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The Páramo Vegetation of Ecuador: the Community Ecology, Dynamics and Productivity of Tropical Grasslands in the Andes.

by

Paul Michael Ramsay

A thesis submitted for the degree of
Philosophiae Doctor of the University of Wales.

December 1992

School of Biological Sciences, University of Wales, Bangor,
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Dedicated to the memory of Jack Higgins, my grandfather.

"... a naturalist's life would be a happy one if he had only to observe and never to write."

Charles Darwin

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Preface

At the beginning of the nineteenth century, Alexander von Humboldt and Aimé Bonpland travelled amongst the Ecuadorian Andes. The 'Avenue of the Volcanoes', as Humboldt described this section of the Andes, proved an excellent outdoor laboratory, generating ideas which have become the foundation for many aspects of plant ecology today. Their plant collection still remains the basis for plant taxonomy in the region (evidenced by the number of species in this work with the authority of "H.B.K.", the abbreviated names of Humboldt, Bonpland and Kuntze). Richard Spruce was collecting in the high páramo grasslands above the Ecuadorian forests around the time of Humboldt's death. Soon afterwards, the golden age of plant collecting in South America had begun to decline.

Since then, a number of trips have been made to the Ecuadorian páramos by collectors, but their work has tended to be small-scale (by comparison with the efforts of Humboldt *et al.*) and concentrated in the more accessible regions. More recently, scientific interest in the páramos has increased. A project to produce a *Flora of Ecuador* is now in progress, based on international research coordinated in Scandinavia.

Taxonomically, therefore, the páramo flora is relatively well-known, though in the absence of a complete guide to the flora, obtaining identifications still requires lengthy research in herbaria. However, other aspects of páramo vegetation have been neglected. Lately, the Centro de Investigaciones Ecológicas de los Andes Tropicales (CIELAT) based at the Universidad de los Andes in Mérida has concentrated on Venezuelan páramo vegetation, with particular emphasis on environmental conditions, productivity, population and reproductive ecology. A co-operative research programme involving Colombia and the Netherlands (Investigaciones de Ecosistemas Tropandinos – ECOANDES) has produced major contributions to our knowledge of the community composition and biogeography of the Colombian páramos.

Despite this intense effort elsewhere in the Northern Andes, the páramos of Ecuador have not been subjected to the same degree of detailed study as those in neighbouring countries. The country is well-known as a centre of biological diversity and this has perhaps led research programmes away from the highlands to the species-rich forests. The miserable climate at high altitudes cannot have helped the case for the páramo in this respect (locals have coined the term *parameando* to mean "It's raining").

During the course of three student expeditions to Ecuador I had the opportunity to make extensive observations in the high altitude grasslands of the Andes. The work was of necessity broad-based: so little is known about páramo vegetation that it was difficult to plan the research programme with any confidence. Access to remote areas of páramo was difficult to assess from the reference sources available. A low budget, coupled with these access difficulties and the terrible weather conditions, limited the technical equipment it was possible to use (warm, rainproof clothing, camping equipment, food and plant presses constituted a heavy pack without additional scientific equipment).

However, a number of projects were carried out and will hopefully act as a catalyst in encouraging further research in this unique ecosystem. The páramo is an ideal place to study plant responses to environmental gradients and a set of interesting climatic conditions with pronounced daily rather than seasonal cycles. It is also an environment where, in the future, biological monitoring of the greenhouse effect might be possible via the response of plant communities to the changing climate.

Paul M. Ramsay,

December 1992.

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First and foremost, I would like to thank Mr. Ralph Oxley for proposing me for a studentship at the University of Wales, Bangor, and for his supervision. The programme owed much to his advice and encouragement, not only academically but also in the planning and execution of the three expeditions which formed the basis for this thesis. I was fortunate to have him for company (albeit briefly) on one of these expeditions.

My involvement in the field of Ecuadorian botany was the result of a chance liaison with Adrian Barnett – at the time, a fellow student at the University of Wales, Bangor. His work on the small mammal populations of the Ecuadorian Andes led me to consider a botanical excursion to Ecuador. Adrian's help in the crucial, early stages of my exposure to expedition organisation and logistics was invaluable. The U.C.N.W. El "CAJAS" Expedition to Ecuador in 1985 was the result.

The work was supported by a College Studentship maintenance grant from the University of Wales, Bangor. The fieldwork for the research presented in this thesis was funded by many organisations, from trust funds to academic institutions, from large multinationals to local commercial companies. The donations ranged from £25 to £1,124. I would like to express my gratitude to the following organisations for their support:

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Summary

Páramo vegetation was quantitatively surveyed in 192 samples on altitudinal gradients in twelve sites in Ecuador. Thirty-one communities were identified, comprising 348 vascular plant taxa (voucher specimens deposited at Kew and QCA, Quito). These communities could be assigned to eight general types of páramo vegetation located between the upper forest limit and the snow-line: Shrubby Sub-páramo, High Altitude Dwarfshrub Páramo, Tussock Páramo, Bamboo Páramo, *Espeletia* Páramo, Cushion Páramo, Rainshadow Desert Páramo and High Altitude Desert Páramo. Community types were more closely related to altitude than to other variables such as burning, trampling, grazing and pH.

The species were assigned to ten defined growth form categories. The distributions of these categories in 192 páramo vegetation samples were described. Twelve growth form communities were identified. Field temperature measurements of plant parts demonstrated that some plants maintained day and night temperatures several degrees Celsius above ambient levels.

The effect of fire on cyclical and successional processes within páramo vegetation were described. Two experimental páramo fires reached temperatures in excess of 400°C in the upper tussock canopy, while the tussock bases were mostly below 65°C. In a quantitative study, the majority of plant-by-plant replacements soon after a páramo fire did not depart from those expected by chance, though some trends were observed and described.

Field trials in Central Ecuador provided net aboveground grassland community productivity estimates for five sites. Estimates ranged from 1,359 g m^{-2} yr^{-1} at 3,100 m to 512 g m^{-2} yr^{-1} at 3,950 m.

In greenhouse experiments, tussock grasses from *Calamagrostis* spp. at three altitudes in the páramo were grown in a diallel design under two watering regimes. In both regimes, the grass from the lower altitude yielded more and had a higher relative yield than that from the higher altitude. RYTs in the wettest treatment lay between 1.2 and 2.5, those of the drier treatments were not greater than 1.0.

Resumen

La vegetación del páramo fue muestreada cuantitativamente en 192 muestras en un gradiente altitudinal en doce sitios en Ecuador. Treinta y una comunidades fueron identificadas, comprendiendo 348 taxa de plantas vasculares (muestras fueron depositadas en Kew y QCA, Quito). Esas comunidades pueden ser asociadas a ocho tipos de vegetación del páramo localizadas entre el limite superior del bosque y la linea de nieve: Sub-páramo Arbustivo, Páramo Arbustivo Enano de Altura, Páramo Macolla, Páramo Bambú, Páramo *Espeletia,* Páramo Almohadillado, Páramo Desértico Seco y Páramo Desértico de Altura.

Los tipos de comunidades estuvieron mas relacionados a la altitud que a otras variables como la quema, pisoteando, pastoreo y pH.

Las especies fueron asignadas a diez categorías definidas por su forma de crecimiento. Las distribuciones de esas categorías en las 192 muestras de vegetación del páramo fueron descritas. Doce comunidades de diferente forma de crecimiento fueron identificadas. Mediciones de temperatura de partes de las plantas en el campo demostraron que algunas plantas mantienen temperaturas, durante el día y la noche, varios grados celsius por encima de los niveles ambientales.

El efecto del fuego en los procesos cíclicos de sucesión y dentro de la vegetación del páramo fueron descritos. Dos fuegos experimentales en el páramo, alcanzaron temperaturas superiores a los 400°C en la parte superior del dosel de la macolla, mientras que en las bases de la macolla fueron menores a 65°C. En un estudio cuantitativo, la mayoría de los remplazamientos planta por planta inmediatamente déspues del fuego en el páramo no fueron distintos de aquellas que se esperaba por suerte, aunque algunas tendencias fueron observadas y descritas.

Pruebas del campo en la parte central del Ecuador provereron estimaciones de productividad neta de la comunidad de pastos encima del suelo para cinco sitios. El rango de las estimaciones fue desde 1,359 g m^{-2} por año a 3,100 m y 512 g m^{-2} por año a 3,950 m.

En experimentos de invernadero, las gramíneas de *Calamagrostis* spp. a tres altitudes en el páramo fueron crecidas en un diseño “diallel” a dos regimenes de regando. En ambos regimenes, el pasto de las altitudes bajas produjeron más y tuvieron mayor cosecha relativo que aquellas de altitudes altas. RYTs en el tratamiento más húmedo estuvieron entre 1.2 y 2.5, aquellas de los tratamientos secos no fueron mayores que 1.0.

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Chapter 1

Introduction to the Ecuadorian Páramos

Ecuador

Ecuador, situated in north-western South America, is the fourth smallest state on the continent (Figure 1.1). It derives its name from the equator which passes through the country which is bounded to the west by the Pacific Ocean, to the north by Colombia and to the south and east by Perú (though there is considerable dispute over this border). The total area has been estimated at 269,178 km^2. There are twenty provinces including the Galapagos Islands and the Banco Central del Ecuador (1990) estimates the population at 10.2 million, about 38 people on average per square kilometre. The capital city is Quito.

The Andes run approximately north-south, bisecting the country. The western coastal region is known as the Costa, the Andean uplands as the Sierra, and the eastern lowlands are often referred to as the Oriente or as Amazonas. The Andes consist of two parallel ranges, the Cordillera Occidental (western range) and the Cordillera Oriental (eastern range). Many peaks are volcanic and snow-covered. The two ranges are connected by transverse ranges (nudos), rather like rungs in a ladder, with the main centres of population occupying the depressions between them (hoyas).

Although rich in natural resources, Ecuador has not been able to sustain the high rates of economic growth it experienced during the early 1970's. The economy was basically agricultural until extensive exploitation of petroleum deposits in 1972 stimulated industrial development. In 1988, agriculture employed 33% of the workforce and provided 17% of the Gross National Product (Banco Central del Ecuador, 1990). In 1984, the land use patterns were as follows: forested, 51.1%; meadows and pastures, 17.0%; agricultural and under permanent cultivation, 9.1%; and other, 22.8%.

Tourism is a growing phenomenon in Ecuador. In 1988 tourism generated US$273 million (Banco Central del Ecuador, 1990). The majority of visitors come from the Americas, though European tourists constitute a significant proportion. Many visitors are interested in the country's natural resources (mountains, flora and fauna). Of course, the Galapagos Islands are responsible for attracting a large proportion of tourists, though their numbers are strictly controlled.

The Páramos of the Andes

Páramo is an ancient Spanish word for "an elevated, barren, treeless plateau", then used to signify the inhospitable plains of Spain (Acosta-Solís, 1984). The term was brought to South America by the conquistadores and colonialists who applied it to the exposed grasslands of the northern Andean ranges.

Páramos occupy the vegetation belt between the upper limit of the montane cloud forest (*Ceja Andina*) and the snow-line (Figure 1.2). They occur from Venezuela to

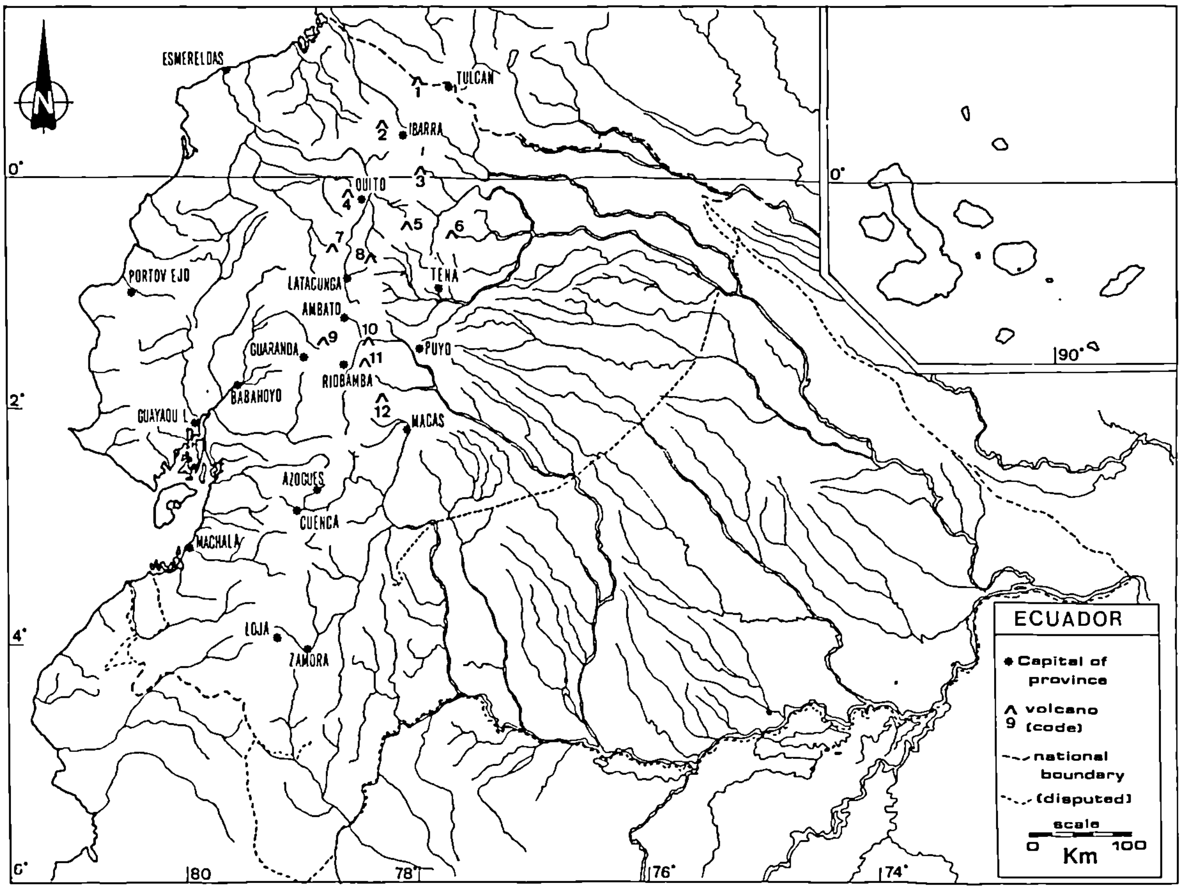


Figure 1.1.

Map of Ecuador, showing volcanoes and principal towns and cities. KEY: 1, Volcán Chiles; 2, Volcán Cotacachi; 3, Volcán Cayambe; 4, Volcán Pichincha; 5, Volcán Antisana; 6, Volcán Sumaco; 7, Volcán Iliniza; 8, Volcán Cotopaxi; 9, Volcán Chimborazo; 10, Volcán Tungurahua; 11, El Altar; 12, Volcán Sangay.

Ecuador and northern Perú (where they are called jalcas), with outliers in other parts of Perú, Bolivia, Panamá and Costa Rica (Cleef, 1978). The páramos show similarities to the vegetation of other high elevation tropical environments (Figure 1.3). These high montane ecosystems are found in the Central Andes (puna), East Africa (afroalpine or moorland), Malaysia (tropical alpine) and Mexico (zacatal, though Gomez-Pampa (1973) and Breedlove (1973) speak of 'páramo' vegetation in Veracruz and Chiapas). Some authors advocate the use of páramo to describe all of these tropical alpine vegetation types (for example, Walter, 1973, and Lind & Morrison, 1974). Monasterio & Vuilleumier (1986) suggest the use of terms such as Andean páramo, African páramo, Papuan páramo, and so forth. The term tropicalpine has lately been used to describe all alpine areas in equatorial regions (for example, Smith & Young, 1987b). Other authors have suggested the use of the term "tundra" for all treeless regions, north and south of latitudinal tree-lines and above natural altitudinal tree-lines (for example, Holdridge, 1957; Tieszen & Detling, 1983). In this work, I will use tropicalpine and the more traditional nomenclature for regional vegetation (páramo, afroalpine, etc.).

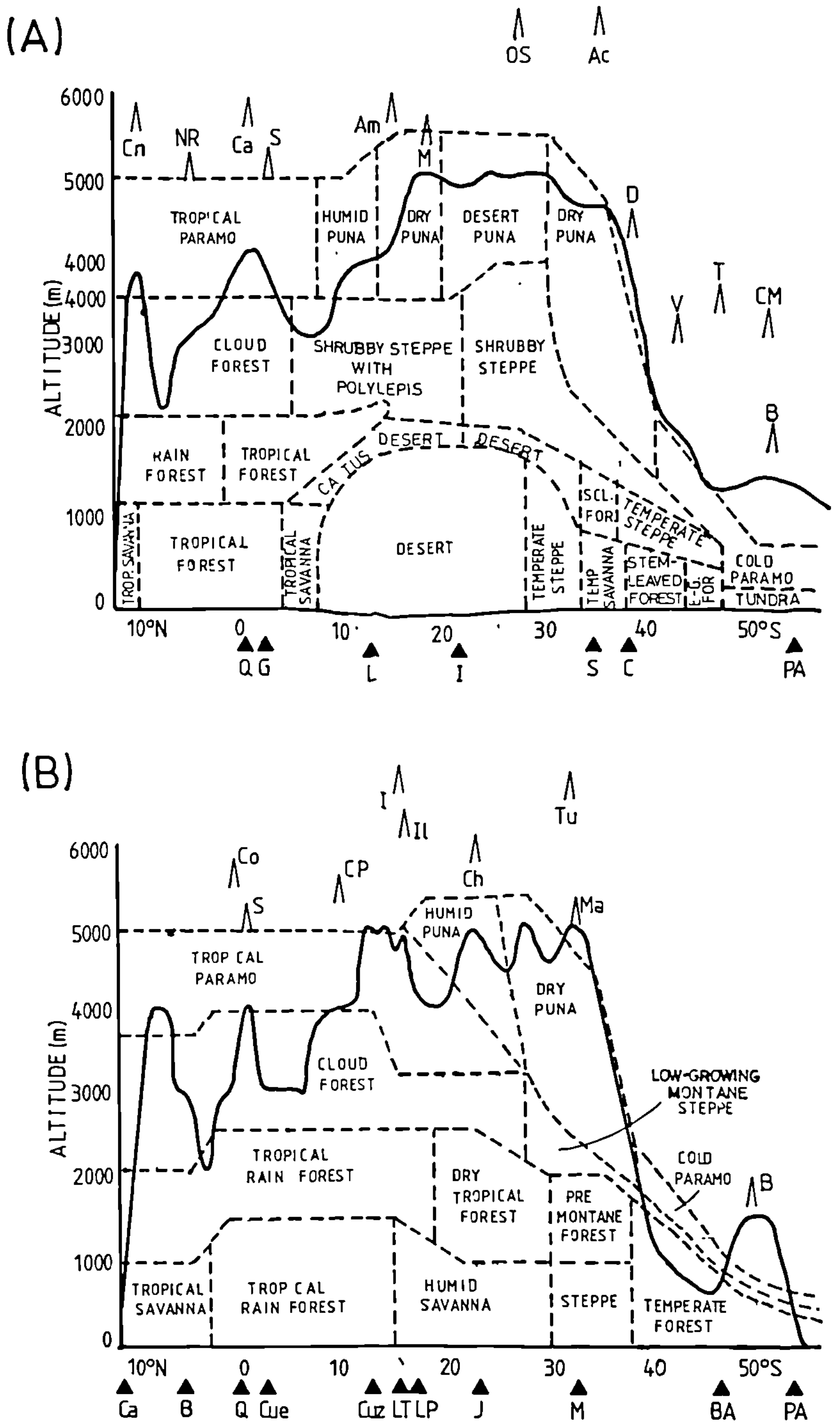


Figure 1.2.

Vegetation zones of the Andes: (A) Western Andes, (B) Eastern Andes, following Mann (1968). The zones are divides by dashed lines. Major mountains are shown at the top of the figure and pricipal cities at the bottom.

Mountain Codes: Ac, Aconcagua; Am, Ampato; B, Balmaceda; Ca, Cayambe; Ch, Chañi; CM, Cerro Muralion; Co, Cotopaxi; Cn, Colón; CP, Cerro de Pasco; D, Domeyco; I, Illampú; Il, Ilimani; M, Misti; Ma, Maipo; NR, Nevado del Ruiz; OS, Ojos del Salado; S, Sangay; T, Tronador; Tu, Tupungato; V, Villarica.

City Codes: B, Bogotá; BA, Buenos Aires; C, Concepción; Ca, Caracas; Cue, Cuenca; Cuz, Cuzco; G, Guayaquil; I, Iquique; J, Jujuy; L, Lima; LP, La Paz; LT, Lake Titicaca; M, Mendoza; PA, Puerto Arenas; Q, Quito; S, Santiago de Chile.

Other abbreviations used in text: E.G. FOR., Evergreen Forest; SCL. FOR., Sclerophyll Forest.; TEMP SAVANNA, Temperate Savanna.

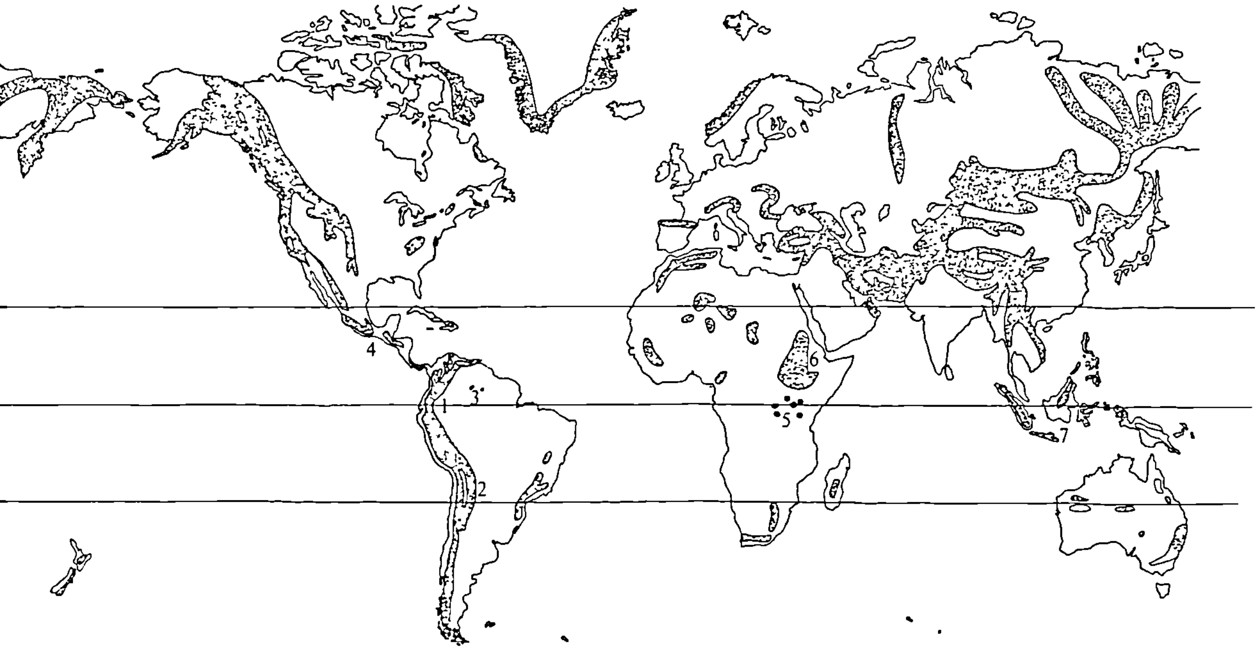


Figure 1.3.
Regions of the world with high altitude tropical vegetation: 1, Northern Andes (páramo); 2, Central and Southern Andes (puna); 3, Guyana Highlands (tepuis); 4, Central American Highlands (páramo and zacatal); 5, East African mountains (afroalpine moorland); 6, Ethiopian Highlands (tableland); 7, Malaysian Highlands (tropical alpine grasslands). Adapted from Monasterio & Vuilleumier (1986).

"Páramo" and "Rain Páramo" appear in Holdridge's (1967) life zone classification system, but many Ecuadorian páramos are found in the "Moist Forest" and "Wet Forest" life zones. Though an adequate category is not found in Fosberg (1967), "Steppe" [2G] would seem to be most appropriate for the majority of páramo vegetation.

The Andean páramos should not be confused with the páramos templados of high latitudes in South America (40°S), which show distinctive dissimilarities from equatorial páramos. They are also distinct from Neotropical savannas which have entirely different floristic, physiognomic and physiological features (Huber, 1987).

Some authors have suggested the limit of distribution of Espeletiinae tribe (Compositae) as a guide for the extent of páramo vegetation (for example, Fosberg, 1944). In Ecuador, only one species of *Espeletia* is found (*Espeletia pycnophylla*). One subspecies is restricted to northern areas, such as the páramos of El Angel, Volcán Chiles and El Playon de San Francisco, the other to a valley in the Llanganatis (Central Ecuador). Elsewhere, *Espeletia* is absent, with *Puya* species becoming more dominant. Ecuadorian páramos generally lack *Chusquea* bamboo species, which is a dominant plant in more humid páramos.

Acosta-Solís (1984) has estimated that the total area of páramo in Ecuador is somewhere between 25,000-28,000 km^2, though this is probably an over-estimate, since he includes the snowcaps and assumes that the lower limit of the páramos is at 3,000-3,300 m. The actual altitude of the upper forest line in Ecuador varies considerably, from under 3,000 m to about 4,000 m, depending mainly on climatic factors and human interference, though most often the transition zone exists between 3,400-3,500 m. The upper limit of the páramo is the snow-line, ranging from 4,400-4,900 m. Encalada (1986) offers 20,000 km^2 as a more reasonable evaluation of the extent of the Ecuadorian páramo, and Bonifaz (1981) goes further with an overall estimate of 19,610 km^2, calculating the area of subpáramo (3,500-4,000 m) as 13,310 km^2, with 6,300 km^2 of páramo occupying the land above 4,000 m.

Some authors believe the existence of the páramos to be the result of man's activities, in particular burning (Ellenberg, 1979; Laegaard, 1992). Without doubt, clearance of forest has had a major impact on the extent of the lower reaches of the páramo grasslands. The presence of pockets of quiñuales (woodlands of *Polylepis* spp. trees) and *Gynoxys* spp. woodlands amidst the extensive grasslands of páramo has been used as support for this argument, stating that such pockets of woodland represent refugia from fire and that without burning, the whole landscape would be dominated by trees. Simpson's (1979) revision of the genus presents a summary of the debate. A.P. Smith (1978) carried out field experiments with *Polylepis sericea* in the Venezuelan Andes and found that seedlings only survived on rocky talus slopes and showed 100% mortality over one year in open páramo and bare soil. He concluded that the cause of mortality was an interaction of competition and climatic stress. Ramsay (1988) also points out that several large islands in lakes in the páramo of Cajas (southern Ecuador) do not support woodland vegetation. This will be discussed in more detail in the final chapter of this thesis.

Geology and Edaphology of the Páramos

The massive Andean range owes its existence to the consumption of the oceanic Nazca tectonic plate beneath the continental South American plate (at a rate of about 6cm per year). It accounts for the crumpling of the stable continental margin to form the belts of fold mountains that now constitute the eastern ranges of the Andes, for the birth of the great Andean volcanic cordillera to the west, and for the continental growth of western South America (James, 1973).

The Ecuadorian highlands or Sierra, according to Baldock (1982), is a composite mountain belt, formed by two (or more) distinct orogenic episodes. In the Palaeozoic, the Cordillera Oriental (also known as the Cordillera Real) was formed as high pressures forced fold mountains upwards in a line roughly north-south. This range is underlain by metamorphic rocks capped by Cenozoic volcanoes. In the late Mesozoic to Cenozoic, the Cordillera Occidental developed, probably as an island arc (Baldock, 1982). This range is comprised of Cretaceous-Lower Tertiary volcanic and volcaniclastic rocks, along with sedimentary rocks which were deposited between the islands. Many of the higher areas are covered by Neogene volcanics. According to Hoffstetter (1986), there are eight active volcanoes in Ecuador, and twenty more have recently become extinct.

The inter-Andean valley is a graben, a fault between two lines of weakness, which appeared during the Neogene uplift and arching of the Andean mountain belt. This 'Avenue of the Volcanoes', averaging 2,500-3,000 m, becomes morphologically less distinct to the south, but is still evident geologically (Baldock, 1982).

During the past there have been several glaciations in highland Ecuador. Glacial features such as moraines, boggy U-shaped valleys, tills, cirques, fluvio-glacial deposits, tarns and glacial lakes, polished bed-rock, roches moutonées and erratic rocks are frequently observed, especially in the super-páramo (Cleef, 1981). Repeated glaciations and catastrophic volcanic events have prevented the undisturbed development of soils over much of the páramo area.

There have been few detailed studies of páramo soils. General works dealing with the soils of South America, have tended to group together the soils of the high Andes (for example, the "páramo soils" of Beek & Bramao, 1968). Studies of particular countries or regions have used similar general terms or local names for the soils present.

Sturm (1978) reviewed previous pedological studies in the northern Andes in his paper on the soil flora and fauna of a Colombian páramo. Cleef (1981) presents an extensive set of soil data, collected during his characterisation of the páramos of the Colombian Cordillera Oriental.

In general, the soils of the páramos of the northern Andes are very dark in colour, acidic, rocky and poorly developed, low in inorganic nutrients but with a high organic content in the uppermost horizon (Sturm, 1978; Baruch, 1979; Cleef, 1981). The decomposition of the vegetation is slow (reflected in high carbon:nitrogen ratios – Cleef, 1981), ascribed by Jenny (1948) to the cold temperatures rather than the soil moisture content. Frei (1958) assigned most Ecuadorian páramo soils to the Black Andean Soil Group. Soils of this type collected in Ecuador were found by Miller and Coleman (1952) to be characterised by a relatively high organic content (9-12% dry weight), high cation exchange capacity, low exchangeable calcium and magnesium, high concentrations of exchangeable aluminium and a high capacity for phosphate adsorption, with a pH of 4.1-4.8. However, pH values from 3.8 (Peña Herrera, quoted in Acosta-Solís, 1984) to 6.2 (Grubb, Lloyd & Pennington, manuscript) have been recorded in Ecuadorian páramos. Clearly, this variation in pH will alter soil properties such as cation exchange capacity.

Horizon A can be thick, 30cm to 2m in depth (Acosta-Solís, 1984). Boundaries between horizons are not usually pronounced (Jenny, 1948; Acosta-Solís, 1984).

A common component of páramo soils is cangagua, a mixed loessal volcanic fallout deposit related to volcanic eruptions and cold, possibly dry periods of glaciation (Clapperton & McEwan, 1985; Vera & López, 1986). If the soil is deep enough, particularly if cangagua is present in large amounts, there is little influence of the bedrock on the vegetation (for example, the Nevado de Sumapaz, Colombia, is underlain by limestone but the soil pH is not markedly different than elsewhere; Cleef, 1981).

In general, these descriptions refer only to the páramo soils beneath tussock grassland at intermediate altitudes. In fact, a mosaic of soil types occur, under the influence of factors such as topography, geological history and altitude. Under very wet conditions, clays and peat may develop. Though Sturm (1978) found little or no podzolic soils in the páramos, the Cambridge Llanganati Expedition 1969 (1970) found podzols at 4,200 m in Cerro Hermoso, Ecuador, where a distinct iron pan had formed 4-10cm below the surface. They also described iron-oxide mottling in soils with restricted drainage. Furrer & Graf (1978) studied glacial and periglacial phenomena in the higher reaches of the Ecuadorian Andes where stony soils are common, sometimes showing periglacial features such as needle ice, structured soils (stripes and polygons) and screes.

Climate

From the outset, it is important to differentiate between the alpine climate of temperate regions and the tropicalpine environment of the Andes. Tropical climates do not show as much seasonal variation in temperature and day length as the mid- and high-latitude climates (Sarmiento, 1986). A characteristic feature of the tropical climate is that the yearly variation in temperature is not so great as the daily variation. The main climatic pattern is, therefore, the marked circadian cycle rather than the seasonal pattern. This is the diurnal temperature climate described by Troll (1968).

The seasonal constancy of temperature holds true for all altitudes. However, temperature decreases on average with increasing altitude with a lapse rate of around 0.6°C per 100 m of altitude. Although there is a constancy of mean temperature, the minima do vary seasonally. This is particularly important with regard to the number of frost days.

Rainfall is much more variable than temperature, since it depends on a whole range of factors relating to the geography of each mountain system. Most tropical regions have two to four seasons with heavy rainfall alternating with dry, almost rainless conditions. The tropical mountains are subject to this rainfall seasonality too, in all but the wettest and most arid regions. The circulation patterns of the atmosphere have a direct influence on the climate of the Andes (Eidt, 1968). The Andean range is not just a watershed between east and west, it is also a climatic dividing line, bisecting the major air masses of the southern hemisphere (Sick, 1969). Sarmiento (1986) summarized rainfall patterns along the Andean chain. From Venezuela to Central

Colombia rainfall follows a bimodal pattern, with the main dry season from December to March. Around the thermal equator, between 4°N and 5°N, the rainfall pattern is still bimodal, but the major dry season shifts to the middle months of the year. In northern Ecuador, the secondary dry season tends to disappear and the climate becomes more or less two seasonal, showing a pronounced mid-year minimum. This bi-seasonality is reinforced southward, so that southern Ecuador experiences drier weather from June to January. The trend culminates in a two-season regime in the Peruvian Andes. Emphasising this bi-seasonality, Sarmiento (1986) reports that in the Andes of Ecuador, 70% of the annual total precipitation falls in the wet season, compared with 80% and 90% for parts of southern Peru and Bolivia, respectively.

Johnson (1976) noted several other climatic gradients along the Andes from Ecuador to Bolivia. Total rainfall decreases smoothly from north to south. In northern Ecuador, the páramos are quite humid, but in southern Ecuador (at about 2°S) conditions become semi-arid (Johnson, 1976). This is accompanied by unreliability of rainfall. Schwabe (1968) relates this to the position of the Intertropical Front (responsible for convection rain patterns) which is located near the thermal equator, and so lies close to Colombia and Ecuador all year round, resulting in rainfall throughout the year. Further south, away from the continuous influence of the ITF, rainfall becomes more seasonal. A further trend is the appearance of a cold season during the southern hemisphere winter as one moves south. However, despite this N-S variation, the main axis of environmental variation is E-W (Troll, 1968). This results in climatic zones parallel to the Andes (see Sarmiento, 1986: Fig. 7).

The temperature regime can be governed to a large degree by the rainfall patterns, since rainfall is associated with cloudiness. Tropicalpine environments rely heavily on direct solar radiation as a temperature input and cloud cover dramatically reduces insolation. At night, the cloud cover reduces thermal loss via long-wave radiation. Thus, cloudiness buffers temperature variation, restricting the amplitudes of maximum and minimum temperatures. In this way, seasonality in rainfall leads to thermoperiodism, an annual cycle with dampened temperature oscillations and higher night minima during wet seasons and greater temperature fluctuations and lower night minima during dry seasons (Sarmiento, 1986).

Precipitation is, therefore, of great importance in determining a host of climatic conditions. Rainfall pattern is dependent on a range of factors, most influential of which are altitude, topography and geographic position. Weischet (1969) and Lauer (1976) showed that, in general, there is a maximum amount of precipitation at middle altitudes, occurring a few hundred metres above the cloud base where drops begin to form and corresponds to the position of montane cloud forests. Above and below this altitude, the amount of rainfall steadily decreases.

The Andes are characterised, like other mountain ranges, by irregular topography. Their geological youth means that slopes are still very steep and level ground is rarely found. As Troll (1968) points out, under such circumstances, meteorological data collected in one valley may be completely different to that in the next valley: the so-called "Troll effect". Locating meteorological stations in valleys leads to an underestimation of rainfall, and run-off data show that in many mountain areas, as a result of the "Troll effect", precipitation measurements are utterly unrepresentative (Flohn, 1974).

Topoclimates may be more important than regional climates. Geiger (1966, 1969) and Barry & Van Wie (1974) stress three key topoclimatic factors. Slope aspect and slope angle modify diurnal temperature and humidity changes through their action on insolation. This was well-known in the Alps where agriculture was located on sunny ('adret'), south-facing slopes whilst shaded ('ubac'), north-facing slopes remained under forest (Garnett, 1937). This is more important in tropical mountains where diffuse radiation accounts for much less a proportion of the total radiation, and direct sunlight is consequently more influential. Therefore, steep slopes receive less radiation than flatter ones. Holland & Steyn (1975) demonstrated that differences between equator-facing and pole-facing slopes (in the absence of cloud) are greatest on steep slopes and at mid-latitudes – and least in equatorial and polar regions. Their studies suggest that thermal microclimatic differences at tropical latitudes are generally insignificant. However, these studies did not take into account cloudiness. In the tropics, E-W slope aspect is more important than N-S slope aspect, mainly as a result of differences in precipitation on lee- and windward slopes and the effect of afternoon cloudiness (a common situation) on western-facing slopes (Smith, J.M.B., 1978; Azócar & Monasterio, 1979, 1980b). The result is that east-facing slopes receive more sunlight. A third factor is topography, with its relation to catabatic and anabatic winds and night-time inverted temperature regimes (cold valley bottoms).

Winds are usually gentle, but can influence plant growth (Smith, 1972). Strong winds can be a continual presence locally, where consistent directionality can create distinct microclimates on leeward and adjacent windward slopes (Smith, 1972). The absence of strong winds in the páramos has been used to explain why stem rosette species are dominant in many regions (Cleef, 1978 – reply to Hnatiuk).

The fall in atmospheric pressure with altitude leads to a lowering of the air water-vapour pressure at high elevations. This may be limiting to plant growth at these altitudes. High UV-B input is, to some extent, compensated by reduced epidermal UV transmissivity (Robberecht, Caldwell & Billings, 1980). Barnes, Flint & Caldwell (1987) provide corroborative evidence for this but suggest that other factors, in addition to the shielding of UV-B radiation by UV absorbing pigments and/or leaf structures, are also involved.

Vegetation types are clearly related to prevailing climatic conditions. Cuatrecasas (1968) and Monasterio & Reyes (1980) report that a mean temperature of 10°C roughly corresponds to the climatic boundary between montane and páramo climates, which, according to Sarmiento (1986) corresponds (on wet slopes at least) to the first appearance of a few days of night frosts (that can occur at any time of the year). The number of days of frost increases sharply around 3,300 m, which coincides approximately with the upper limit of montane forests. By 4,500 m, the number of frost days per year rises to about 100, and the nival limit is usually reached between 4,700-4,900 m. On drier slopes, frosts appear at lower elevations, but the permanent snow-line may be much higher.

For a plant to be a successful colonist of the páramos, it must be able to cope with several climatic factors which present difficulties to plant existence. Sarmiento (1986) considers freezing temperatures at night and insufficient radiation and sub-optimal temperatures during daylight hours as the main constraints on life in tropical mountains. Plants may evolve several responses to these factors: modifications in form, function, behaviour or all three (Sarmiento, 1986). These adaptations will be discussed in more detail in a later chapter on páramo growth forms. Particularly important to many species is the exploitation of microclimates.

Flora

The present páramo vegetation is at least four million years old (Van der Hammen & Cleef, 1986). These authors estimate that the páramo has 30 endemic genera out of 300 (10%), while in the Cordillera Oriental of Colombia 35% of the species are endemic (Van der Hammen & Cleef, 1986).

Central to the understanding of páramo vegetation is a knowledge of its development. Van der Hammen & Cleef (1986) present a valuable account of the evolution of the high altitude vegetation of the northern Andes. About 4-5 million years BP (before present), lowland and mountain savannas and other tepui-like grasslands, determined by edaphic and/or climatic (other than temperature) factors, existed amongst the forest. This "pre-páramo" was made up of floristic elements from Andean, even Sub-Andean forest vegetation. It was to be an important source of (Neo)tropical and Andean elements of later páramo vegetation types, once the final upheaval of the Andes took place.

During this great uplift in the Pliocene and Early Pleistocene (some 4-2 million years BP), night frosts became important above 2,300 m and the flora became adapted to the new conditions. The "proto-páramo" vegetation was wider in extent than today's páramo since, despite milder temperatures, the forest line was low owing to an undeveloped upper Andean forest flora. Some evidence for the existence of a "proto-páramo" flora is provided by pollen analysis. Though poor in genera, some of the taxa are characteristic of the present-day páramo, while others are now absent. Half of the floral elements were of tropical origin, the remaining 50% temperate (mostly from the south).

The immigration of temperate species then proceeded more rapidly (both from the south and north) leading to the appearance of páramo vegetation much as we know it today. During interglacial times, the páramo had an archipelago-like distribution, similar to that at present. During the glacials, however, the extent of the páramo resembled that of the proto-páramo, possibly even larger.

Since proto-páramo times (2-0.5 million years BP), there have been 15-20 major climatic cycles (each of approximately 100,000 years duration), which have displaced the forest line. Maximum opportunities for the migration of páramo plants were afforded when the upper forest line was around 2,000 m (some 5-10% of the time): the area of páramo being increased several times. Immigration to the páramo was also optimum at this time. For 40% of the time, the páramo occupied its present position (or slightly higher), and migration and immigration were minimal. For the remaining 50% of the time, the extent of the páramo was intermediate.

The altitudinal movement of vegetation belts was not merely a vertical displacement: the flora had to contend with different soil types (sometimes after a glaciation there was no soil at all) and wetter/drier conditions. In this way, extinction of elements of the flora could occur when their niches were temporarily unavailable. In Ecuador and parts of Colombia, further extinctions may have resulted from the continual, often catastrophic effects of volcanic activity.

Tropical alpine environments may, therefore, be thought of as typically insular and short-lived (Smith & Cleef, 1988), relying on long distance dispersal rather than local adaptation as the primary source of recruitment to tropical alpine floras. The equilibrium theory of island biogeography (MacArthur & Wilson, 1967) has been used to calculate the expected number of species for different páramo regions. Vuilleumier (1970) found good correlation between expected and observed numbers of species for Andean birds. Simpson (1974) found that plant species diversity conformed to the theory of island biogeography (though greater correlation was found using páramo area and distance measures at glacial times than those of the present day). It is probable that the continual displacement of páramo vegetation belts prevents a state of equilibrium from being reached in all but the most rapidly colonizing groups (such as birds).

Cabrera (1957) places the 'Páramo Province' within the 'Andean Domain', which in turn is a part of the 'Neotropical Region'. The most important families in the 'Páramo Province' are Compositae (Asteraceae), Gramineae (Poaceae), Cyperaceae, Cruciferae (Brassicaceae), Geraniaceae, Valerianaceae, Bromeliaceae, Caryophyllaceae, Umbelliferae (Apiaceae), Leguminosae (Fabaceae) and Rosaceae. All páramos merit their amalgamation into a single biotic Province because of similarities in evolutionary history, environmental conditions, fauna, flora and vegetation (Monasterio, 1980c). However, despite these likenesses, there are clear sub-divisions within the Province. For example, Monasterio (1980c) differentiates the Province into three groups: the jalca and Ecuadorian páramos, consisting mainly of tussock grasses with genera from extra-tropical regions; the páramo of Colombia, with equal importance of grasses and rosettes; and the Venezuelan páramos, where some dualism exists but the rosettes are more dominant.

Cleef (1981) reports that more than 300 native vascular plant genera are represented in the páramos of the northern Andes (with 260 of them in the Colombian Cordillera Oriental – comprising about 700 species). There have been numerous collections of plants made in the Ecuadorian páramos, ever since von Humboldt and Bonpland made their way through the "Avenue of the Volcanoes" in 1802 (Sandwith, 1926). As a result, the taxonomy of the region is relatively well-advanced, though plant identification is still only possible by comparing specimens in herbaria as keys are incomplete or unavailable, despite the excellent efforts of the Flora of Ecuador project.

The literature contains several descriptions of páramo flora in Ecuador (for example, Heilborn, 1925; Diels, 1934; Acosta-Solís, 1937, 1966, 1984, 1985; Penland, 1941; Drew, 1944; Svensen, 1945; Paredes, 1962; Løjtnant & Molau, 1982; Cerón, 1985). More recently, some quantitative descriptions using methods of Braun-Blanquet have been published (Øllgaard & Balslev, 1979; Balslev & de Vries, 1982; Black, 1982; Ramsay, 1988). However, these researches are still far behind progress in Venezuela and Colombia, where some extensive quantitative comparisons have been made (for example, Fariñas & Monasterio, 1980; Cleef, 1981; Baruch, 1984; Rangel & Franco, 1985; Franco, Rangel & Lozano, 1986).

Harling (1979) recognizes three types of páramo in Ecuador. Grass páramos or pajonales occupy most ground below 4,000 m. Cushion páramos are found above 4,000 m, as the tussock grasses are replaced by cushion plants. Harling's third category contains the desert páramos or arenales, which inhabit the higher reaches of the Andean ranges, where conditions restrict plant growth.

The páramo vegetation of Latin America characteristically shows altitudinal zonation, resulting from progressively higher stress factors with increasing elevation. Cuatrecasas (1934, 1958, 1968) classified the typical Colombian páramo into three belts:

- Sub-páramo (3,000-3,500 m) – the transition zone between the upper Andean forest and the open páramo, dominated by bushes of Compositae, Guttiferae and Ericaceae.
- Grassy Páramo (3,500- c.4,100 m) – characterised by tussock grasses (mainly Calamagrostis and Festuca spp.) with thickets of *Hypericum* and *Senecio vaccinioides*. Isolated woodlands exist in this belt, consisting of trees of the genus *Polylepis*. Another feature of this zone is the presence of *Espeletia* spp., though this is not usually true of Ecuadorian páramos.
- Super-páramo (c. 4,100 m and above) – the extreme environmental conditions restrict plant growth and cover is sparse. Characteristic are *Culcitium* spp.

Despite this zonal approach, clear separations between the community types have not generally been found in quantitative studies, rather a continuum of community change (Crawford, Wishart & Campbell, 1970, for Perú; Fariñas & Monasterio, 1980, and Baruch, 1984, for Venezuela).

The geological history of the Andes has left the range with a "small-scale mosaic of types of landscape" (Schwabe, 1968) consisting of high ridges and deep valleys, clearly showing the influence of glaciation. This high topographic diversity is reflected in a wide spectrum of plant communities with azonal distributions. Cliffs, rock outcrops, recent moraines, river-banks and waterlogged ground support their own community types (Grubb *et al.*, unpublished).

Alpha diversity (within habitat species richness) appears to be similar in tropical alpine, temperate alpine and arctic communities (Hanselman, 1975). However, gamma diversity (regional among mountain species richness) appears to be greater in tropical alpine communities (evidenced by high levels of endemism and vicarious species complexes in tropical mountains). This is doubtless a function of the island-like nature of the páramo regions in a sea of tropical vegetation with pulses of migration during glaciations alternating with periods of speciation in the isolated páramos when the climate was warmer (Simpson, 1975). In addition, Janzen (1967), Huey (1978) and Smith (1987) suggest that tropical mountains may be effectively more isolated from each other than are temperate mountains with similar topography. This has wide implications for understanding the processes of plant biogeography and evolution in the high Andes.

Fauna

The diversity of páramo habitats supports a variety of animal species. The grasses of the páramo provide a living for a number of herbivores such as deer (*Odocoileus virginianus*), rabbits (*Sylvilagus brasiliensis*) and numerous small rodents (16 species in three orders have been collected in the páramo of Cajas, southern Ecuador, by Barnett & Gordon, 1985). These herbivores (in addition to hunting by man) provide food for several large carnivorous species: puma (*Felis concolor*), spectacled bear (*Tremarctos ornatus*), Andean fox (*Dusicyon culpacus*) and large birds of prey. Carrion-feeders include the magnificent condor (*Vultur gryphus*). All of these large carnivores, especially the condor, have declined considerably over the last hundred years as a result of hunting and killing practices of farmers with domestic herbivores. Whymper (1892) describes very large populations of condors: for Chimborazo he writes, "When the atmosphere permitted us to look below, we commonly saw a dozen [condors] on the wing at the same time."; and for Antisana, "A score or more continually hovered over the pastures." Such sights have long since disappeared.

Twelve species of hummingbird (Trochilidae) inhabit the páramos (Wolf & Gill, 1986). Cordillera Snipe (*Chubbia jamesoni*) are common, as are the Páramo Pipit and members of the genus *Cinclodes*. Ducks and teals live in some páramo lakes, along with populations of introduced trout (*Salmo gairdnerii* and *S. trutta*).

Descimon (1986) observed a very sharp division in lepidopteran diversity between the upper montane forest and the páramo. He explained this in evolutionary terms: the relatively recent uplift of the Andes had not allowed sufficient time for local species to evolve and take advantage of the páramo habitat and the long distance from the nearest source of preadapted fauna (in Tierra del Fuego) had prevented immigration from this region.

The Influence of Man

Although the páramos are uninhabited, man's influence is strong there. Human communities in the high Andes have been, in general, self-sufficient. Their isolation, coupled with access to a broad resource base, has contributed to this reliance on subsistence agriculture.

Several decades ago, Ecuadorian agricultural systems in the highlands were among the most anachronistic in the hemisphere (Haney & Haney, 1989). An agrarian reform programme was launched to improve the lot of the campesinos (peasant farmers) in 1964 but has been only partially successful. Some rural people own small patches of land (minifundios), which are often incapable of providing even a subsistence living for their owners. In a study of the minifundio community of Santa Lucia Arriba in highland Ecuador, 80% of households owned less than 1 ha of land or were landless, though 61% had purchased land over and above what they had inherited (Forster, 1989). Others work as huasipongueros (tenant farmers) on large haciendas, in return for which they may receive a house and a small plot of land on which they may grow crops.

The diet of the campesinos remains essentially traditional, despite commercialisation of the rural economy and changes in production and eating habits (Herrera, 1987). The main foods are barley meal, potatoes, rice, barley grain, beans and wheat flour, and deficiencies in protein and energy requirements are very common, especially in children (Herrera, 1987).

The campesinos recognize various agricultural zones on the elevational gradient, summarized for northern Perú by Brush (1976). The páramos are not used for cultivation owing to frequent frosts. Instead, the extensive low-value paja (tussock grass) provides forage for cattle, horses and sheep. Below the páramo zone is a belt of tuber cultivation (e.g., potatoes and oca) and below that is a zone of cereal cultivation (*e.g.*, maize and quinoa). The ceja andina provides a source of timber and fuelwood.

The human ecology of the Andes is in a state of flux. In pre-Hispanic times, settlements were higher than at present. The lowering of Andean villages after the Spanish conquest has been attributed to increased dependence on cereal crops under Old World influence (Brush, 1976). In more recent times, this trend away from the páramos has been reversed. The depletion of local natural resources (particularly fuelwood) as a result of increased population pressure, diminishing isolation and the loss of self-sufficiency has generated a need for cash crops. Brush (1976) describes livestock as a "living bank account on the hoof", since cattle can be readily converted into money when required, and the páramo zone has seen an increase in grazing pressure.

As Brush also points out, the tuber zone has traditionally been the major focus of subsistence activity in the Andes. Pressure to increase production has resulted in pushing crops away from their effective limits to their absolute limits in the sub-páramo (where risks of frost damage and disease are higher). Gondard (1988) also identified this trend – of advancing pioneer fringes of agriculture along the edge of natural vegetation formations – throughout the Andean region of Ecuador.

In a study of perceived stress factors in Ecuadorian Andean campesinos, Stadel (1989) found that low temperatures at high elevations and isolation were seen as major worries, but steep slopes and erosion were not. This is perhaps a consequence of the modern view of maximization of yields, rather than of sustainability.

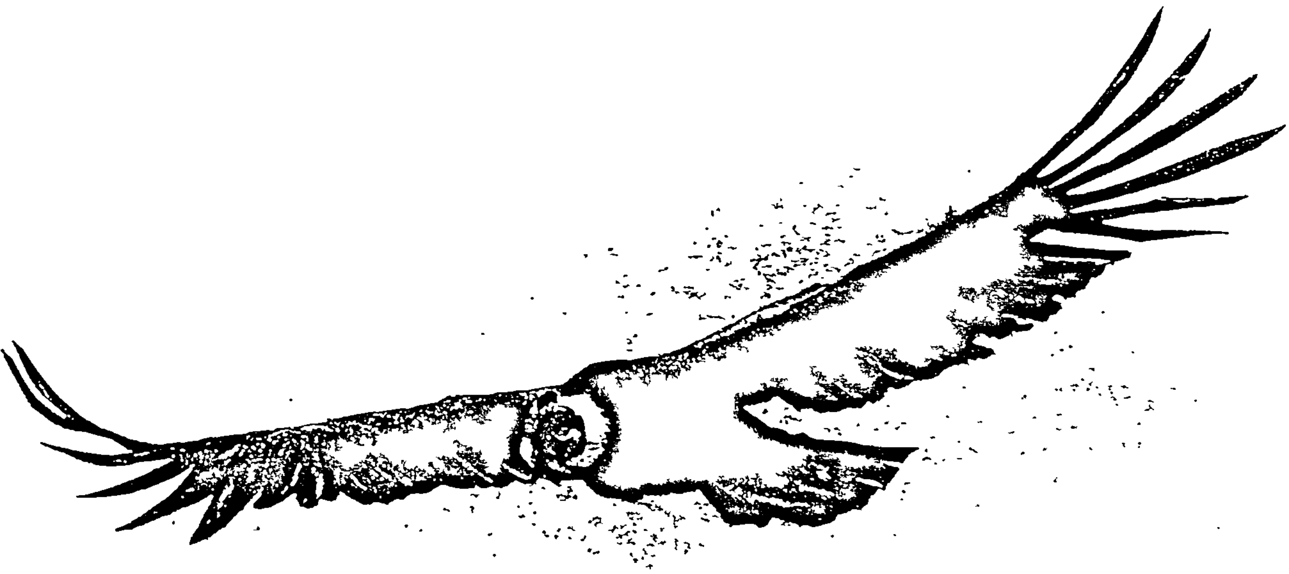
The treatment of montane forest is a prime example of a non-sustainable approach to local natural resources. Day-to-day survival has forced many communities to destroy the ceja andina completely in the quest for wood, now leaving them without fuelwood – "the poor man's energy crisis" (Brandbyge & Holm-Nielsen, 1987). In some of the drier páramos, where trees are absent, shrubs are collected for fuel. This happens, for example, on the slopes of Volcán Chimborazo, where each household collects a horse-load of *Chuquiraga jussieui* branches every five days or so, for cooking and heating. A similar practice has been observed in puna vegetation types in parts of highland Perú and Bolivia (West, 1987). This practice can cause degradation of the ecosystem if the shrubs are over-utilized.

With increasing utilization of the páramos as pastures, burning has become more widespread in an effort to alter the nutritional value of the paja tussocks by removing choking dead leaves and stimulating the growth of succulent new shoots. Ellenberg (1979) puts forward a case for the extreme modification of tropical mountain ecosystems of the Andes by burning and trampling. As he points out, nearly all regions of the Andean countries are composed of mixtures of ecosystems, representing different stages of landscape history and different levels of human interference.

Despite the hostile climate, the páramos will become increasingly important to Andean peoples as a result of population pressures in a country with the greatest density of humans per cultivable unit and the highest birthrate on the continent.

Chapter 2

The Community Ecology of the Ecuadorian Páramos



Introduction

The high altitude grasslands of the northern Andes of South America are characterised by two great vegetation types, the páramo and the puna. They both cover similar altitudinal ranges, but are fundamentally distinct, largely in terms of humidity (Quintanilla, 1983; Acosta-Solís, 1984). The páramos stretch from Central America to northern Perú and Bolivia, where the drier puna vegetation begins and extends southwards into Chile (Cleef, 1978).

The páramos of Ecuador are interesting in that they occur towards the southernmost limit of páramo vegetation, and show a trend from humid páramos in the north to drier páramos in the south (Acosta-Solís, 1984). There is also a similar trend from the humid vegetation on the eastern Andean range (receiving moisture-laden air from the Amazon basin) to the drier western range (corresponding to the east-west climatic trend described by Sarmiento, 1986). There is a complex interaction of these trends to produce various kinds of páramo vegetation within the same latitude or along one Cordillera. In the northern province of Carchi (and one site in the eastern slopes of the Andes in Central Ecuador), there are páramos with vegetation more typical of Colombia. By contrast, Acosta-Solís (1984) describes various sites in Ecuador with what he considers to be "puna" vegetation, similar to that of Perú (for example, the Grande Arenal of Volcán Chimborazo).

The community composition of the high altitude grasslands of the Andes has been studied in various countries. In Venezuela, most research has been centred on the mountains around Mérida (Vareschi, 1970; Monasterio, 1979, 1980a, 1980b; Fariñas & Monasterio, 1980; Baruch, 1984; Ricardi, Briceño & Adamo, 1987). The widest extent of páramo is found in Colombia and a number of researchers have studied its composition there (Cuatrecasas, 1934, 1958, 1968; Cleef, 1979, 1981, 1983; Sturm & Abouchaar, 1981; Sturm & Rangel, 1985, Rangel & Franco, 1985; Franco, Rangel & Lozano, 1986; Rangel & Lozano, 1986; Rangel & Aguirre, 1987). The puna of Perú has received considerable attention, beginning with the extensive works of Williams (1941) and Weberbauer (1945) and continuing with overviews such as that by Cabrera (1968) and detailed studies of particular areas (for example, Wilcox *et al.*, 1986).

By contrast, the páramos of Ecuador have received relatively little attention. Humboldt and Bonpland were the first to make a serious attempt at collecting Ecuadorian páramo plants in 1802 (Sandwith, 1926). A succession of plant collectors followed, including Jameson and Spruce, and collections have continued throughout this century. General descriptions of páramo vegetation have been produced by Diels (1934), Acosta-Solís (1937, 1966, 1984, 1985), Penland (1941), Drew (1944), Svensen (1945), Paredes (1962), Løjtnant & Molau (1982) and Cerón (1985). Until recently, access to many páramo areas has been difficult. Lately, as new roads have appeared, collecting has been carried out with renewed vigour to complete our knowledge of plant distributions in the more remote páramos and to provide herbarium material for identification purposes (for example, Holm-Nielsen, Øllgaard &

Molau, 1984). This activity has resulted in quite detailed plant inventories of some páramo areas and the beginnings of a Flora of Ecuador (Harling & Sparre, 1973-).

Very few quantitative descriptions of Ecuadorian páramos have been attempted. Balslev & de Vries (1982) described the vegetation at a single altitude on Volcán Cotopaxi by means of four 100m2 quadrats. Muñoz, Balslev & de Vries (1985) provided the same treatment for plots on Volcán Antisana and Black (1982) presented a preliminary account of a detailed study carried out on Volcán Antisana over a number of years, but as yet no further information is available.

Within any one páramo region in Ecuador, the vegetation can be expected to be comprised of a number of altitudinally-related vegetation zones. Within this zonal pattern, other vegetation types may be found which are independent of altitude, their presence governed by such factors as soil moisture, topography and the like. This expectation is based on the studies of páramo vegetation in neighbouring Andean countries which have already been cited (but particularly Cleef, 1979) and descriptions of mountainous regions throughout the world (for example, J.M.B. Smith, 1975, and Coe, 1967).

Mills (1975) described plant distribution over an altitudinal transect on Volcán Cotopaxi in terms of presence or absence of species, and this represents the only published study to date which looks at the community composition of an Ecuadorian páramo in relation to altitude.

Cuatrecasas (1934, 1958, 1968) defined three altitudinal belts of páramo vegetation with reference to the vegetation of Colombia. The transition zone between the upper Andean forest and the open grassland is dominated by shrubs and grasses, and Cuatrecasas termed this **sub-páramo**. Above the sub-páramo, he described the **grassy páramo** or **páramo proper**, characterized by tussock grasses and giant rosette plants. Finally, at the highest altitudes, the extreme environmental conditions restrict plant growth and cover is reduced. This is the **super-páramo**.

In describing the vegetation types of Ecuador, Harling (1979) also defined three altitudinal belts. Above the montane forest scrub, the **grass páramo** (*pajonal*) is located between 3,400 and 4,000 m, dominated by tussock grasses of *Calamagrostis, Festuca* and *Stipa*, with herbs and shrubs from the genera *Ranunculus, Lupinus, Gentiana, Halenia, Castilleja, Valeriana, Baccharis, Oritrophium, Chuquiraga, Hypochaeris* and in some cases *Espeletia*. The **shrub and cushion páramo** is found between 4,000 and 4,500 m. Tussock grasses are less extensive, being replaced by shrubs, herbs of various kinds, mats, rosette plants and cushions. Small trees may also occur. Most characteristic genera of this zone are *Chuquiraga, Diplostephium, Baccharis, Valeriana, Calceolaria, Astragalus, Loricaria, Senecio, Culcitium, Werneria, Oritrophium, Gentiana, Halenia, Viola, Lachemilla, Draba, Bomarea, Jamesonia* and *Lycopodium*. The most important cushion-forming species are *Azorella pedunculata, Azorella aretoides, Azorella corymbosa, Plantago rigida, Draba aretioides, Werneria humilis* and *Distichia tolimensis*. At the highest altitudes (above 4,500 m), Harling classifies the sparse vegetation of xerophytic grasses, alternating with herbs, shrubs, mosses and lichens as **desert páramo**. At these altitudes, species such as *Ephedra americana, Poa cucullata, Rhopalopodium guzmanii, Lupinus microphyllus, Lupinus smithianus, Nototriche* *pichinchensis, Senecio microdon, Senecio comosus, Culcitium nivale* and *Werneria rigida* are found. Harling also describes the much lower altitude páramo on the western and southern slopes of Volcán Chimborazo (from about 4,000 m) as desert páramo. Here he describes a community with scattered clumps of *Stipa* and a few shrubs and herbs (for example, *Calceolaria ericoides, Azorella pedunculata, Calandrina acaulis, Chuquiraga jussieui* and *Hypochaeris sonchoides*).

The divisions between these vegetation zones have been arbitrarily devised, based on many years' experience of studying páramo vegetation. Cleef (1981) described in great detail 121 community types of the Colombian Cordillera Oriental, using the Zürich-Montpellier classification methods. However, there are only a few other cases of páramo classification using quantitative methodology, these examining the Venezuelan páramo (Fariñas & Monasterio, 1980; Baruch, 1984).

The present study aims to give a quantitative description of the grassy páramo vegetation of Ecuador, linking the distribution of species and páramo types to environmental variation, including those factors relating to altitude. Azonal vegetation types, such as bogs or woodlands, were excluded from the study in order to simplify the relationship between vegetation and altitude.

Methods

Study Sites

Twelve páramo localities were sampled in total: these areas selected to encompass a range of páramo types from north to south and east to west (Figure 2.1). In north-western Ecuador, two páramos were sampled. Volcán Chiles straddles the Colombia-Ecuador border and maintains an extensive páramo, notable as one of the few in Ecuador with *Espeletia* giant rosette plants. The area is very humid and was sampled from 4,200m (between the summit and the crest of the pass 38km from Tulcán) to 3,600m near Tufiño (Figure 2.2). Volcán Cotacachi in Imbabura province supports a moderately humid páramo. It was studied from the shoulder above the crater at 4,200m to the area just above Laguna Cuicocha at 3,600m (Figure 2.3).

Only one páramo was studied in north-eastern Ecuador. To the north of the pass on the Quito-Baeza road is a very humid páramo on a lakeland plateau, the Páramo de Guamaní (Figure 2.4). It was sampled from 4,400m on the main jagged ridge to 3,800m in agricultural páramo below Laguna de Hoyas.

In Central Ecuador, four páramos were sampled in or close to Parque Nacional Sangay on the Cordillera Oriental. Volcán Tungurahua is still active, its tephra and ash deposits in this humid area supporting a modified páramo flora. Along the route to the summit on the northern flank of the volcano, the vegetation was investigated from 4,300m to 3,900m (Figure 2.5). Further south, the west-facing caldera of El Altar dominates a more usual páramo vegetation. A transect from 4,200m beneath

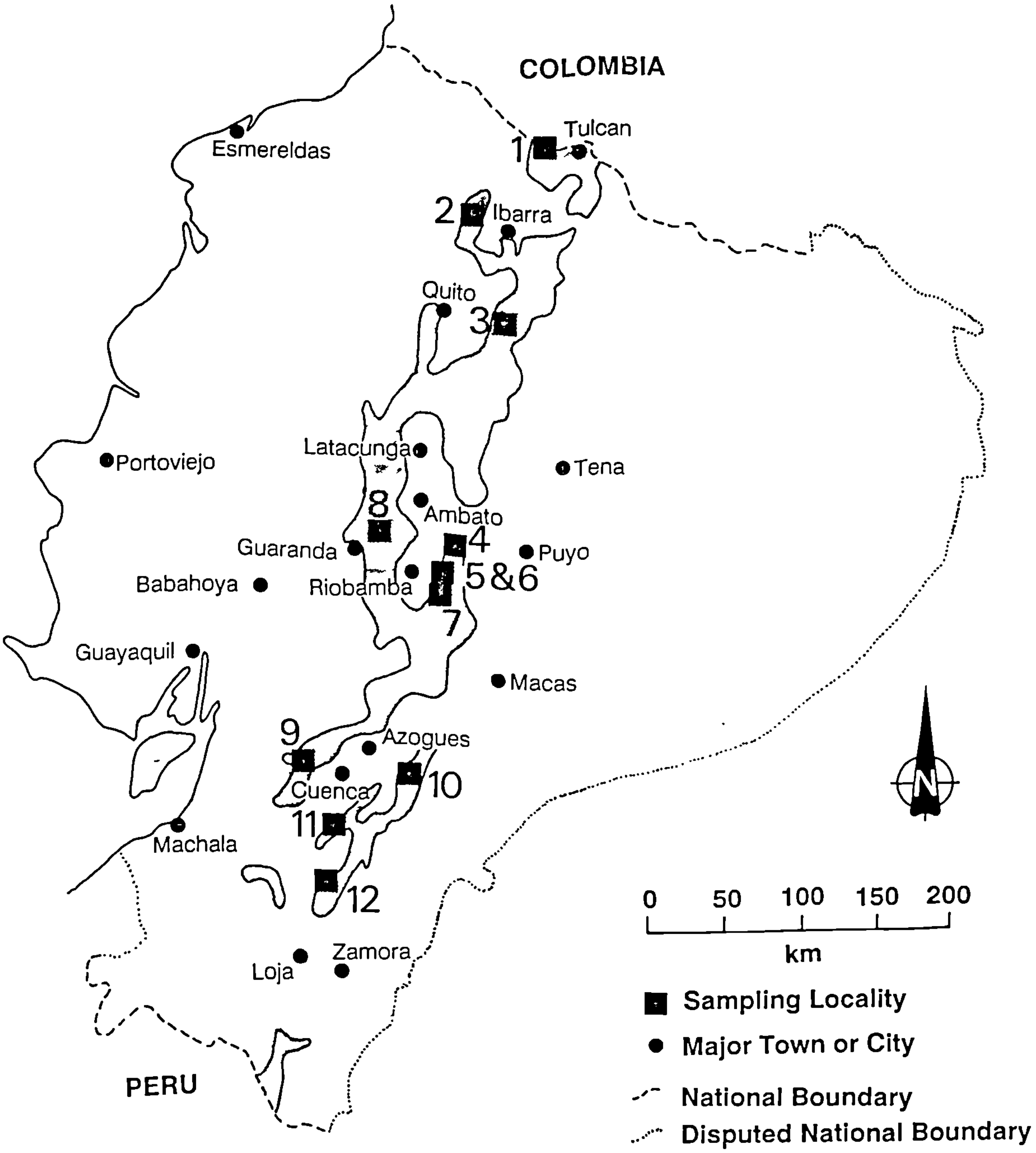


Figure 2.1.
Map of Ecuador showing the location of the twelve study sites. Site codes: 1, Volcán Chiles; 2, Volcán Cotacachi; 3, Páramo de Guamaní; 4, Volcán Tungurahua; 5 & 6, El Altar (2 sites); 7, Páramo de Daldal; 8, Volcán Chimborazo; 9, Páramo de Zapote Naida; 10, El Area Nacional de Recreación Cajas; 11, Páramo near Cumbe; 12, Páramo near Oña. Land above the 3,000 m contour line is shaded.

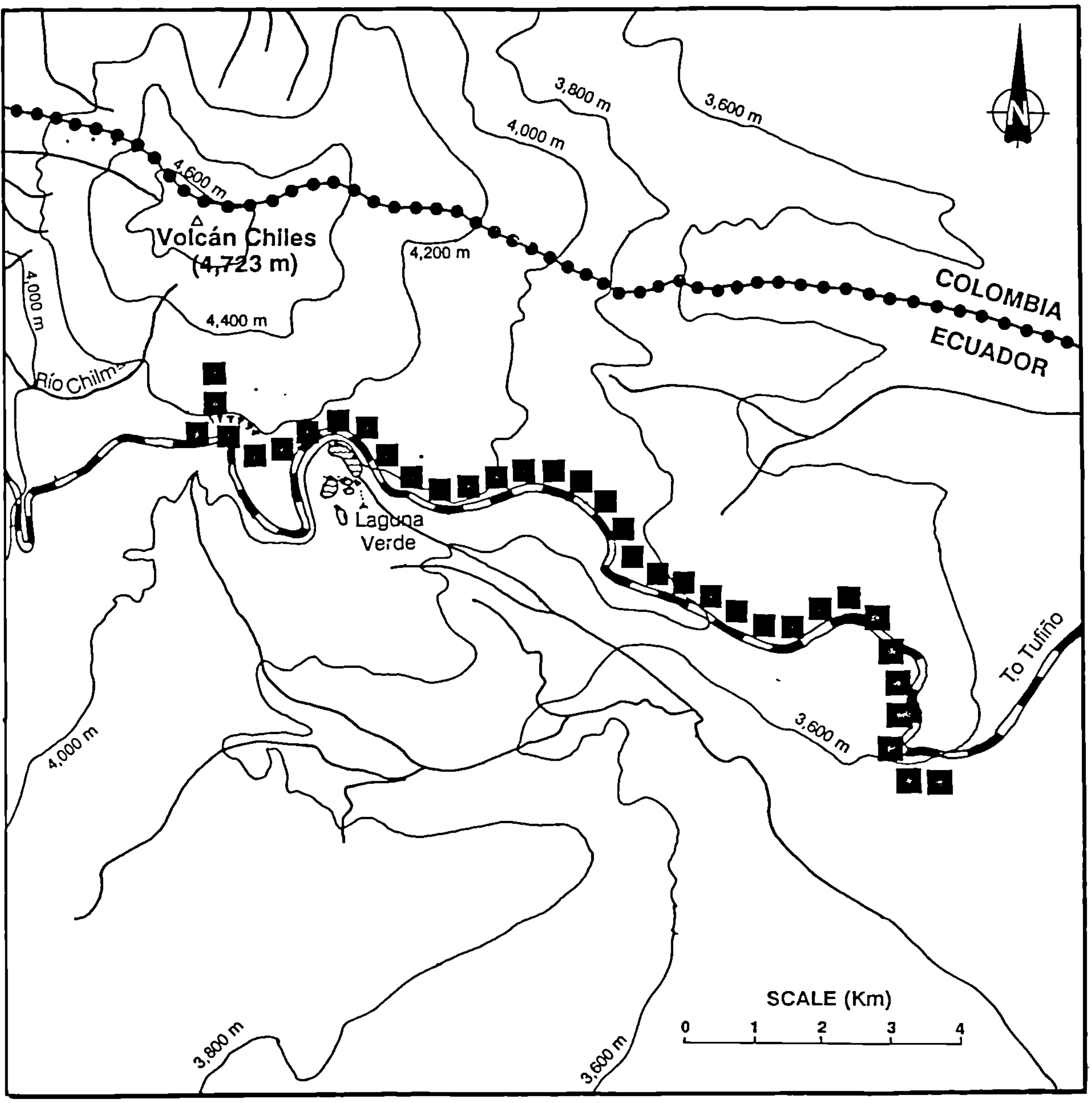


Figure 2.2.
The location of the sampling transect on Volcán Chiles (■). Based on the Instituto Geográfico Militar (Quito) map for Tufiño. The scale is 1: 100,000.

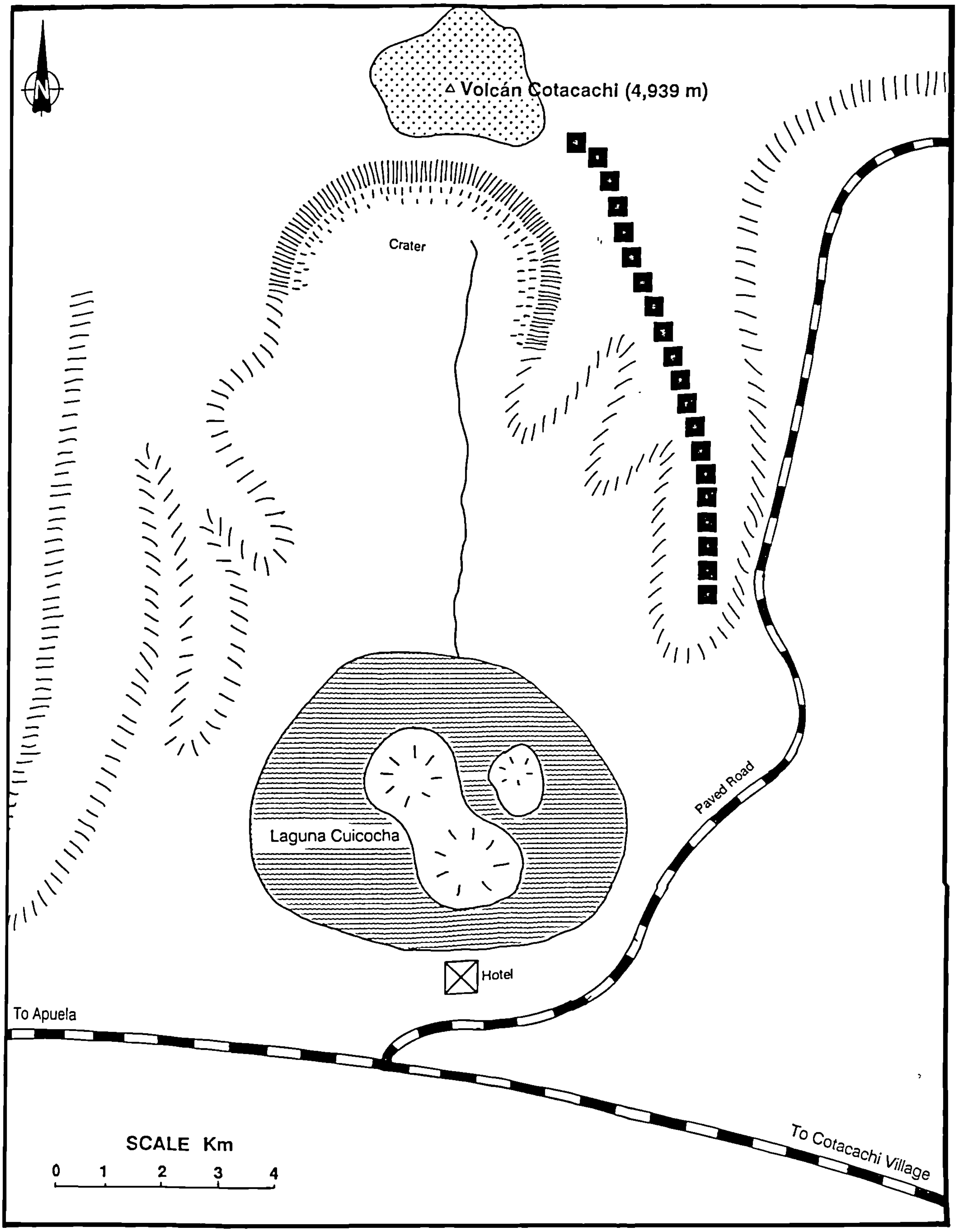


Figure 2.3.
Sketch map showing the location of the sampling transect on Volcán Cotacachi (■). The dotted area represents permanent snow cover. The scale is approximately 1:100,000.

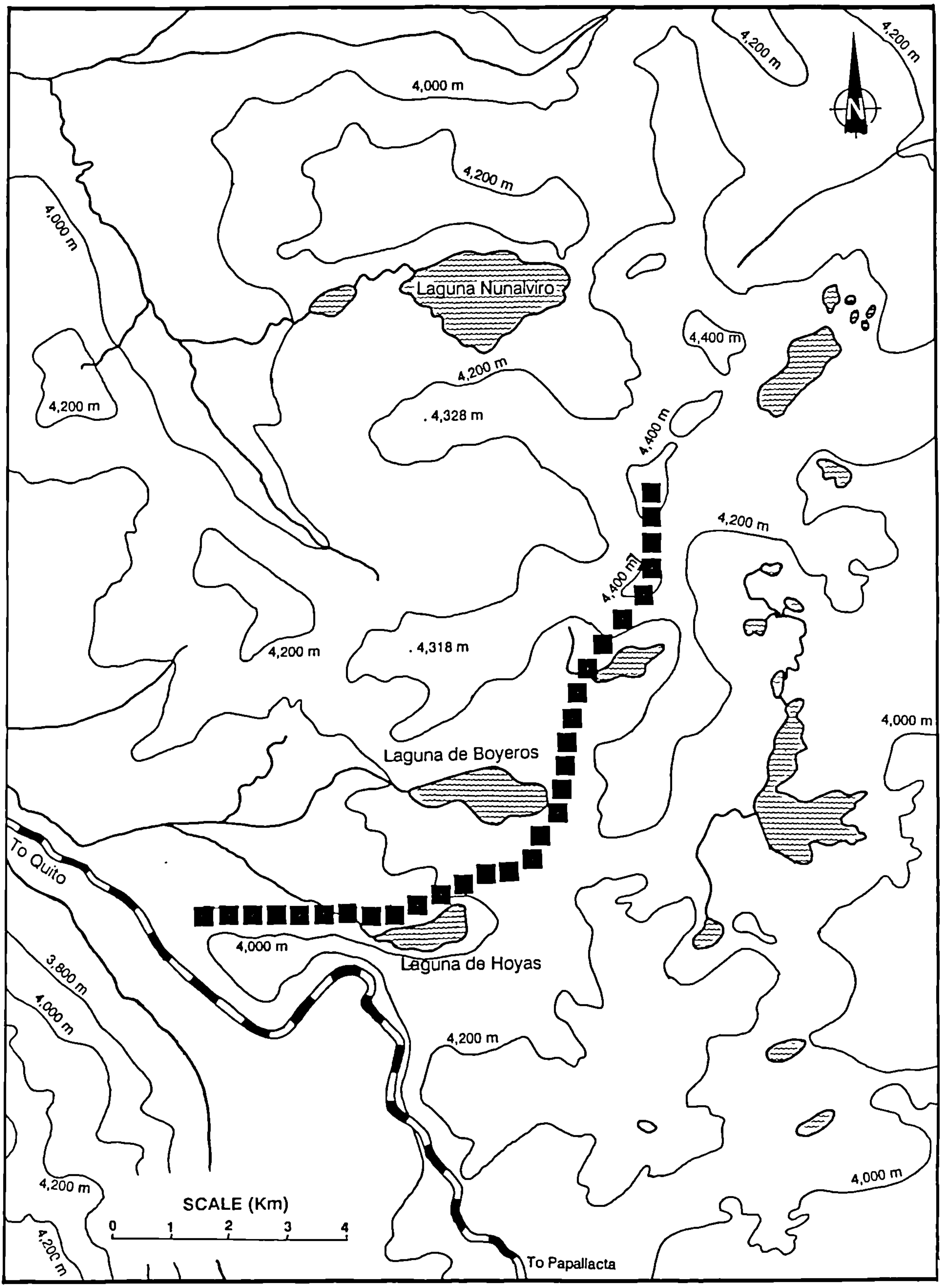


Figure 2.4.
The location of the sampling transect in the Páramo de Guamaní (■). Based on the Instituto Geográfico Militar (Quito) map for Oyacachi. The scale is 1: 100,000.

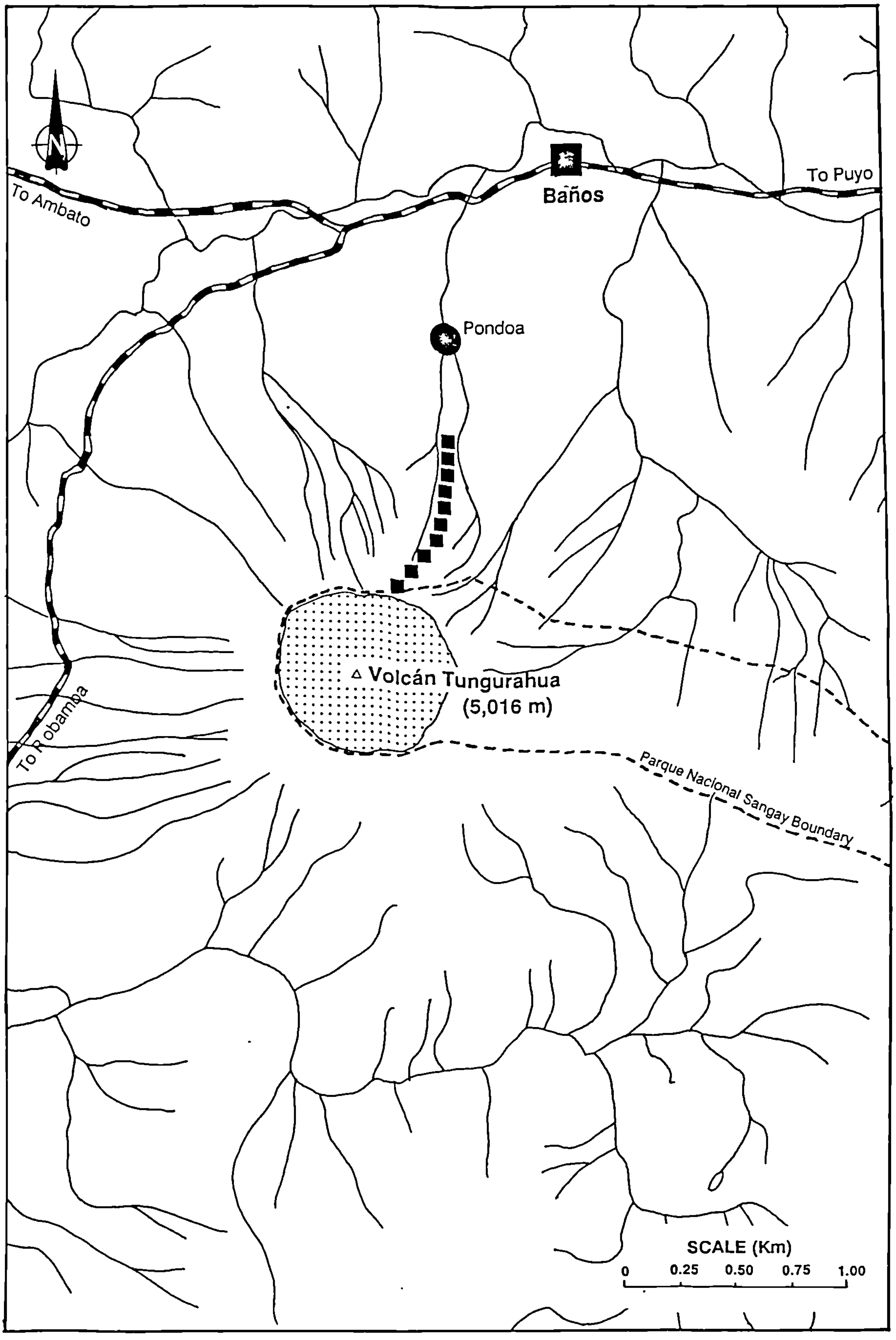


Figure 2.5.
The location of the sampling transect on Volcán Tungurahua (■). The dotted area represents permanent snow cover. The scale is approximately 1:25,000.

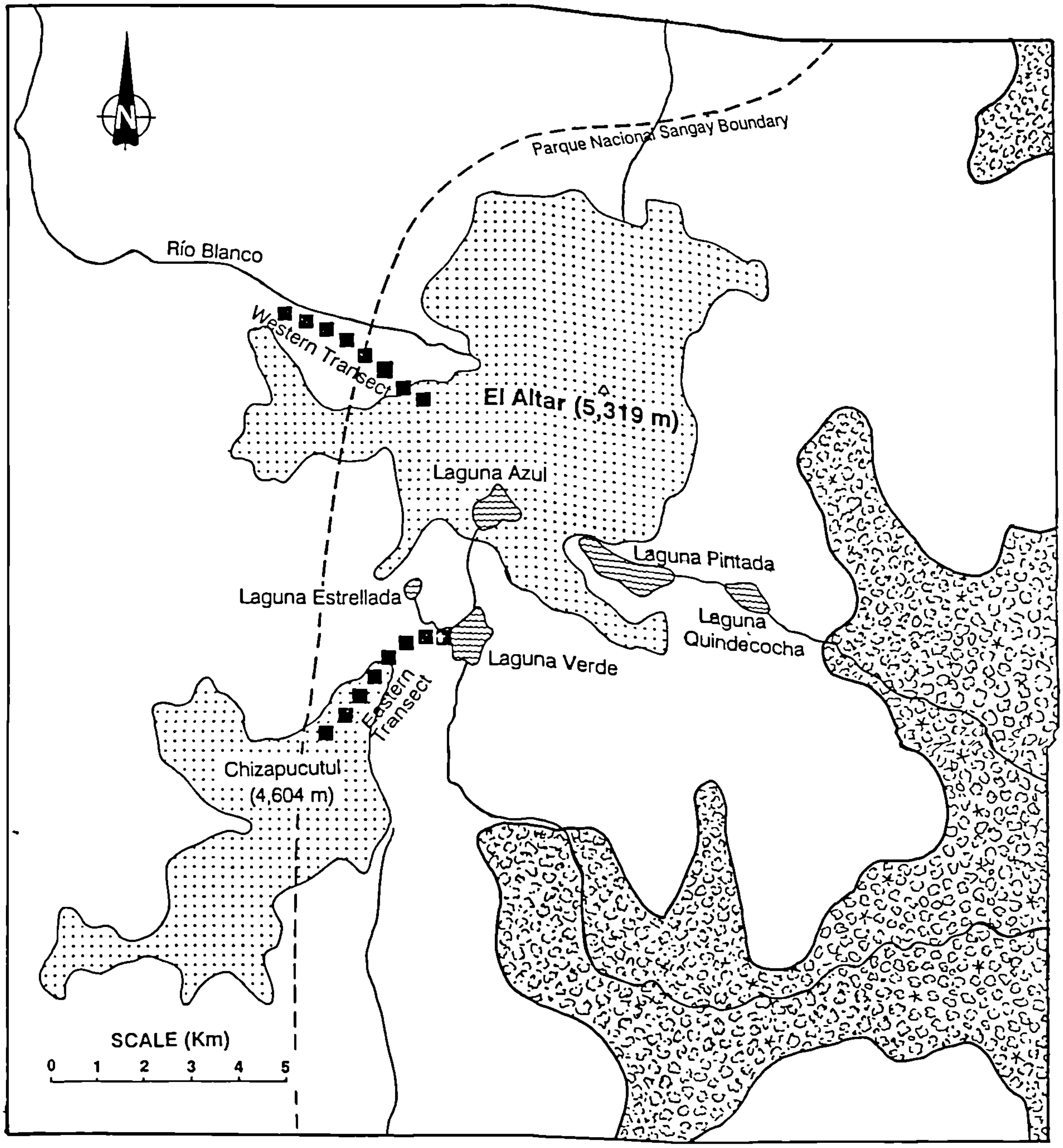


Figure 2.6.
The location of the two sampling transects on El Altar (■). The dotted area represents (semi-)permanent snow cover, and the forest is shown to the east. Based on the PRONAREG-ORSTOM Mapa Ecológico for Riobamba. The scale is approximately 1:142,800.

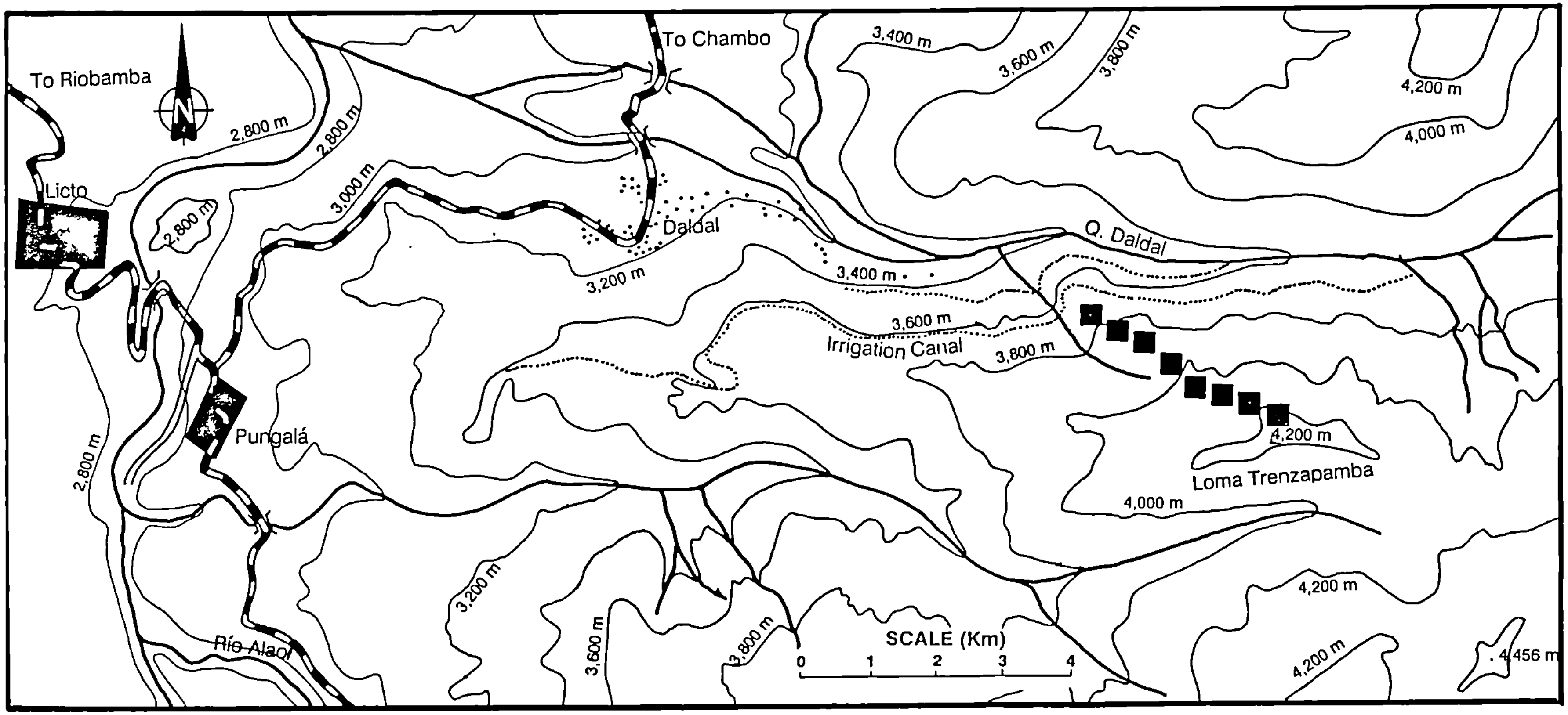


Figure 2.7.
The location of the sampling transects in the Páramo de Daldal (■). Based on the Instituto Geográfico Militar map for Riobamba. The scale is 1: 100,000.

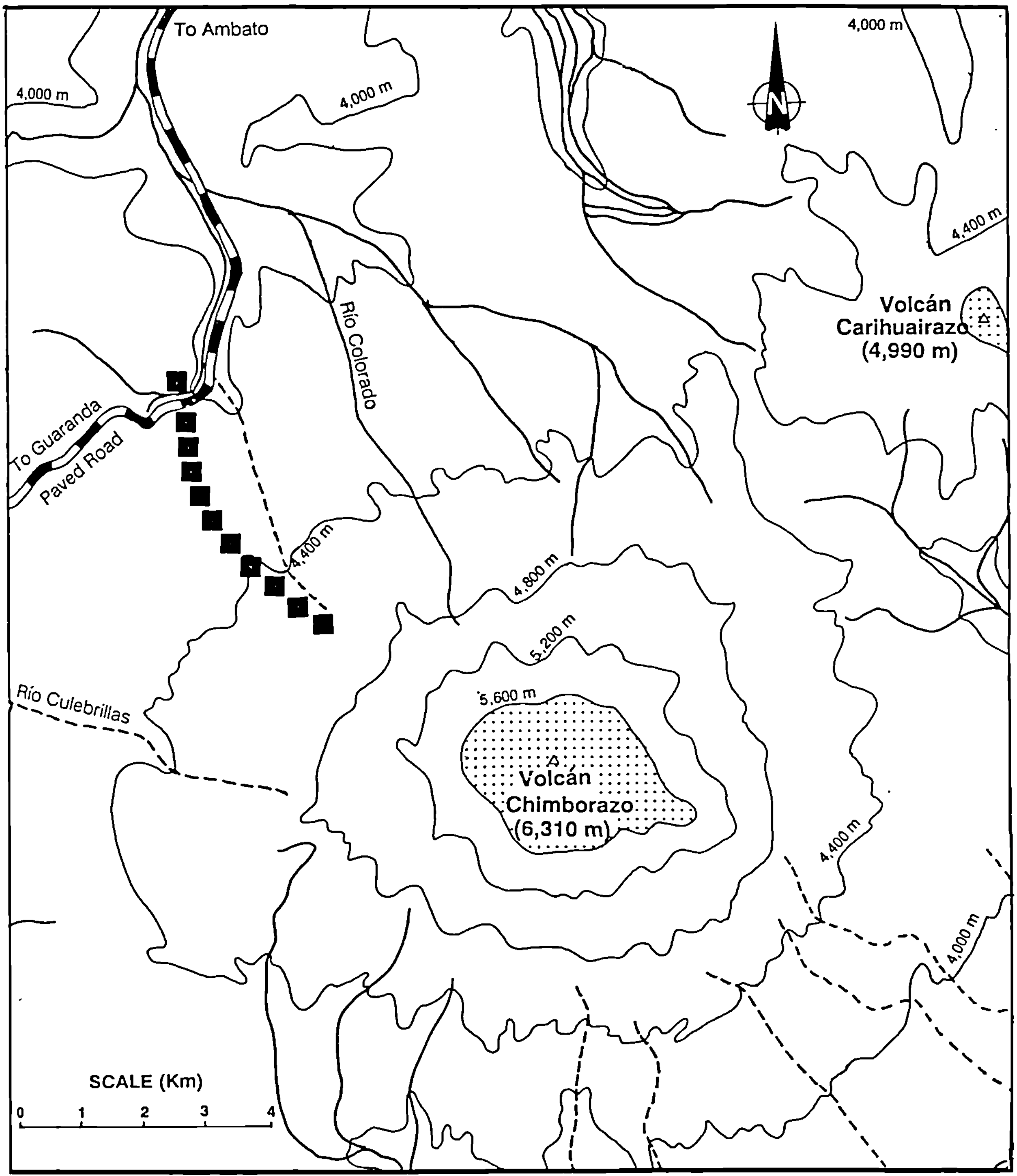


Figure 2.8.
The location of the sampling transect on Volcán Chimborazo (■). The dotted areas denote permanent snow cover. Based on the Instituto Geográfico Militar (Quito) map for Chimborazo. The scale is 1: 100,000.

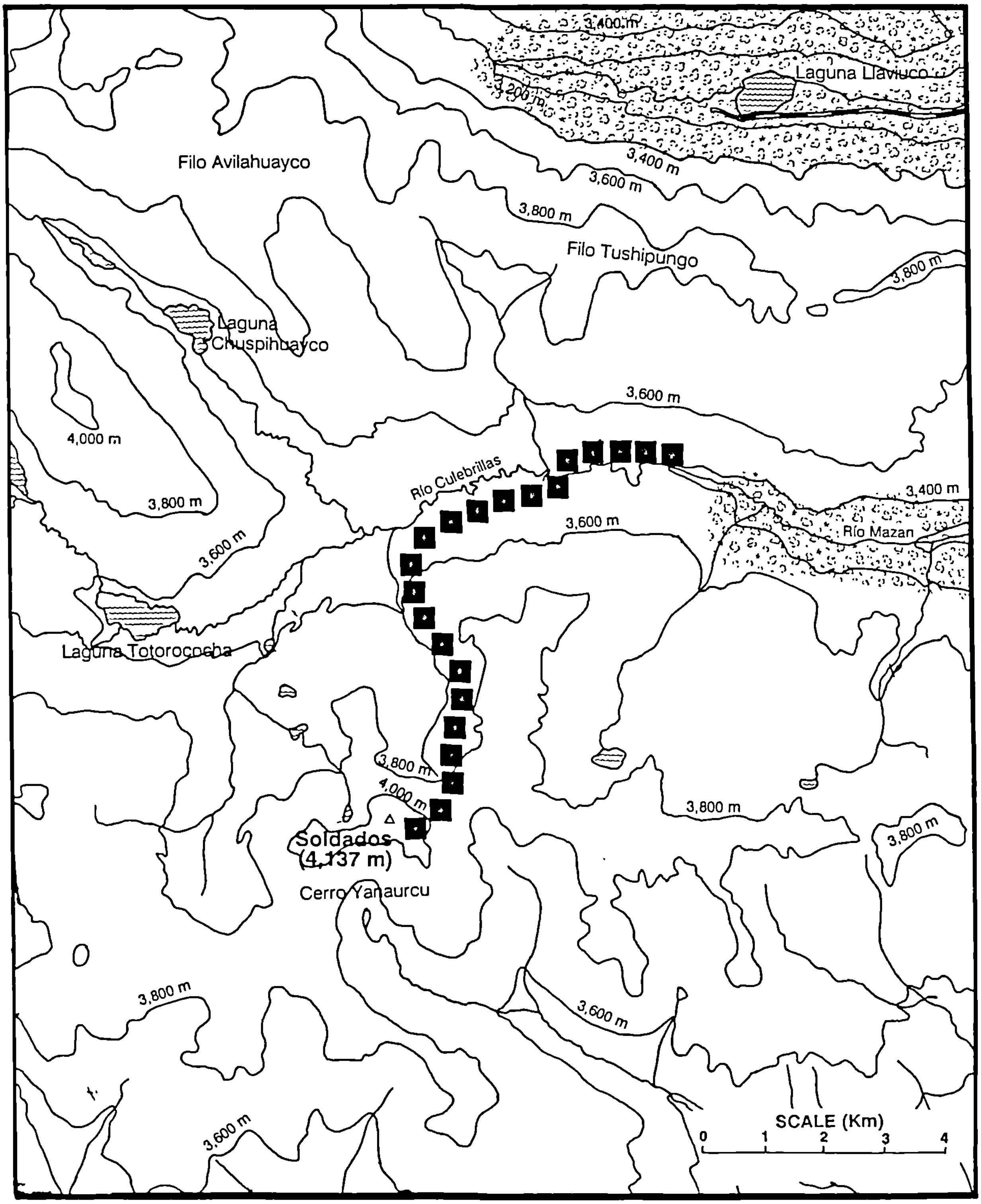


Figure 2.9.
The location of the sampling transect in the Páramo de Cajas (■). Based on the Instituto Geográfico Militar (Quito) map for Cuenca. The scale is 1: 100,000.

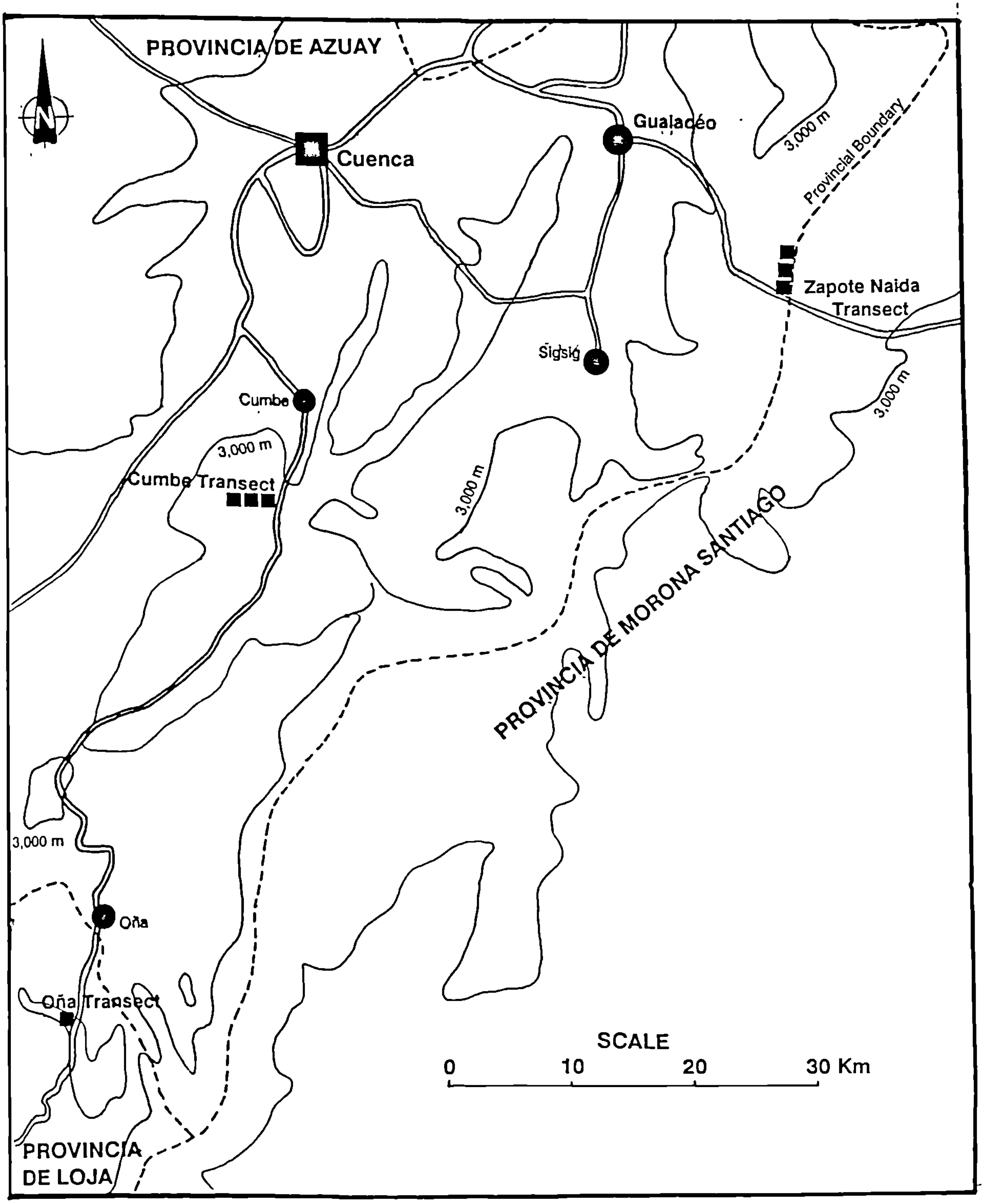


Figure 2.10.
The location of three sampling transects in southern Ecuador: the Páramo de Zapote Naida, Cumbe and Oña (■). Based on the Instituto Geográfico Militar (Quito) map of Ecuador (at 1: 1,000,000). The scale here is 1: 500,000.

Obispo to the Collanes Plain at 3,800m was the basis for the study in this area (Figure 2.6). On the eastern slopes of the El Altar massif, a much more humid páramo exists and was studied from 4,300m beneath Chizapucutul to 3,800m beside Laguna Verde (Figure 2.6). Above the village of Daldal an area of typical agricultural páramo was investigated. The Lomo de Trenzapamba at 4,200m was the highest study point at this location with the sub-páramo at 3,700m the lowest (Figure 2.7).

On the Cordillera Occidental in Central Ecuador stands Volcán Chimborazo, at 6,310m the highest peak in the country. The famous Grande Arenal ("Great Beach") was sampled from 4,600m to 4,000m on the northern slopes of the volcano (Figure 2.8). A highly modified páramo is found here on a sandy substrate in a comparatively dry region.

Finally, four páramos made up the southern section of the study sites. All four areas were comparatively dry and low-lying. El Area Nacional de Recreación Cajas is situated to the west of Cuenca on the Cordillera Occidental. It is a lakeland plateau averaging around 3,800m. The highest elevation studied was at 4,000m on Soldados above Totorococha, the transect descending from there to 3,400m towards the treeline above the Río Mazan forest reserve (Figure 2.9). On the pass between Cuenca and Limón on the Cordillera Oriental is the Páramo de Zapote Naida (Figure 2.10). It was studied from 3,500m to 3,200m, though no sampling was conducted at 3,300m because of a belt of shrubby vegetation. A páramo region south of Cumbe from 3,400m to 3,200m and a small patch of páramo at 3,100m south of Oña (Figure 2.10) completed the study sites. These two areas were both situated on the Cuenca to Loja road.

Table 2.1 provides a summary of the study sites. The grid references quoted are for guidance only, since the studies were conducted along transects rather than at points.

	Province	Altitude (m)		Latitude & Longitude	Sampling Dates
		Min	Max		
Volcán Chiles	Carchi	3,600	4,200	1°49'N 77°57'W	20–22 Oct 1987
Volcán Cotacachi	Imbabura	3,600	4,200	0°35'N 78°20'W	11–12 Oct 1987
Páramo de Guamaní	Pichincha	3,800	4,400	1°15'S 78°12'W	7-8 Oct 1987
Volcán Tungurahua	Tungurahua	3,900	4,300	1°29'S 78°23'W	28–29 Aug 1987
El Altar (west)	Chimborazo	3,800	4,200	1°40'S 78°24'W	2–3 Sep 1987
El Altar (east)	Chimborazo	3,800	4,300	1°43'S 78°25'W	12–13 Aug 1989
Daldal	Chimborazo	3,700	4,200	1°48'S 78°32'W	30 Oct 1987
Volcán Chimborazo	Chimborazo	4,000	4,600	1°30'S 77°50'W	25 Oct 1987
Páramo de Zapote Naida	Azuay/Morona Santiago	3,200	3,500	3°00'S 78°40'W	21 Sep 1987
Cajas	Azuay	3,400	4,000	2°53'S 79°10'W	12–14 Sep 1987
Cumbe	Azuay	3,200	3,400	3°20'S 79°10'W	21 Sep 1987
Oña	Loja	3,100	-	3°35'S 79°15'W	16 Sep 1987

Table 2.1.
Study sites used in the phytosociological study of the Ecuadorian páramos.

Plant Collection

Since a comprehensive flora of the Ecuadorian páramos has yet to be produced, it was necessary to collect voucher specimens of plant taxa and cross-reference them with plants cited in this study. Therefore, in cases where species have not been fully-named, they are identified by a code number shown in square braces, which permits cross-reference of the species to voucher specimens via Appendix 1. Thus, for *Cerastium* sp. [197], the code number 197 in Appendix 1 shows that this species is represented by two voucher specimens numbered 454 and 536.

A collecting licence was obtained from the Ministerio de Agricultura y Ganadería, with the support of the Pontificia Universidad Católica del Ecuador (PUCE) and the Museo Ecuatoriano de Ciencias Naturales (MECN).

During the course of the fieldwork, representative vascular plant material was collected. Ideally, fertile specimens were taken, but occasionally only sterile material was available. The material was placed in polythene bags until it could be pressed. The pressing usually took place within one day, though in difficult circumstances up to three days elapsed before some specimens were pressed.

Plant material was sandwiched between sheets of newsprint or, when available, proprietary ‘flimsies’, with a drying unit (consisting of a corrugated aluminium sheet between two blotting papers) separating specimens. Repeating this pattern, the press was filled and bound using straps.

Whenever possible, the presses were transported to Quito for drying in the drying room of the PUCE herbarium. The presses were placed over low-power electric heaters for 3-7 days. On many occasions, however, drying had to be carried out away from Quito. For this purpose, a wooden frame was constructed to support the press at the right height and a paraffin pressure stove used as a heat source. This proved very effective, though the stove was prone to flare up from time to time, requiring constant vigilance.

When possible, four duplicates were collected for each specimen, and numbered on collection. Duplicate specimens are housed in the collections at the Royal Botanic Gardens, Kew (K) or the Royal Botanic Garden, Edinburgh (E), the herbarium of the Pontificia Universidad Católica del Ecuador, Quito (QCA) and the Ecuadorian national collection at the Museo Ecuatoriano de Ciencias Naturales, Quito (QCNE). The remaining duplicate set was deposited with the Ministerio de Agricultura y Ganadería in Quito.

Preliminary identifications were carried out at the QCA herbarium, but most of the taxonomic work took place at the herbarium of the Royal Botanic Gardens, Kew. Many specimens have only been identified to generic level, though it has been possible in nearly all cases to assign these to more precise taxa without actually naming them (for example, *Calamagrostis* A, *Calamagrostis* B, *etc.*). Where specimens could not be differentiated with confidence, species aggregates have been formed. For example, there is a possibility that *Bromus pitensis* was confused with *Bromus lanatus* in the field, and therefore this species has been amalgamated into *Bromus lanatus* aggregate. Similarly, *Lachemilla andina* has been added to *Lachemilla rupestris* aggregate in the analysis.

A complete moss and macro-lichen collection was made for each quadrat and later used to produce comparative species lists for each páramo area. A portion of the moss collection was stolen in Ecuador, rendering full comparisons impossible. The remainder of the mosses and macro-lichens are housed in the British Museum of Natural History (BMNH), the Royal Botanic Gardens, Edinburgh (E), QCA and QCNE, but have yet to be determined. The following analyses were, therefore, only performed on the vascular plant composition of the quadrats.

Sampling Procedure

Only zonal páramo was studied. Azonal vegetation, such as that found in bogs, was deliberately excluded from the sampling. The vegetation was investigated by means of 5m x 5m quadrats, randomly located at each 100m of elevation over the range studied (which depended upon the páramo coverage at each site). At each altitude, a 100m transect was established along the contours and the three quadrats located according to random co-ordinates previously generated. This was not always possible, however, particularly in the super-páramo where the vegetation was sometimes confined to smaller patches (by rocky outcrops, unfavourable conditions or merely by the small size of the peak). In such cases the horizontal transect was shortened and the random co-ordinates scaled accordingly.

For each 25m2 sampling unit, a complete list of the vascular plants present was compiled, along with the corresponding Braun-Blanquet abundance scores (1, <5%; 2, 6-25%; 3, 26-50%; 4, 51-75%; 5, >75% – 'r' and '+' were not used owing to the small size of the sample area). The species present were cross-referenced with voucher specimens in the plant collection.

Estimates of the coverage (as a percentage) of bare ground and rock cover, including scree, were made for each sample unit. Plant litter coverage was not estimated because most of the tussock grass material decays while still attached to the plant, making accurate judgement difficult. The abundance scores for tussocks of this sort included such standing dead material.

A number of environmental variables were recorded for each quadrat. Altitude was measured as the mean of two Thommen 6,000m aneroid altimeters set at Quito observatory (2,818m). It was not possible to account for meteorological changes in atmospheric pressure. Aspect was assigned to 8 compass points (N, NE, E, SE, S, SW, W and NW) using a prismatic compass and slopes were measured in degrees from the horizontal using a clinometer. A soil sample was taken from each quadrat (10cm depth), air-dried and the pH measured with a Whatman pH meter (2:1 ratio of water to soil by volume). However, some soil samples were stolen along with the mosses, and therefore pH data is unavailable for the southern sites.

Finally, exposure, burning intensity, grazing intensity, trampling intensity and overall disturbance were estimated for each quadrat on subjective, semi-quantitative scales from 0 to 5 (where 0 represents the absence of the influence and 5 the highest influence).

Exposure was judged using the local topography: a sample surrounded by ridges on all sides was considered to be of low exposure whereas a sample plot on a ridge received a high exposure score. Burning intensity scores were determined from visible indicators of fire. These included ash deposits, charred remains and the loss of soil caused by the combustion of its organic material. Indicators of grazing included visible signs (cropping of vegetation, *etc.*) and indirect signs (droppings). Trampling scores were based on the presence of micro-terracing, paths, poaching (hoof-prints), broken branches of shrubs and cattle-scrapes.

Overall disturbance was recorded in an attempt to deal with the interactive effects of burning, trampling and grazing, where the combined impact of these variables can result in higher disturbance than the individual effects might suggest. Thus, a disturbance score was assessed with reference to compounded disturbance, irrespective of its source.

The majority of the data was collected from August to October 1987, though one of the sites was visited in August 1989 (Table 2.1).

Data-Handling and Analysis

In order to simplify the dataset, the vegetation samples were classified according to a polythetic divisive cluster analysis technique. This was achieved using the TWINSPAN algorithm (Hill, 1979), forming part of the VESPAN-II package (Malloch, 1988). The plant taxa were also classified using this programme, based on their presence in the stand classes.

Multivariate direct gradient analysis (canonical ordination) was employed to determine the relationship between species distributions and the measured environmental variables. This combination of regression and ordination was carried out using the CANOCO programme (ter Braak, 1988). The analysis was performed on all taxa and all stands, then the TWINSPAN classes were superimposed (as centroids) upon the resulting ordination. The first axis of this ordination and the trace statistic (the sum of all axes) were tested for statistical significance by means of a Monte-Carlo permutation test (Hope, 1968) with 99 permutations, also part of the CANOCO package.

α-diversity was estimated for each stand using an adapted version of the Simpson index:

$$D = \frac{\Sigma\, p(p-1)}{A(A-1)}$$

where p represents the percentage cover of each species (using the mid-point of its Braun-Blanquet score), and A is the total coverage of all the species in the quadrat (that is, Σp). This only represents an approximation of the diversity of the stands, since Braun-Blanquet scores are not 'linear'. Diversity was expressed as the reciprocal of D.

β-diversity, measuring "the extent of species change along environmental gradients" (Whittaker, 1975), was calculated according to the measure proposed by Wilson & Smida (1984):

$$\beta_T = \frac{[g(H) + l(H)]}{2\alpha} .$$

where g(H) represents the number of species gained along the gradient and l(H) the number of species lost. α is the average number of species found within the samples. β-diversity is essentially the same as MacArthur's (1965) between habitat diversity. To calculate β-diversity values, the three replicate quadrats at each altitude were combined (three 25 m2 quadrats becoming one sample of 75 m2).

Results

Twelve páramo regions were studied. The number of quadrats and summary statistics on the number of vascular taxa ("species") recognised for each of these regions is given in Table 2.2. The number of altitude levels sampled in each study area ranged from one (3,100 m at Oña) up to seven for several of the sites. In total, 64 altitudes were sampled using 192 quadrats. The 21 stands sampled in the páramo at Cajas included more species (117) than any of the other study areas, whilst the three quadrats at Oña yielded just 24 species. On average, a 25 m2 sample of the vegetation contained 21.11 species, though this varied from site to site (only 6.90 species per quadrat on Volcán Chimborazo to 29.22 species in the páramo at Daldal). The number of species recorded in the three replicate quadrats at each altitude averaged 29.41. On Volcán Chimborazo, this mean was 10.71 whilst in the páramo around the crater of El Altar it reached 42.60 species.

Site	No of Altitude Levels	No of Quadrats	No of Species in all Quadrats	Mean No of Species per Quadrat	Mean No of Species per Altitude (3 Quadrats)
Volcán Chiles	7	21	94	22.10	31.86
Volcán Cotacachi	7	21	89	20.10	27.43
Páramo de Guamaní	7	21	97	23.52	35.57
Volcán Tungurahua	5	15	52	17.67	25.40
El Altar (west)	5	15	92	27.54	42.60
El Altar (east)	6	18	71	19.44	25.83
Daldal	6	18	91	29.22	36.57
Volcán Chimborazo	7	21	37	6.90	10.71
Páramo de Zapote Naida	3	9	47	24.56	33.67
Cajas	7	21	117	22.86	36.29
Cumbe	3	9	71	24.76	36.33
Oña	1	3	24	16.33	24.00
Overall	64	192	348	21.11	29.41

Table 2.2.

The location and summarised vascular plant composition of 192 páramo quadrats. For each locality the number of altitude levels sampled and the number of quadrats used are stated. The total number of vascular plant species found in the stands at each locality are given. The mean number of species found in each stand and at each altitude level (three quadrats combined) are shown.

Altogether, 348 taxa of vascular plants have been recognised in these sample stands (Appendix 1). Table 2.3 indicates the composition of the 192 stands in terms of family, and Table 2.4 shows the genera comprising these families. Almost 20% of the species found in the quadrats belong to the family Compositae. 25 genera of composites were present in the vegetation samples, the best-represented being *Senecio, Baccharis, Culcitium, Gnaphalium, Diplostephium* and *Gynoxys.*

Family	Number of Taxa in Family	Percentage of all Taxa
Unidentified to Family	6	1.7
Compositae	69	19.8
Gramineae	47	13.5
Cyperaceae	19	5.5
Lycopodiaceae	15	4.3
Scrophulariaceae	15	4.3
Gentianaceae	14	4.0
Leguminosae	12	3.4
Umbelliferae	11	3.2
Valerianaceae	11	3.2
Ericaceae	10	2.9
Rosaceae	10	2.9
Rubiaceae	10	2.9
Caryophyllaceae	8	2.3
Cruciferae	8	2.3
Geraniaceae	6	1.7
Plantaginaceae	6	1.7
Violaceae	6	1.7
Bromeliaceae	5	1.4
Guttiferae	5	1.4
Hemionitidaceae	5	1.4
Juncaceae	5	1.4
Melastomataceae	5	1.4
Ranunculaceae	5	1.4
Iridaceae	4	1.1
Orchidaceae	4	1.1
Lomariopsidaceae	3	0.9
Alstroemeriaceae	2	0.6
Labiatae	2	0.6
Oxalidaceae	2	0.6
Polygalaceae	2	0.6
Alliaceae	1	0.3
Aspleniaceae	1	0.3
Blechnaceae	1	0.3
Campanulaceae	1	0.3
Equisetaceae	1	0.3
Filicopsida	1	0.3
Grossulariaceae	1	0.3
Isoetaceae	1	0.3
Lentibulariaceae	1	0.3
Malvaceae	1	0.3
Melanthiaceae	1	0.3
Onagraceae	1	0.3
Ophioglossaceae	1	0.3
Polygonaceae	1	0.3
Thelypteridaceae	1	0.3
Xyridaceae	1	0.3
Total	348	100.0

Table 2.3.
A summary of the 348 recognised taxa in 192 páramo quadrats. The number of taxa ("species") in each family is given, along with the percentage of all taxa this represents. There are 46 families. Six voucher specimens could not be identified to family level.

The Gramineae accounted for 13.5% of the taxa with 15 genera determined. *Agrostis, Poa, Calamagrostis* and *Festuca* were the most important genera. The Cyperaceae

No Family (6 unidentified taxa)
- Unidentified (6 taxa)

Alliaceae (1 unidentified genus)
- Unidentified (1 taxon)

Alstroemeriaceae (1 genus)
- *Bomarea* (2 taxa)

Aspleniaceae (1 genus)
- *Asplenium* (1 taxon)

Blechnaceae (1 genus)
- *Blechnum* (1 taxon)

Bromeliaceae (1 genus)
- *Puya* (5 taxa)

Campanulaceae (1 genus)
- *Lobelia* (1 taxon)

Caryophyllaceae (2 genera)
- *Cerastium* (7 taxa)
- *Stellaria* (1 taxon)

Compositae (25 genera + 2 unidentified taxa)
- Unidentified (2 taxa)
- *Senecio* (8 taxa)
- *Baccharis* (7 taxa)
- *Culcitium* (6 taxa)
- *Gnaphalium* (6 taxa)
- *Diplostephium* (5 taxa)
- *Gynoxys* (5 taxa)
- *Oritrophium* (4 taxa)
- *Werneria* (4 taxa)
- *Loricaria* (3 taxa)
- *Erigeron* (2 taxa)
- *Hypochaeris* (2 taxa)
- *Lucilia* (2 taxa)
- *Aphanactis* (1 taxon)
- *Bidens* (1 taxon)
- *Chrysactinium* (1 taxon)
- *Chuquiraga* (1 taxon)
- *Conyza* (1 taxon)
- *Cotula* (1 taxon)
- *Espeletia* (1 taxon)
- *Hieracium* (1 taxon)
- *Perezia* (1 taxon)
- *Sonchus* (1 taxon)
- *Stevia* (1 taxon)
- *Taraxacum* (1 taxon)
- *Vernonia* (1 taxon)

Cruciferae (4 genera + 2 unidentified genera)
- Unidentified (2 taxa)
- *Draba* (2 taxa)
- *Eudema* (2 taxa)
- *Cardamine* (1 taxon)
- *Lepidium* (1 taxon)

Cyperaceae (5 genera)
- *Carex* (9 taxa)
- *Uncinia* (4 taxa)
- *Oreobolus* (3 taxa)
- *Rhynchospora* (2 taxa)
- *Eleocharis* (1 taxon)

Equisetaceae (1 genus)
- *Equisetum* (1 taxon)

Ericaceae (3 genera + 7 unidentified genera)
- Unidentified (7 taxa)
- *Disterigma* (1 taxon)
- *Pernettya* (1 taxon)
- *Vaccinium* (1 taxon)

Filicopsida (1 genus)
- *Eriosorus* (1 taxon)

Gentianaceae (3 genera)
- *Gentianella* (9 taxa)
- *Halenia* (4 taxa)
- *Gentiana* (1 taxon)

Geraniaceae (1 genus)
- *Geranium* (6 taxa)

Gramineae (15 genera + 2 unidentified taxa)
- Unidentified (2 taxa)
- *Agrostis* (12 taxa)
- *Poa* (10 taxa)
- *Calamagrostis* (5 taxa)
- *Festuca* (4 taxa)
- *Muhlenbergia* (2 taxa)
- *Paspalum* (2 taxa)
- *Stipa* (2 taxa)
- *Aciachne* (1 taxon)
- *Anthoxanthum* (1 taxon)
- *Bromus* (1 taxon)
- *Cortaderia* (1 taxon)
- *Elymus* (1 taxon)
- *Holcus* (1 taxon)
- *Neurolepis* (1 taxon)
- *Trisetum* (1 taxon)

Table 2.4.

Genera in the 192 páramo quadrats. For each family the number of genera (plus any unidentified specimens, which may or may not represent further genera) are shown. Within each family, the genera are listed along with the number of taxa assigned to them. In total there are 117 genera in 46 families, with 27 taxa as yet unidentified. [Continued Overleaf]

Grossulariaceae (1 genus)
- *Ribes* (1 taxon)

Guttiferae (1 genus)
- *Hypericum* (5 taxa)

Hemionitidaceae (1 genus)
- *Jamesonia* (5 taxa)

Iridaceae (2 genera)
- *Sisyrinchium* (3 taxa)
- *Orthosanthus* (1 taxon)

Isoetaceae (1 genus)
- *Isoetes* (1 taxon)

Juncaceae (2 genera + 1 unidentified genus)
- Unidentified (1 taxon)
- *Luzula* (3 taxa)
- *Distichia* (1 taxon)

Labiatae (2 genera)
- *Satureja* (1 taxon)
- *Stachys* (1 taxon)

Leguminosae (4 genera)
- *Lupinus* (7 taxa)
- *Vicia* (3 taxa)
- *Astragalus* (1 taxon)
- *Trifolium* (1 taxon)

Lentibulariaceae (1 genus)
- *Pinguicula* (1 taxon)

Lomariopsidaceae (1 genus)
- *Elaphaglossum* (3 taxa)

Lycopodiaceae (2 genera)
- *Lycopodium* (12 taxa)
- *Huperzia* (3 taxa)

Malvaceae (1 genus)
- *Nototriche* (1 taxon)

Melanthiaceae (1 genus)
- *Tofieldia* (1 taxon)

Melastomataceae (1 genus + 2 unidentified genera)
- Unidentified (2 taxa)
- *Brachyotum* (3 taxa)

Onagraceae (1 genus)
- *Epilobium* (1 taxon)

Ophioglossaceae (1 genus)
- *Ophioglossum* (1 taxon)

Orchidaceae (2 genera + 2 unidentified genera)
- Unidentified (2 taxa)
- *Altensteinia* (1 taxon)
- *Myrosmodes* (1 taxon)

Oxalidaceae (1 genus)
- *Oxalis* (2 taxa)

Plantaginaceae (1 genus)
- *Plantago* (6 taxa)

Polygalaceae (1 genus)
- *Monnina* (2 taxa)

Polygonaceae (1 genus)
- *Rumex* (1 taxon)

Ranunculaceae (2 genera)
- *Ranunculus* (4 taxa)
- *Anemone* (1 taxon)

Rosaceae (1 genus)
- *Lachemilla* (10 taxa)

Rubiaceae (4 genera)
- *Arcytophyllum* (4 taxa)
- *Relbunium* (4 taxa)
- *Galium* (1 taxon)
- *Nertera* (1 taxon)

Scrophulariaceae (7 genera)
- *Bartsia* (4 taxa)
- *Castilleja* (4 taxa)
- *Veronica* (3 taxa)
- *Calceolaria* (1 taxon)
- *Ourisia* (1 taxon)
- *Pedicularis* (1 taxon)
- *Sibthorpia (1 taxon)*

Thelypteridaceae (1 genus)
- *Thelypteris* (1 taxon)

Umbelliferae (5 genera + 2 unidentified genus)
- Unidentified (2 taxa)
- *Azorella* (5 taxa)
- *Eryngium* (1 taxon)
- *Hydocotyle* (1 taxon)
- *Niphogeton* (1 taxon)
- *Oreomyrrhis* (1 taxon)

Valerianaceae (1 genus)
- *Valeriana* (11 taxa)

Violaceae (1 genus)
- *Viola* (6 taxa)

Xyridaceae (1 genus)
- *Xyris* (1 taxon)

Table 2.4. (Continued)
Genera in the 192 páramo quadrats.

provided 5.2% of the taxa found in the quadrats, with the Lycopodiaceae, Scrophulariaceae and Gentianaceae just below this figure.

Table 2.5 lists the thirty most frequent species occurring in the samples. By far the commonest species is *Calamagrostis* sp. [251], which is present in 94.27% of the quadrats, with a mean Braun-Blanquet score between 2 and 3 (5-50% cover). Other common grasses were *Paspalum tuberosum* (present in 40% of the sample stands), *Poa* sp. [262] (26%), *Agrostis nigritella* (20%) and *Bromus lanatus* (18%). *Pernettya prostrata* and *Disterigma empetrifolium* were growing in 56% and 46% of the quadrats respectively.

Species number and name		Family	Mean B-B Score	Const %	N
251	*Calamagrostis* sp.	Gramineae	2.7	94.27	181
185	*Pernettya* sp.	Ericaceae	0.6	56.25	108
79	*Disterigma empetrifolium*	Ericaceae	0.5	46.35	89
91	*Geranium sibbaldioides*	Geraniaceae	0.4	44.79	86
40	*Hypochaeris sessiliflora*	Compositae	0.4	42.19	81
97	*Paspalum tuberosum*	Gramineae	0.5	39.58	76
143	*Eryngium humile*	Umbelliferae	0.4	38.54	74
48	*Oritrophium peruvianum*	Compositae	0.3	33.85	65
72	*Carex tristicha*	Cyperaceae	0.3	29.17	56
146	*Oreomyrrhis andicola*	Umbelliferae	0.3	28.13	54
80	*Gentiana sedifolia*	Gentianaceae	0.3	27.60	53
64	*Werneria humilis*	Compositae	0.3	27.08	52
134	*Bartsia laticrenata*	Scrophulariaceae	0.3	26.56	51
161	*Hypericum* sp.	Guttiferae	0.3	26.56	51
88	*Halenia weddelliana*	Gentianaceae	0.3	26.04	50
262	*Poa* sp.	Gramineae	0.3	26.04	50
150	*Valeriana bonplandiana*	Valerianaceae	0.2	24.48	47
130	*Lachemilla orbiculata*	Rosaceae	0.3	23.96	46
99	*Sisyrinchium jamesonii*	Iridaceae	0.2	22.92	44
106	*Lupinus sarmentosus*	Leguminosae	0.2	22.92	44
29	*Gnaphalium pensylvanicum*	Compositae	0.2	22.40	43
15	*Bidens andicola*	Compositae	0.2	21.88	42
39	*Hieracium frigidum*	Compositae	0.2	21.88	42
139	*Azorella aretoides*	Umbelliferae	0.2	20.31	39
124	*Lachemilla rupestris*	Rosaceae	0.2	19.79	38
142	*Azorella pedunculata*	Umbelliferae	0.2	19.79	38
244	*Agrostis nigritella*	Gramineae	0.2	19.79	38
103	*Satureja nubigena*	Labiatae	0.2	19.27	37
94	*Bromus lanatus*	Gramineae	0.2	18.23	35
153	*Valeriana microphylla*	Valerianaceae	0.2	18.23	35

Table 2.5.
The 30 most frequent species found in the 192 páramo quadrats. The species number, name and family are shown, along with the mean Braun-Blanquet value, the frequency (N, out of 192) and the percentage constancy in the sample stands.

The Compositae made an important contribution to the list of most frequent species: *Hypochaeris sessiliflora*, *Oritrophium peruvianum* and *Werneria humilis* were all present in over 25% of the sample stands. *Geranium sibbaldioides* and *Eryngium humile* were each found in over 30% of the vegetation samples.

	Slope	Expos	Bare	Rock	Burn	Trampl	Graz	Disturb	pH	Cond	Cover	Diversity	
Altitude (3920 m)	2.2+ *	22.4+ ***	18.4+ ***	3.6+ **	29.6- ***	20.3- ***	35.6- ***	38.2- ***	11.1+ ***	0.6- NS	24.2- ***	8.0+ ***	
Slope (24°)		4.0+ **	3.2- *	0.0 NS	0.4+ NS	0.0 NS	0.0 NS	0.0 NS	5.8+ **	1.9+ NS	0.2 NS	+1.3+ NS	
Exposure (Index score 3.2)			0.9+ NS	10.9+ ***	23.5- ***	22.4- ***	19.8- ***	25.3- ***	0.0 NS	0.7- NS	11.6- ***	9.4+ ***	
Bare Ground (11% cover)				0.1- NS	6.7- ***	11.1- ***	23.9- ***	12.5- ***	18.7+ ***	1.7- NS	38.3- ***	0.2- NS	
Rock cover (2% cover)					3.8- **	5.4- ***	4.4- **	5.6- ***	3.8+ **	0.4+ NS	7.3- ***	1.3+ NS	
Burning (Index score 2.0)						53.5+ ***	70.2+ ***	81.6+ ***	12.2- ***	0.2+ NS	30.8+ ***	20.0- ***	
Trampling (Index score 2.0)							66.2+ ***	73.9+ ***	15.7- ***	0.1+ NS	32.5+ ***	14.4- ***	
Grazing (Index score 1.8)								83.8+ ***	20.1- ***	0.7+ NS	50.4+ ***	19.7- ***	
Disturbance (Index score 2.3)									12.4- ***	0.3+ NS	40.0+ ***	20.6- ***	
pH (132 samples only) (5.2 units)										5.3+ **	15.9- ***	0.7+ NS	
Conductivity (132 samples only) (1.2 mS s-1)											1.8+	0.3+ NS	NS
Vegetation Cover (97% cover)												11.4- ***	
Diversity (8.4)													

Table 2.6.
Correlations between environmental variables, vegetation cover and diversity. Correlations are based on 192 observations for each of the variables (with the exception of soil pH and conductivity with 132 observations). The overall mean for each of the environmental variables is shown in the left-hand column. The r2 values are given on the first line and the '+' or '-' indicates a positive and negative correlation respectively. The second line shows if the correlation is significant (*, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$) or not significant (NS).

The eleven environmental variables which were measured for each quadrat were subjected to a correlation test (Table 2.6), the distributions of six of these variables are shown in Figure 2.11. Vegetation cover and species diversity values, derived from species abundance data for each stand, were also correlated with the environmental variables in Table 2.6. It is immediately apparent that these environmental variables are interdependent. All variables except soil conductivity show a significant relationship with altitude. Exposure is greater at higher altitudes ($r2 = 22.4\%, p < 0.001$) and the cover of bare rock increases ($r2 = 3.6\%, p = 0.008$). The amount of bare ground also rises with altitude ($r2 = 18.4\%, p < 0.001$) and slopes become steeper ($r2 = 2.2\%$, $p = 0.038$). The soils are less acidic at higher altitudes than those lower down ($r2 = 11.1\%, p < 0.001$).

The semi-subjective assessment of overall disturbance was a very good predictor of burning ($r2 = 81.6\%, p < 0.001$), trampling ($r2 = 73.9\%, p < 0.001$) and grazing ($r2 = 83.8\%, p < 0.001$). All of these variables were highly correlated with each other. Clearly, trampling and grazing are linked ($r2 = 66.2\%, p < 0.001$) and these forms of disturbance are concentrated in areas which have been burned ($r2 = 53.5\%$, $p < 0.001$; $r2 = 70.2\%, p < 0.001$, respectively). It is reasonable, therefore, to use overall disturbance alone as an indicator of burning, trampling and grazing pressures. These disturbances show an inverse relationship with altitude ($r2 = 38.2\%$, $p < 0.001$): disturbance decreases up the elevational gradient.

Vegetation cover, calculated as the sum of the Braun-Blanquet mid-point cover values for each quadrat, decreases at higher altitudes ($r2 = 24.2\%, p < 0.001$). Species diversity ("evenness") tends to increase with altitude ($r2 = 8.0\%, p < 0.001$), as dominance by a few species diminishes. Exposure decreases vegetation cover ($r2 = 11.6\%, p < 0.001$) but increases species diversity ($r2 = 11.6, p < 0.001$). Vegetation cover is greater on more acidic soils ($r2 = 15.9\%, p < 0.001$), which are more common on flatter ground ($r2 = 5.8\%, p = 0.005$).

The 192 vegetation samples were classified using TWINSPAN. The dendrogram showing the divisions leading to the stand classification is presented in Figure 2.12. A group of three samples was found to be sufficiently different from the other plots to split away from them at the first division. At the next division, another small group (containing 15 stands) was separated from the main group of samples. Then, by a number of successive divisions, the large group of 174 samples was divided into five groupings of 10, 24, 79, 46 and 15 plots. Ultimately, the classification resulted in 31 stand groups. These end groups may be interpreted as types of páramo vegetation. It should be remembered that this analysis does not rely on presence or absence of species alone for the divisions. Instead, it is the combination of species present that determines the end groupings. Thus, one species may be diagnostic of several groups, but in each group its association with other characteristic species is unique. A description for each of these páramo types is provided later.

Figure 2.13 shows the CANOCO ordination biplot of the 348 species plotted against the first two constrained axes. In the figure, the species are displayed as points in a two-dimensional subspace (there are many more dimensions that could be displayed if it were possible). These points represent their approximate optima in this space, that is, the points where they are most abundant. The environmental variables are shown as arrows: the length of an arrow indicates the magnitude of the correlation between the variable and the distribution of species, whilst the direction of the arrow shows the plane in which the variable increases.

This ordination was subjected to a Monte Carlo permutation test to determine the statistical significance of the relationship between the species distribution and the ordination axes (and, therefore, the environmental variables). The species distribution in the ordination space was found to be related to the environmental variables with a high degree of probability ($p = \leq 0.01$).

Arrows have been drawn on the ordination to show the nature of the relationship between species distribution and vegetation cover ("Area") and species diversity.

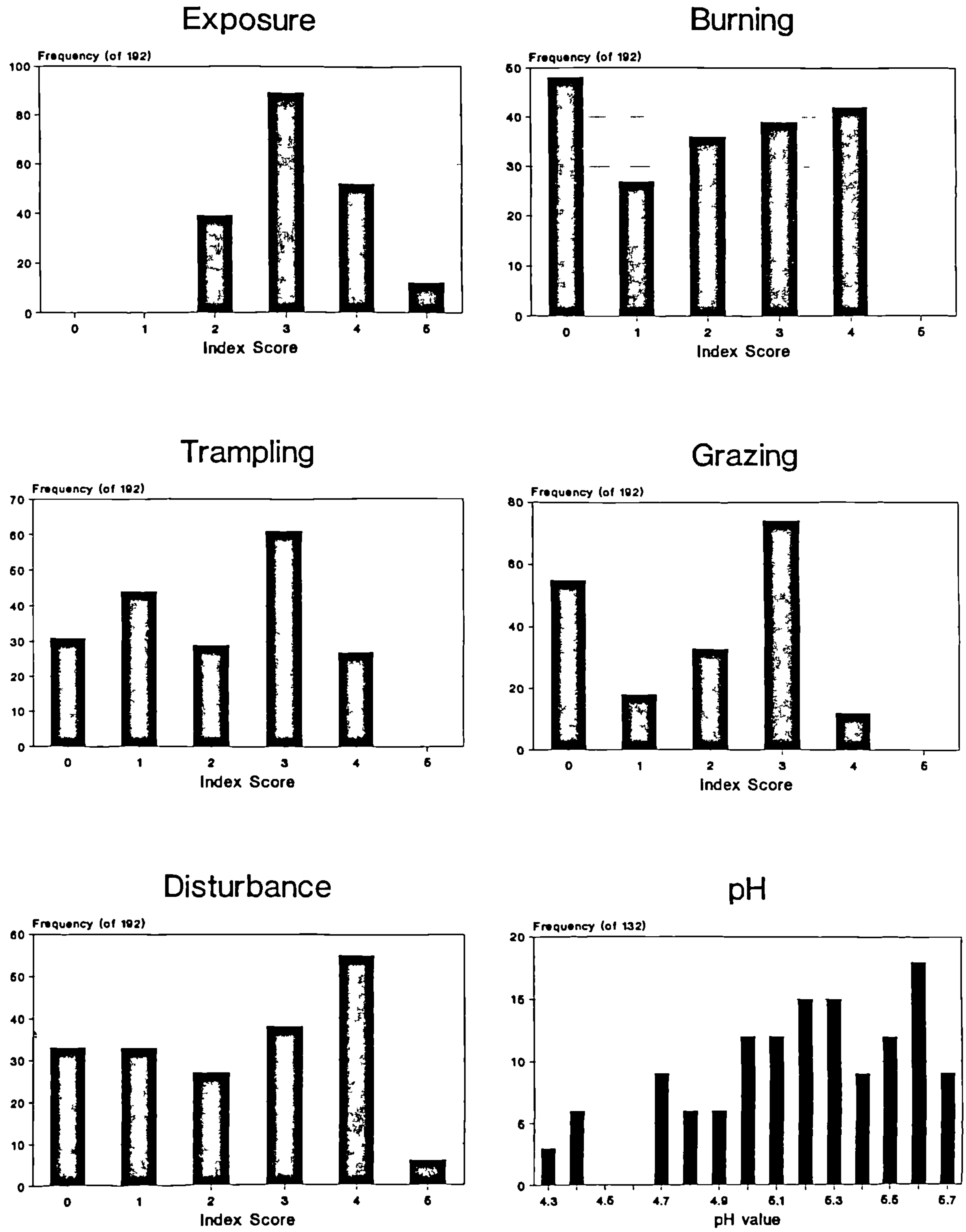


Figure 2.11.

Distribution of six environmental variables in the páramo vegetation samples. Exposure, burning, trampling, grazing and disturbance were measured on a six-point scale (where 0 represents the absence of the influence and 5 the highest influence) for 192 samples. pH values were measured for 132 samples.

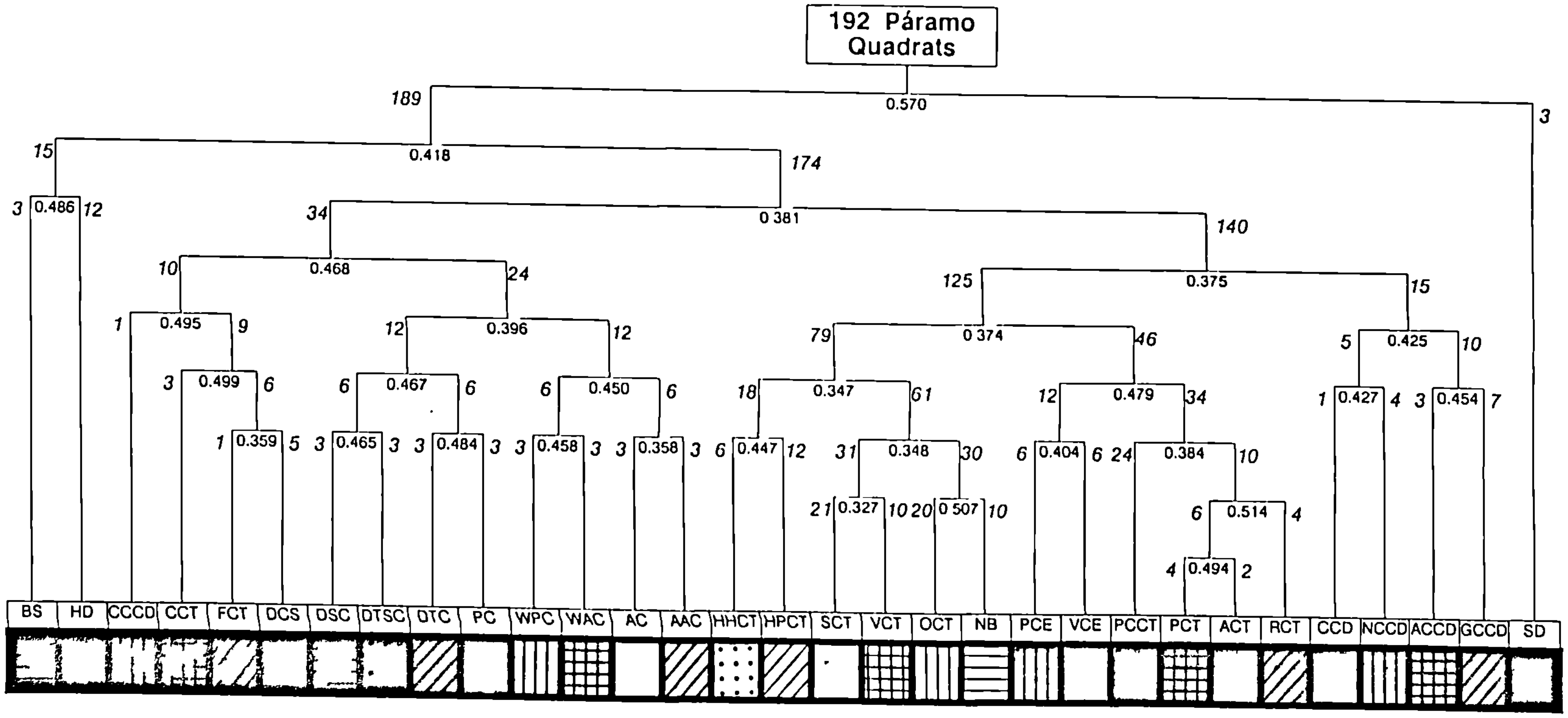


Figure 2.12.

TWINSPAN classification of 192 samples of Ecuadorian páramo vegetation. 31 vegetation types were defined and each of these is described in detail in the text (cross-referenced by the 2-4 letter code). The eigenvalue, which gives an indication of the importance of a division, is shown directly beneath each division. The number of stands in each group is provided either side of a division. The end groups have been colour-coded in the same way as Figures 2.14 and 2.16.

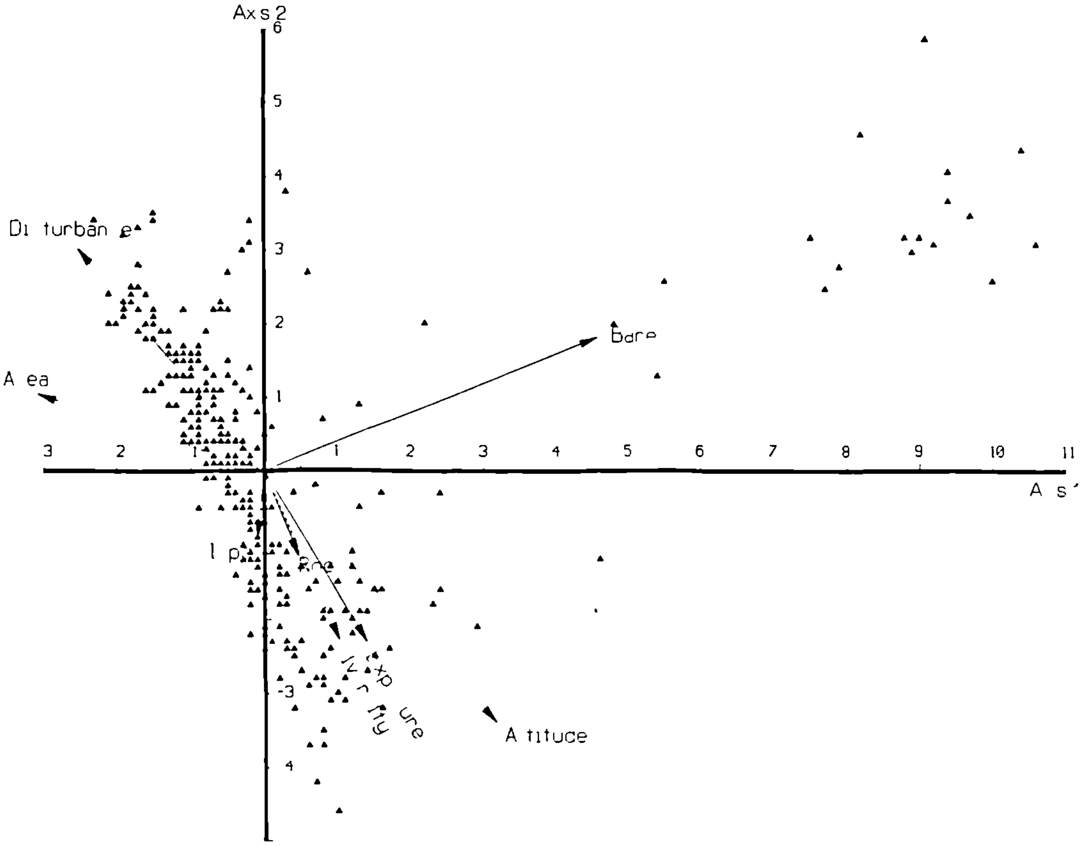


Figure 2.13.
CANOCO biplot ordination of the 348 vascular species present in 192 páramo stands. Environmental variables are depicted as solid arrows. Passive variables, which were not used to calculate the ordination, are superimposed as dashed arrows. The axes are divided into standard deviation units ($\lambda_1 = 0.508$, $\lambda_2 = 0.449$).

These arrows are passive, in that they were not used to determine the ordination (unlike the environmental variables), but have been superimposed onto it after its creation. For this reason they have been drawn with dashed rather than solid lines.

Most of the species in Figure 2.13 lie within a belt running diagonally from the upper left portion of the ordination (with negative values for Axis 1 and positive values for Axis 2) to the lower right part (positive Axis 1 values and negative Axis 2 values). This distribution corresponds well with the environmental variables of altitude, exposure and disturbance, as depicted by their arrows. Those species in the lower right portion of the ordination are most abundant at higher altitudes, where disturbance is minimal but exposure is greater. Species diversity was highest in this region of the biplot. Species located in this part of the ordination include *Oritrophium peruvianum, Culcitium ovatum, Werneria humilis, Werneria pumila, Gentianella foliosa, Lupinus purdianus, Lachemilla holosericea, Cerastium* sp. [198], *Aciachne flagellifera, Agrostis nigritella, Agrostis* sp. [239], *Huperzia hypogoea, Lycopodium* sp. [288], *Lycopodium* sp. [289], *Luzula racemosa, Plantago rigida, Valeriana aretioides, Bartsia laticrenata* and *Azorella aretoides.*

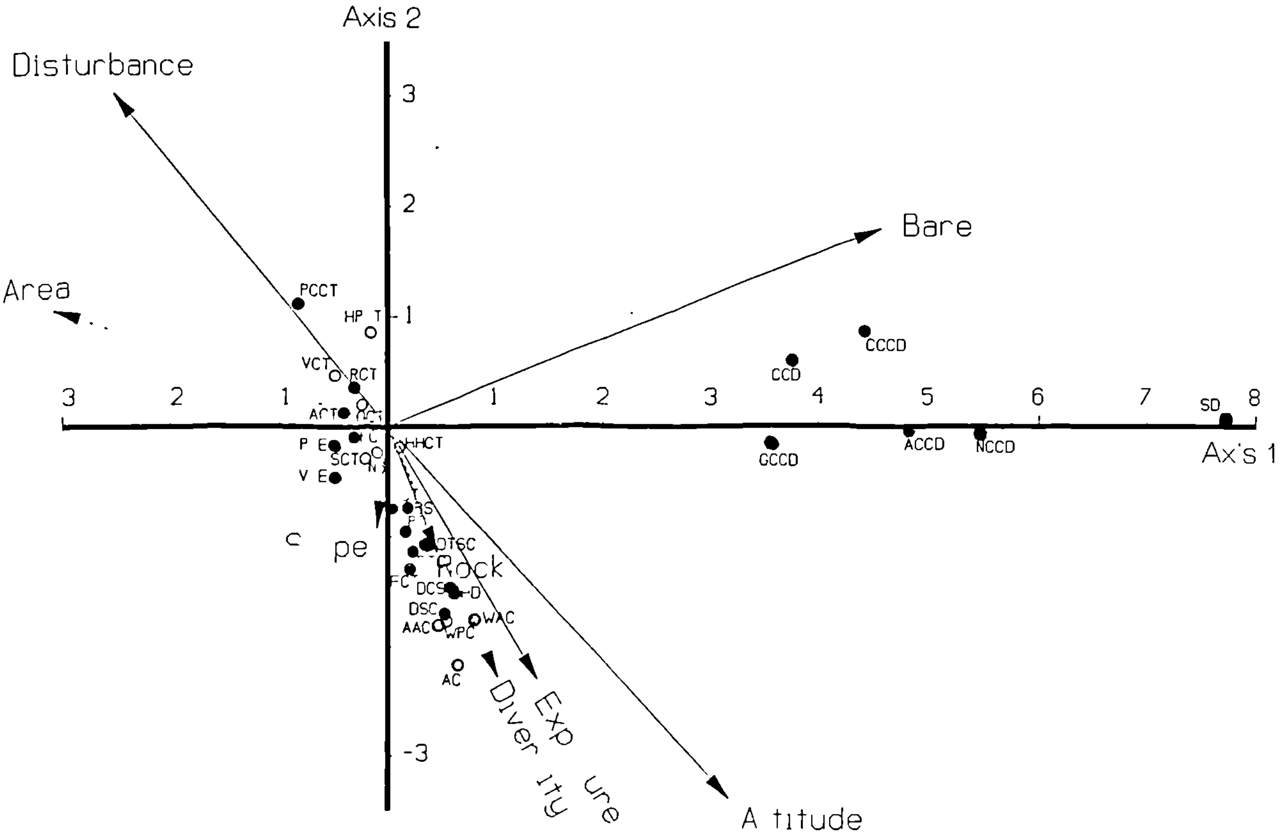


Figure 2.14.

CANOCO biplot ordination of the 31 páramo plant communities. Environmental variables are depicted as solid arrows. Passive variables, which were not used to calculate the ordination, are superimposed as dashed arrows. The axes are divided into standard deviation units ($\lambda_1 = 0.508$, $\lambda_2 = 0.449$). The centroid of each class is colour-coded to match that of Figures 2.12 and 2.16.

Species which are more abundant at lower altitudes, where disturbance is greater but exposure is reduced, are located in the upper left part of the ordination. Species which are located in this portion of the ordination tend to exist in vegetation of lower diversity and include *Paspalum tuberosum, Poa* sp. [266], *Poa* sp. [267], *Stipa* sp. [270], *Chrysactinium acaule, Gynoxys buxifolia, Oritrophium peruvianum* forma intermedium, *Gentianella gracilis, Gentianella hyssopifolia, Orthrosanthus chimboracensis, Sisyrinchium tinctorium, Pinguicula calyptrata, Tofieldia sessiliflora, Brachyotum ledifolium, Viola humboldtii, Puya* sp. [180], *Puya* sp. [181], *Halenia* sp. [187], *Cerastium* sp. [197], *Jamesonia robusta, Lycopodium clavatum* and *Oxalis* sp. [359].

A number of species lie clustered to the upper right of the diagram. The position of these species correlates well with the amount of bare ground present, and are little influenced by the other environmental variables which were measured. These species were all found on Volcán Chimborazo, and include *Chuquiraga jussieui, Erigeron pinnatus, Lucilia radiata, Senecio teretifolius, Werneria crassum, Gentianella cernua, Lupinus smithianus, Valeriana alypifolia* ssp. *alypifolia, Valeriana* sp. [194], *Geranium* sp. [157], *Cerastium* sp. [200], *Plantago* sp. [301], *Stipa* sp. [353] and *Agrostis* sp. [348].

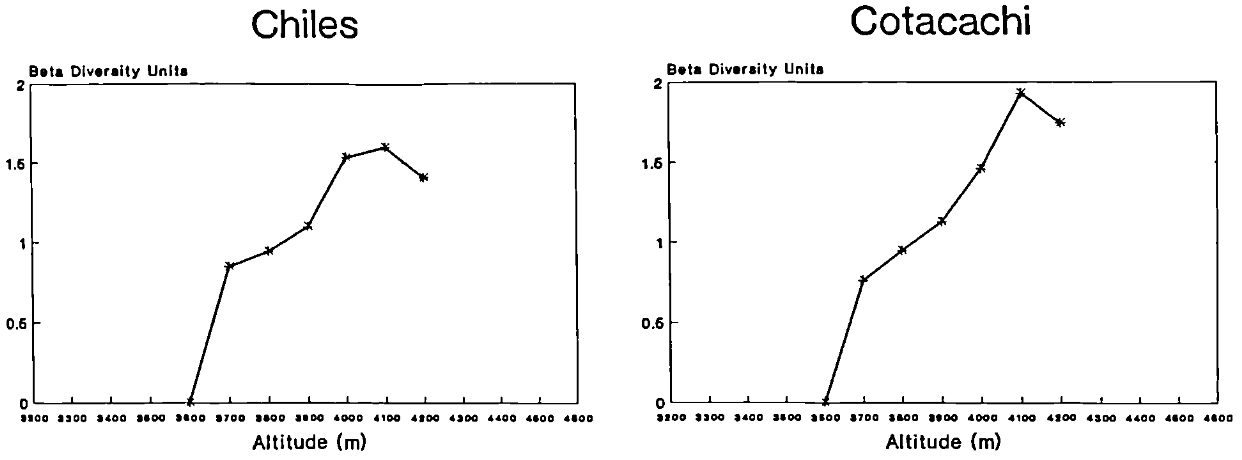
Of the thirty commonest species in the sample quadrats (shown in Table 2.5), almost all (24) are located around the origin of the ordination. Reference has already been made to the exceptions.

The species ordination was used to calculate the centroids of the TWINSPAN classes and to infer their correlation with the environmental variables, vegetation cover and species diversity. The resulting biplot, showing the ordinated vegetation classes and the environmental variables, is displayed in Figure 2.14. The mean values of the environmental variables for each vegetation class are shown in Table 2.7.

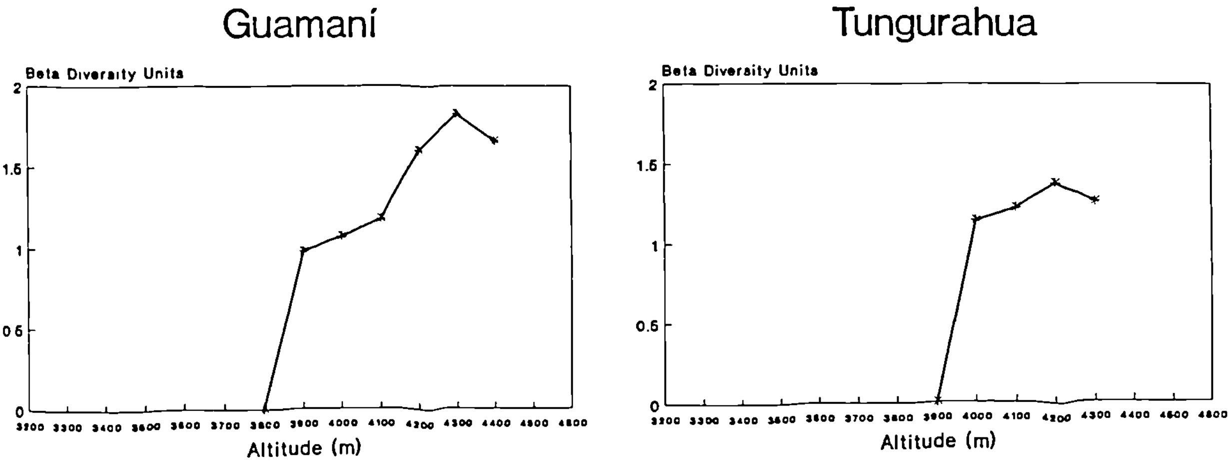
Class	Exposure	Burning	Trampling	Grazing	Disturb'ce	pH	Slope	Bare	Rock
BS (n = 3)	4.00					5.60	28		
HD (n = 12)	4.25		1.00		0.75	5.48	32	10.2	0.8
CCCD (n = 1)	5.00					5.70	19	90.0	0.8
CCT (n = 3)	3.00		2.00	2.00	2.00	4.40	15		
DCS (n = 5)	4.00		1.00			4.94	25	11.0	1.4
FCT (n = 1)	4.00		1.00			5.00	22	1.0	
AC (n = 3)	5.00					-	20	81.7	
AAC (n = 3)	4.00			1.00		-	20		
WAC (n = 3)	5.00					5.50	41	23.3	14.0
WPC (n = 3)	4.00		1.00	1.00	1.00	5.10	5	3.0	
DTSC (n = 3)	3.00			1.00		5.10	37	4.0	
DSC (n = 3)	4.00					5.10	35	2.7	0.3
DTC (n = 3)	2 00					-	15		
PC (n – 3)	3.00		3.00	3.00	2.00	5.30	18	2.0	
HHCT (n = 6)	3.17	2.67	2.50	2.00	2.17	5.35	36	9.2	5.0
HPCT (n = 12)	2.75	4.00	3.75	3.50	4.50	5.15	34	9.9	
NB (n = 10)	3.40	1.80	1.90	1.80	2.40	4.90*	26	4.0	
OCT (n = 20)	2.20	3.10	2.95	2.75	3.45	5.40*	19	2.0	
VCT (n = 10)	2.80	3.40	3 00	3.00	3.80	5.23*	22	0.4	
SCT (n = 21)	3.14	2.52	2.90	2.67	3.14	5.05	29	1.3	
RCT (n = 4)	2.00	2.50	1.75	1.50	2.50	5.50*	29	18.8	
PCT (n = 4)	3.75	2.25	2.25	2.25	2.50	-	25	0.8	0.5
ACT (n = 2)	3.00	3.00	3.00	3.00	4.00	-	5		
PCCT (n = 24)	3.04	2.42	2.00	2.38	2.95	-	22	3.2	0.3
PCE (n = 6)	3.00	4.00	4.00	3.00	4.00	4.50	17	3.0	
VCE (n = 6)	3.50	3.50	3.00	3.50	4.00	4.55	15	1.0	
GCCD (n – 7)	2.71	0.86	0 86		0.86	5.50	14	62.4	
ACCD (n = 3)	3 67	1.00	1.00		1.00	5.50	20	68.3	3.3
CCD (n = 1)	5.00					5.70	19	80.0	
NCCD (n = 4)	4.00	1.75	0.50		1.00	5.33	19	82.5	
SD (n = 3)	2.00	1.00	1.00		1.00	5.60	5	80.0	
Overall	3.19	2.00	2.05	1.84	2.35	5.19	24	11.1	1.8

Table 2.7.
Mean environmental variable values for the 31 páramo plant communities identified by TWINSPAN. pH values marked with * are derived from fewer values than the other variables for that class. A blank represents zero, and '-' indicates that no measurements were made.

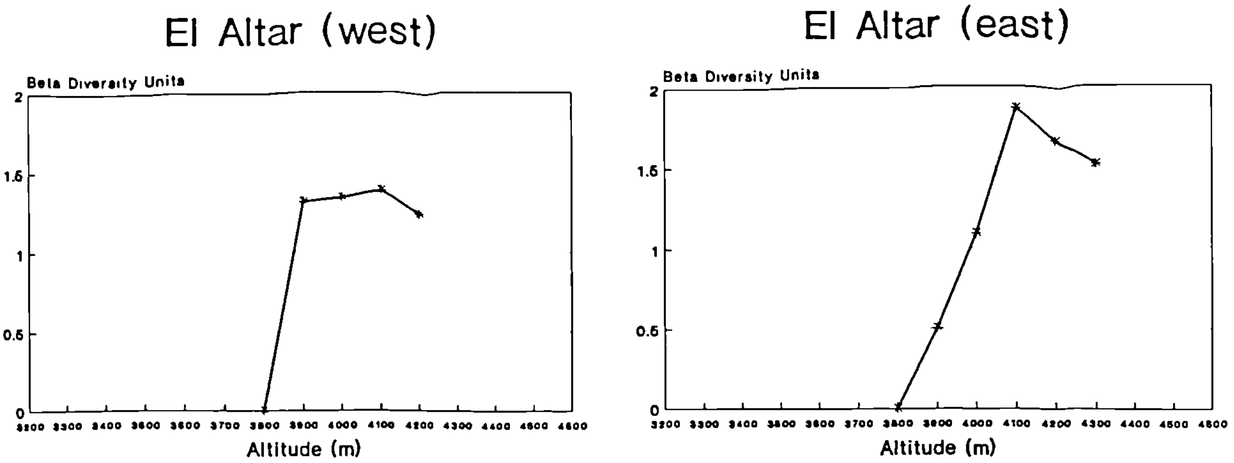
Most of the classes are clustered around the origin and, in a similar pattern to that shown by their constituent species, they extend along a plane from the upper left side of the ordination to the lower right. This pattern corresponds well with the directions of the arrows for disturbance, altitude and exposure. It can be inferred, therefore, that Class PCCT was highly disturbed, of low altitude with a low exposure score. By comparison, Class AC was composed of plots from exposed, high-elevation situations with low disturbance.


Chiles

Cotacachi


Guamaní

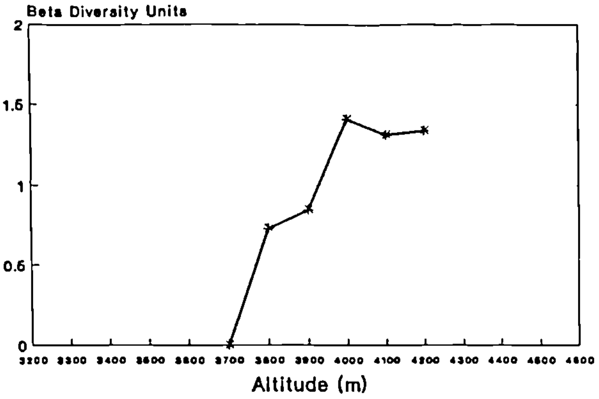
Tungurahua


El Altar (west)

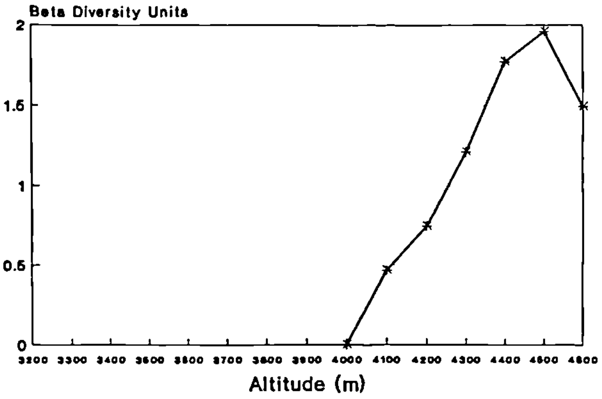
El Altar (east)

Figure 2.15. (Continued overleaf)
β-diversity values along the altitudinal gradient in twelve páramo areas.

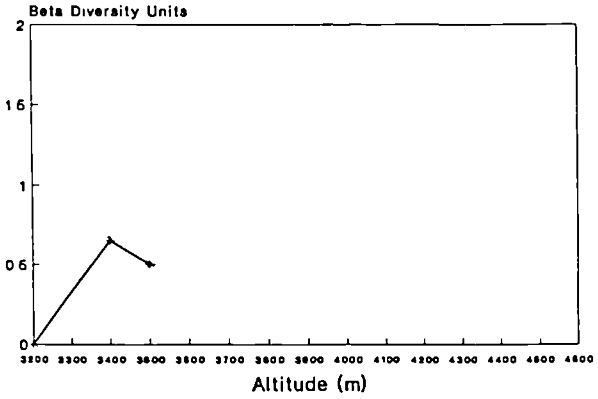
Daldal



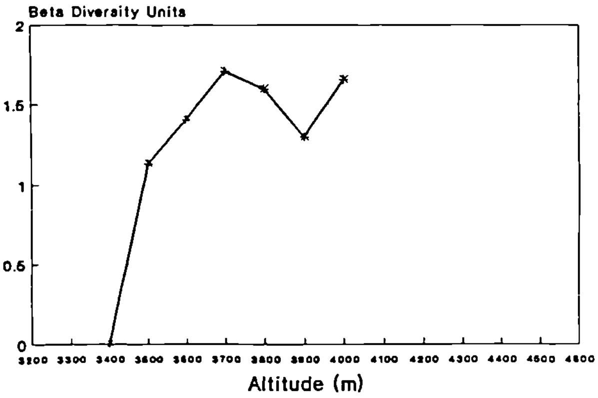
Chimborazo



Zapote Naida



Cajas



Cumbe

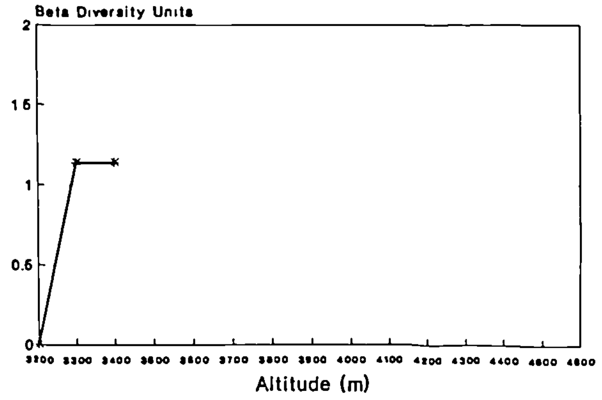


Figure 2.15. (Continued)
β-diversity values along the altitudinal gradient in twelve páramo areas.

Again following the pattern established in the species ordination, a second cluster of TWINSPAN classes is located in the upper right of the ordination space, roughly perpendicular to the plane of the main cluster. These stand groups are characterised by those species from Volcán Chimborazo, described earlier for this portion of the ordination, and are correlated with the amount of bare ground present. These outlying groups were very different from those around the origin. Class SD, which split off from the rest of the stands in the first TWINSPAN division, has been placed furthest from the main cluster of groups. Similarly, Classes GCCD, ACCD, CCD and NCCD are set apart from the others in the classification as well as in the ordination, confirming their distinctive composition.

The β-diversity values for each of the study areas are given in Figure 2.15. Generally, for any one altitudinal gradient, the β-diversity values continue to increase as the elevational difference increases. This indicates that plant community composition changes continuously along the gradient, though the rate of change varies. Almost all of the β-diversity curves show a decrease in value at the end of the altitudinal range. This is an artefact of the β-diversity formula, where the value depends on the species lost plus the species gained. At higher altitudes, the number of species lost becomes almost constant (perhaps even reaching its maximum, with no species in common with the lowest altitude), but the number of species gained decreases as conditions reduce plant cover. Thus a reduction in plant cover may result in a decrease in β-diversity. The maximum value of the β-diversity units obtained is dependent to a large extent on the altitudinal range covered. Maximum values of 1.5-2.0 units are found for all sites covering a 600m range and one with a 500m range. The lowest maximal value (0.65) is produced for Zapote Naida, with samples taken from only three altitudinal levels.

A total of 31 vegetation types or plant communities have been defined in this study. The definition of each of these communities is dependent upon assemblages of species, rather than the presence or absence of key species. This is important, in that a single species may occur in many different communities, and furthermore, may play an important part in defining them (but only in conjunction with other species).

The term ‘species’ is used loosely in this context, since full identification of the voucher specimens has not yet been achieved. Despite this, some attempt has been made to define distinct taxa, even where a name has not been determined. In order to avoid the situation of a ‘species’, so defined, requiring separation into real species at a later date, taxa have been defined cautiously. As a result, it is possible that some taxa may ultimately become merged into one, once full taxonomic studies have been completed.

Of the commonest species in this study, a number have yet to be fully named. From an examination of unpublished species lists and herbarium material, it is possible to speculate upon the identity of some of these. It is likely, for example, that *Calamagrostis* sp. [251] is *Calamagrostis effusa* H.B.K., that *Pernettya* sp. [185] represents *Pernettya prostrata* H.B.K., and *Hypericum* sp. [161] is *Hypericum laricifolium* H.B.K. It is also worth noting that four *Castilleja* sp. (Scrophulariaceae) taxa were defined in this study, some or all of which may represent *Castilleja fissifolia*. If all of these taxa were to be *C. fissifolia*, then this species would become frequent enough to merit a place in Table 2.5 of the commonest species in the vegetation samples, with 46 occurrences in the 192 plots (23.96%).

Descriptions of the plant communities derived from the TWINSPAN analysis are described below. Figure 2.16 shows the distribution of these communities in the twelve study areas. Each description is accompanied by an abbreviation to allow cross-referencing with Figures 2.12, 2.14 and 2.16. The number of sample stands within each community is also indicated.

The Zonal Vegetation of the Ecuadorian Páramos

Blechnum loxense Shrub Páramo (BS, 3 Stands)

This community was found at 3,900 m, just above the treeline on the flanks of Volcán Tungurahua. The community was dominated by the small (up to 1 m tall) tree fern, *Blechnum loxense*, which covered between 50-75% of the surface area. *Thelypteris* sp. [229] ferns were also strong indicators of this community. Other important species in this group were *Disterigma empetrifolium, Geranium reptans, Calceolaria ferruginea, Baccharis genistelloides, Gynoxys baccharioides, Pentacalia arbutifolius, Sisyrinchium jamesonia, Luzula gigantea, Relbunium hypocarpium, Oreomyrrhis andicola, Ranunculus* sp. [304], *Culcitium ovatum* and *Eryngium humile.* A number of other species were present but did not show a preference for this particular community, including *Elaphaglossum* sp. [282], *Agrostis* sp. [243], *Azorella pedunculata, Erigeron* sp. [333] and *Baccharis alpinum* each with a cover value of about 5%, and *Culcitium ovatum* with over 25% cover. There was no *Calamagrostis* sp. [251].

The ground sloped 28° and soil pH was measured at 5.6. Exposure was high with an index score of 4. There were no signs of human influence on the vegetation, direct or indirect, though a track to the summit, in regular use, passed nearby.

Humid Desert Páramo (HD, 12 Stands)

A rapid change in the plant community occurred between 3,900 m and 4,000 m, demonstrated by the steepness of the β-diversity curve between these altitudes on Volcán Tungurahua (Figure 2.15). By 4,000 m both *Blechnum loxense* and *Thelypteris* sp. [229] had disappeared completely. No single species was dominant on Volcán Tungurahua from 4,000 m to 4,300 m; instead a low carpet of vegetation was found, characterised by the presence of *Lachemilla hispidula, Agrostis nigritella, Eriosorus* sp. [288], *Baccharis alpinum, Oritrophium peruvianum, Luzula racemosa, Bartsia* sp. [167], *Asplenium* sp. [230], *Culcitium ovatum* and *Erigeron* sp. [333], each covering between 5 and 25% of the area. Furthermore, the lower part of this community was characterised by species such as *Hypochaeris sessiliflora*, Ericaceae sp. [335], *Azorella pedunculata* and *Agrostis* sp. [243], and to a lesser extent by *Elaphaglossum* sp. [282] and *Lupinus purdianus*. On the other hand, *Culcitium nivalis* (with a cover of more than 25% at 4,300 m), *Ophioglossum crotalophoroides* and *Cerastium floccosum* tended to occur most often in the upper part of the community. There was no *Calamagrostis* sp. [251].

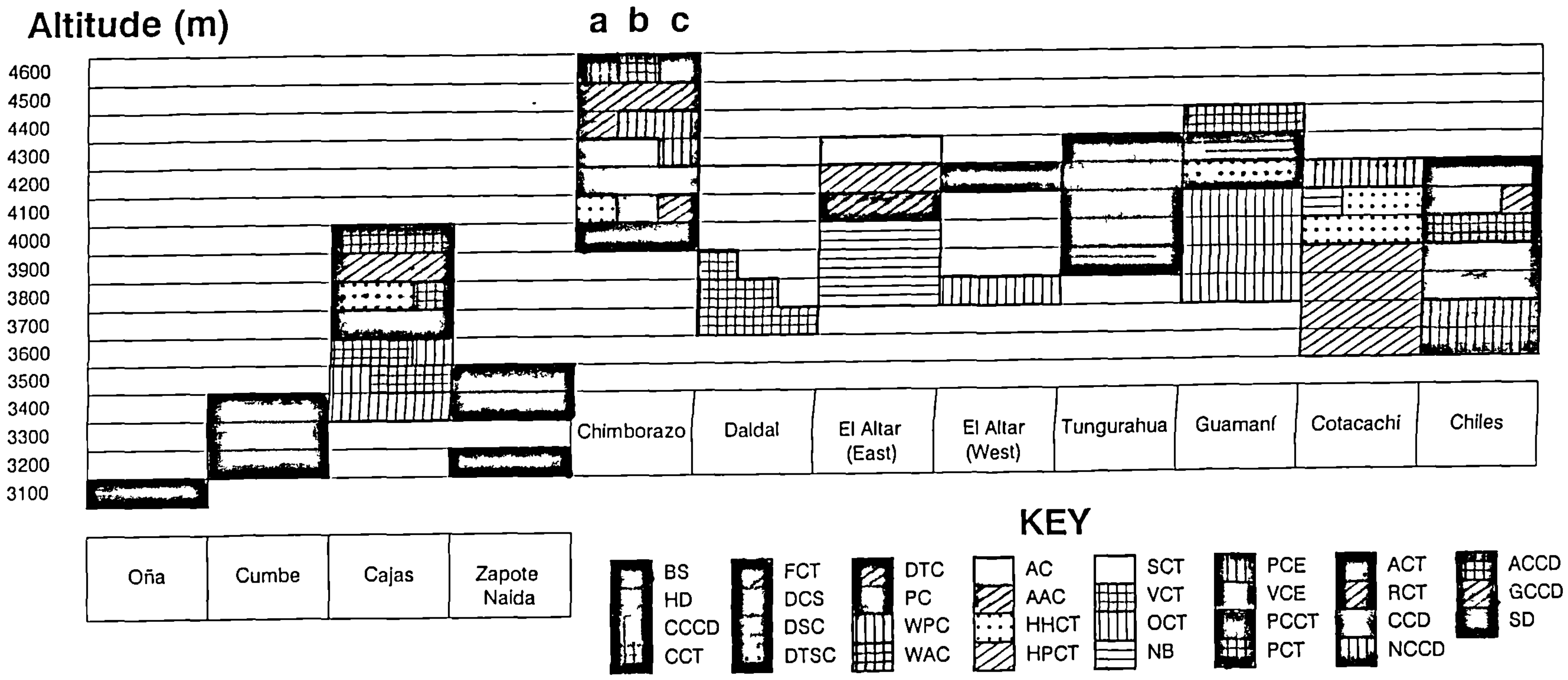


Figure 2.16.
The distribution of the 31 TWINSPAN vegetation classes which are defined and described in detail in the text (cross-referenced by the 2-4 letter code). All 192 vegetation samples are displayed and are colour-coded in the same way as Figures 2.12 and 2.14.

The terrain was fairly constant on the volcanic cone, mostly determined by the angle of repose of the ash and its erosion by water into gullies. The gradient varied from 29° to 38° and exposure was high (4 or 5). Any disturbance was low (1) and consisted of occasional trampling damage by mountaineers *en route* to the summit. The ash substrate was found to have a pH varying from 5.3 to 5.7, with a mean of 5.5.

Calamagrostis sp. [251] and *Chuquiraga jussieui* Desert Páramo with *Cerastium* sp. [200] (CCCD, 1 Stand)

Not far beneath the snow-line on Volcán Chimborazo, a patchy vegetation was found among the scree at 4,600 m, dominated, like so much of the vegetation on this mountain, by shrubs of *Chuquiraga jussieui* and *Calamagrostis* sp. [251] tussocks (both less than 25% cover). Indicators of this group were *Cerastium* sp. [200] and *Relbunium croceum,* plus cushions of *Geranium* sp. [157] and a small grey species [178] with red leaf margins which remains unidentified. *Werneria humilis* cushions, *Hypochaeris sessiliflora, Agrostis nigritella* and *Culcitium ovatum* were also present.

The slope of the ground was 19°. Exposure was very great (5) and there was no evidence of any disturbance. The pH of the soil beneath this stand was found to be 5.7.

Calamagrostis sp. [251] and *Culcitium ovatum* Humid Tussock Grassland (CCT, 3 Stands)

On the Colombian border in the far north of Ecuador, the vegetation at 4,000 m on Volcán Chiles was distinguished by the presence of *Calamagrostis* sp. [251] tussocks (with a cover of 50-75%), with *Culcitium ovatum, Lachemilla orbiculata, Lachemilla pinnata* and *Geranium* sp. [160], all with cover values between 5-25%. Other constant members of this community were *Pentacalia andicola, Werneria pumila, Carex tristicha, Valeriana plantaginea, Jamesonia* sp. [342] and *Geranium sibbaldioides.* Other species of importance in this group were *Perezia pungens, Lachemilla nivalis, Niphogeton dissecta* and *Valeriana bonplandii.*

The slope of the ground was 15°. The vegetation was subject to moderate exposure and disturbance (with index scores of 3 and 2, respectively). Soil pH was measured at 4.4.

Calamagrostis sp. [251] and *Festuca* sp. [255] Tussock Grassland (FCT, 1 Stand)

In places at 4,100 m, amongst the *Diplostephium rupestre* and *Calamagrostis* sp. [251] High Altitude Shrub Community on Volcán Chiles (described below), was a somewhat different vegetation type, lacking the shrubs of *Diplostephium rupestre.* Instead, *Festuca* sp. [255] tussocks were co-dominant with those of *Calamagrostis* sp. [251] (each with a cover of 25-50%). Between the tussocks, the characteristic species were *Lachemilla rupestris, Valeriana plantaginea, Poa* sp. [262] *Valeriana ? niphobia, Oritrophium peruvianum, Pentacalia andicola, Senecio chionageton, Werneria pumila, Bartsia laticrenata, Cerastium* sp. [199], *Valeriana* sp. [312], *Jamesonia* sp. [342], *Agrostis nigritella, Agrostis* sp. [239], *Lachemilla nivalis, Geranium sibbaldioides, Disterigma empetrifolium* and *Carex pichinchensis.*

The slope of this plot was 22°, exposure was high (4) and there were no signs of disturbance. The soil pH was 5.0.

Diplostephium rupestre and *Calamagrostis* sp. [251] High Altitude Shrub Community (DCS, 5 Stands)

Diplostephium rupestre, Werneria humilis and *Gentianella foliosa* characterised the plant community at the highest altitudes sampled on Volcán Chiles (4,200 and 4,100 m). A low cover of *Calamagrostis* sp. [251] tussocks was present, with *Jamesonia* sp. [342], *Agrostis* sp. [239], *Disterigma empetrifolium, Lycopodium* sp. [289], *Gentiana sedifolia, Niphogeton dissecta, Valeriana bonplandiana, Azorella* sp. [195], *Carex pichinchensis, Geranium sibbaldioides, Lachemilla nivalis, Agrostis nigritella, Festuca* sp. [255], small mats of *Aciachne flagellifera* and cushions of *Plantago rigida.*

Slope varied from 22° to 28°. No indications of disturbance were found and the exposure index was judged to be 4 in all cases. The soil pH of these plots was 4.9 or 5.0.

High Altitude *Diplostephium rupestre* Shrub and Cushion Community (DSC, 3 Stands)

At 4,300 m in the Páramo de Guamaní, *Ranunculus* sp. [304] and *Cerastium* sp. [198] were the major diagnostic species, with cushions of *Plantago rigida* (having a cover of greater than 50% in one plot) and *Azorella corymbosa* prominent. *Culcitium ovatum, Lachemilla hispidula, Gentiana sedifolia, Niphogeton dissecta, Eryngium humile, Castilleja* sp. [168], *Halenia* sp. [189], *Ophioglossum crotalophoroides* and *Draba* sp. [234] were also typical of this community, though to a lesser extent. *Diplostephium rupestre* shrubs were a constant and conspicuous feature of the community. *Hypochaeris sonchoides, Oritrophium peruvianum, Oreomyrrhis andicola, Valeriana adscendens, Valeriana bonplandiana, Agrostis nigritella* and *Poa* sp. [261] were present in all three plots, and *Werneria humilis, Disterigma empetrifolium* and *Geranium* sp. [160] were present in two-thirds of the samples.

A slope of 35° was consistent for all three plots. Exposure was high (4). No symptoms of disturbance were encountered in any of the three stands, and the pH was determined as 5.1.

Tussock and Cushion Páramo with *Diplostephium rupestre* (DTSC, 3 Stands)

At 4,200 m in the Páramo de Guamaní, one hundred metres below the community just described and similar to it in many respects, the vegetation differed in one major way: it was dominated by *Calamagrostis* sp. [251] tussocks, covering 50-75% of the sample plots. Co-dominant were shrubs of *Diplostephium rupestre.* The presence of *Oritrophium hieracioides* and *Pernettya* sp. [185] was also characteristic of this community. *Werneria humilis* was notable, forming cushions covering 25-50% of the area. Other distinguishing members of the community were *Carex lemanniana, Geranium sibbaldioides, Luzula racemosa, Satureja nubigena, Bartsia laticrenata, Lycopodium* sp. [189] and *Loricaria* sp. [334]. Many species present were equally common in the community described previously at 4,300 m in the Páramo de Guamaní: *Valeriana* *bonplandiana, Valeriana adscendens, Agrostis nigritella, Poa* sp. [261], *Disterigma empetrifolium, Geranium* sp. [160], *Oreomyrrhis andicola, Oritrophium peruvianum* and *Hypochaeris sonchoides.*

The gradient was generally steep at 32°, 34° and 46° for the individual stands. None of the plots had been recently disturbed and exposure was judged to be moderate (3). The pH was measured at 5.1.

Distichia muscoides, Azorella corymbosa and *Werneria humilis* Cushion Páramo (DTC, 3 Stands)

On the eastern slopes of El Altar at 4,100 m, a diverse community existed with no one species dominating. *Calamagrostis* sp. [251] tussocks varied in cover from 5-15%. A strong cushion and mat component, consisting of *Distichia muscoides, Azorella corymbosa* and *Werneria humilis,* was responsible for much of the vegetation cover. Between these plants, other diagnostic species were growing: *Ranunculus* sp. [303], *Baccharis caespitosa, Valeriana adscendens, Lachemilla orbiculata, Luzula racemosa, Oreomyrrhis andicola, Senecio repens, Oritrophium peruvianum, Isoëtes* sp. [323], *Eleochaeris* sp. [363], *Nertera granadensis* and *Lachemilla nivalis.* Also present were *Pernettya* sp. [185], *Eryngium humile, Azorella aretoides, Bromus lanatus, Geranium sibbaldioides, Gentiana sedifolia, Disterigma empetrifolium, Hypochaeris sessiliflora, Sisyrinchium jamesonia, Plantago rigida, Bartsia laticrenata* and *Hypericum* sp. [273], none of which was indicative of this community.

The slope was the same for all three quadrats in this community (15°). Exposure was fairly low with an index score of 2. No indications of disturbance were observed and no pH reading was possible for these plots.

Plantago rigida Cushion Páramo (PC, 3 Stands)

At 4,200 m on the western slopes of El Altar, near the crater, the vegetation was dominated by cushions of *Plantago rigida,* covering 50-75% of the ground surface, and in one case more than 75%. Associated with this community were tussocks of *Calamagrostis* sp. [251], which covered 25-50% of the area. *Poa* sp. [261], *Agrostis* sp. [238], *Lachemilla hispidula* and *Carex pichinchensis* were indicative of this community, and to a lesser degree *Culcitium ovatum, Loricaria thuyoides, Oritrophium limnophilum, Halenia weddelliana, Ranunculus peruvianus, Lachemilla* sp. [209], *Agrostis nigritella, Festuca* sp. [254], *Poa* sp. [262] and *Uncinia* sp. [329]. *Azorella aretoides, Bartsia laticrenata, Sisyrinchium jamesonia, Bromus lanatus, Disterigma empetrifolium, Werneria humilis* and *Hypochaeris sessiliflora* were constant species in the community, though have no value in defining it. Other important species in the community were *Gentiana sedifolia, Geranium sibbaldioides, Eryngium humile, Pernettya* sp. [185] and *Hypericum* sp. [273].

The slope of these plots was 18°, exposure was 3 and disturbance moderate at 2. The soil pH was 5.3.

Werneria humilis & *Plantago rigida* Cushion Páramo (WPC, 3 Stands)

At the highest sampling altitude (4,200 m) on Volcán Cotacachi, cushions of *Werneria humilis* were co-dominant with *Plantago rigida* cushions and patches of *Lycopodium* sp. [289] (each of these species covering between 25-50% of the area). *Calamagrostis* sp. [251] was present in two-thirds of the samples, though with less than 25% cover. *Agrostis nigritella, Bartsia laticrenata, Geranium sibbaldioides, Aciachne flagellifera, Oritrophium peruvianum, Valeriana aretioides, Luzula racemosa, Disterigma empetrifolium* and *Hypochaeris sonchoides* were also present. This community was differentiated from similar cushion páramos by the presence of *Loricaria* sp. [334], *Calamagrostis* sp. [246], *Halenia* sp. [189], *Azorella aretoides, Lachemilla nivalis* and *Diplostephium rupestre.*

The terrain was reasonably flat (4° to 6°). Exposure was high (4) and disturbance low (1). Soil pH was found to be 5.1.

Werneria humilis & *Azorella corymbosa* Cushion Páramo (WAC, 3 Stands)

At 4,400 m in the Páramo de Guamaní, a similar-looking vegetation to that described above on Cotacachi was found. *Werneria humilis* was co-dominant, this time with *Azorella corymbosa,* their cushions jointly covering more than 50% of the ground surface. *Lachemilla hispidula, Lachemilla holosericea, Cerastium* sp. [198], *Oritrophium hieracioides* and *Oreomyrrhis andicola* were also key components of the vegetation. Other species in the community were *Lycopodium* sp. [289], *Agrostis nigritella, Bartsia laticrenata, Oritrophium peruvianum, Aciachne flagellifera* and *Geranium sibbaldioides.* There were no tussocks of *Calamagrostis* sp. [251] in these samples.

These plots were located on very steep slopes, 35° to 45° from the horizontal, and in a very exposed situation which merited the maximum index score of 5. There were no visible signs of disturbance. Soil pH was 5.5.

Lachemilla holosericea Cushion Páramo (AC, 3 Stands)

On the eastern flanks of El Altar at 4,300 m, a thin covering of vegetation lay on the mineral substrate, with no one species occupying more than about 15% of the sample plots. Indicators of this vegetation were *Luzula racemosa, Lachemilla holosericea* and *Culcitium adscendens.* Also present were *Werneria humilis, Azorella corymbosa, Oreomyrrhis andicola, Huperzia hypogoea, Hypochaeris sessiliflora, Oritrophium hieracioides* and *Bartsia laticrenata.* Once more, *Calamagrostis* sp. [251] was absent from these plots.

On a 20° slope, these three stands were located in a very exposed situation and given an exposure score of 5. No indications of disturbance were observed. Measurement of pH was not possible for these stands.

Aciachne flagellifera & *Valeriana aretioides* Cushion Páramo (AAC, 3 Stands)

100 m below the desert páramo community on the eastern side of El Altar, at 4,200 m, there existed a vegetation dominated by cushion and mat plants. Most indicative of this community were the cushion and mats of *Aciachne flagellifera, Plantago rigida* and *Valeriana aretioides*, with *Geranium sibbaldioides, Baccharis caespitosa* and *Poa cucullata. Oritrophium peruvianum, Azorella aretioides, Lachemilla nivalis, Carex* sp. [319] and *Eudema nubigena* were also characteristic. *Huperzia hypogoea, Oreomyrrhis andicola, Azorella corymbosa, Bartsia laticrenata, Werneria humilis, Oritrophium hieracioides* and *Hypochaeris sessiliflora* were present in these stands, but were not diagnostic of this community.

The slope of the plots was measured at 20° from the horizontal. Exposure was high, at 4, and no evidence was observed to suggest disturbance of the sites by burning, trampling or grazing.

Calamagrostis sp. [251] Tussock Grassland with *Hypochaeris sonchoides, Halenia* sp. [189] and *Satureja nubigena* (HHCT, 6 Stands)

On Volcán Cotacachi at 4,000 m and in two of the three replicate quadrats at 4,100 m, plus one stand from 4,100 m on Volcán Chimborazo, *Calamagrostis* sp. [251] tussocks were almost completely dominant. In most cases the tussocks formed a completely closed canopy about 1-1.2 m above the ground. Associated with the tussocks, beneath the canopy, were *Cerastium danguyi, Satureja nubigena, Halenia* sp. [189], *Agrostis* sp. [242], *Bartsia laticrenata, Castilleja* sp. [168], *Poa* sp. [268], *Elaphaglossum* sp. [281], *Lycopodium* sp. [293] and *Lycopodium* sp. [295]. In addition to these species, a number of others were present, but were not indicative of the community: *Pernettya* sp. [185], Alliaceae sp. [175], *Valeriana microphylla, Valeriana rigida, Eryngium humile, Lupinus sarmentosus, Hypochaeris sonchoides* and *Gnaphalium luteoalbum.*

In general, slopes were steep in these plots, between 35° and 46° (though one stand was found on reasonably flat ground with a slope of only 5°). Exposure was variable, ranging from 2 to 4 with a mean of 3.2. Mean disturbance was 2.2. Measurements of pH were determined at 4.9, 5.5 or 5.6 for these stands, the mean value being 5.4.

Calamagrostis sp. [251] Tussock Grassland with *Hypochaeris sonchoides, Plantago linearis* and *Relbunium croceum* (HPCT, 12 Stands)

Calamagrostis sp. [251] tussocks were again dominant from 3,600 to 3,900 m on Volcán Cotacachi, though they were not so dense as those higher on the mountain. With a cover of 50-75%, the tussocks did not form a completely closed canopy. *Plantago linearis, Bidens andicola, Hieracium frigidum, Relbunium croceum, Equisetum bogotense, Paspalum tuberosum, Poa* sp. [269] and *Gnaphalium coarctatum* were characteristic species between the *Calamagrostis* sp. [251] plants. Though commonly linked with dense *Calamagrostis* sp. [251] tussocks elsewhere, *Pernettya* sp. [185], *Valeriana microphylla, Valeriana rigida, Hypochaeris sonchoides* and *Eryngium humile* were constant members of this community.

These stands grew on slopes which varied from 29° to 37° (mean, 34). Exposure was moderate with a mean index score of 2.75. Disturbance was high (4 or 5) with a mean score of 4.5. pH varied from 4.7 to 5.6; the mean value for the twelve stands was 5.2.

Calamagrostis sp. [251] Tussock Grassland with *Sisyrinchium jamesonia* (SCT, 21 Stands)

The remaining stands in the páramo of Daldal, from 3,800 to 4,200 m, and the western slopes of El Altar from 3,900 to 4,100 m consisted of a community dominated by *Calamagrostis* sp. [251] (50-75% cover). Key floristic components of this community were *Hypericum* sp. [161], *Sisyrinchium jamesoni, Oritrophium peruvianum, Carex pichinchensis, Lupinus sarmentosus, Azorella aretoides, Castilleja* sp. [171], *Aphanactis jamesonia* and *Uncinia* sp. [329]. In addition, *Hieracium frigidum, Hypochaeris sessiliflora, Carex tristicha, Disterigma empetrifolium, Gentiana sedifolia, Halenia weddelliana, Geranium multipartitum, Geranium sibbaldioides, Bromus lanatus, Paspalum tuberosum, Ranunculus peruvianum, Lachemilla rupestre, Valeriana microphylla* and *Pernettya* sp. [185] were present, but did not serve to distinguish this community from other similar ones.

This large group of plots was found on slopes of 17° to 42°, averaging 28.6°. Exposure was intermediate, with a mean score of 3.1. Disturbance was more variable, from 2 to 4, though again centred on 3.1. pH measurements extended from 4.8 to 5.4. The mean pH value for all 21 stands was 5.0.

Calamagrostis sp. [251] Tussock Grassland with *Viola humboldtii* (VCT, 10 Stands)

Four plots from 3,500 and 3,600 m in the páramo of Cajas and six more from 3,700 to 3,900 m in the páramo of Daldal, belonged to a community characterised by the presence of *Viola humboldtii*. The dominant species was the tussock grass *Calamagrostis* sp. [251] (often with a cover greater than 75%) with *Paspalum tuberosum* a constant associate. Other species which were consistent members of the community were *Bidens andicola, Carex crinalis, Geranium reptans, Azorella pedunculata, Sibthorpia reptans, Poa* sp. [262], *Gnaphalium pensylvanicum, Carex tristicha, Disterigma empetrifolium, Halenia weddelliana, Geranium multipartitum, Geranium sibbaldioides, Ranunculus peruvianus, Lachemilla rupestris, Lachemilla orbiculata, Oreomyrrhis andicola, Pernettya* sp. [185] and *Hypochaeris sessiliflora.*

The slopes of these ten plots were very variable, ranging from quite flat terrain with a slope of only 3° to steep, 37° valley sides. Exposure was moderate, with a mean score of 2.8, and disturbance was moderate to high (3, mostly 4). The mean disturbance score was 3.8. pH measurements could only be assigned to six of the ten plots in this community: the mean of these plots was 5.2.

Calamagrostis sp. [251] Tussock Grassland with *Oreomyrrhis andicola* and *Gnaphalium pensylvanicum* (OCT, 20 Stands)

A plant community dominated by *Calamagrostis* sp. [251] with *Oreomyrrhis andicola, Gnaphalium pensylvanicum* and *Lachemilla orbiculata* was found in three páramo areas. In the north-east, this community was found from 3,800 to 4,100 m in the Páramo de Guamaní; in central Ecuador it was found at 3,800 m on the Collanes Plain below the crater of El Altar; and in the south it was found in the páramo of Cajas at 3,400 m and less extensively at 3,500 and 3,600 m.

In these stands, *Calamagrostis* sp. [251] tussocks were responsible for more than half the vegetation coverage, often for more than three-quarters of it. Associated species were *Oreomyrrhis andicola, Gnaphalium pensylvanicum, Lachemilla orbiculata, Bidens andicola, Azorella pedunculata, Aphanactis jamesonia, Agrostis* sp. [242], *Poa* sp. [261], *Poa* sp. [262], *Satureja nubigena* and *Eryngium humile.*

This community was found on almost flat ground as well as on steep slopes up to 33°. Exposure was moderate with a mean score of 2.2. Disturbance was mostly rated at 3 or 4, the mean of the twenty stands was 3.5. Once again, soil samples were not available for one-quarter of the plots. Those that were available had pH values which varied from 5.1 to 5.6, with a mean of 5.4.

Neurolepis elata Bamboo Páramo (NB, 10 Stands)

This group of stands comprised those plots recorded from 3,800 to 4,000 m on the eastern slopes of El Altar plus one plot from 4,100 m on Volcán Cotacachi. In the El Altar stands, the dominant species was the bamboo grass, *Neurolepis elata,* which formed dense tussocks covering up to 75% of the plots. *Neurolepis* was absent from the Cotacachi community, but the remainder of the flora was similar enough for it to be joined with those from the eastern flanks of El Altar. Characteristic species of this community were *Culcitium adscendens, Diplostephium hartwegii, Diplostephium glutinosum, Carex lemanniana, Rhynchospora macrochaeta, Disterigma empetrifolium, Geranium sibbaldioides, Lupinus sarmentosus, Pernettya* sp. [185], *Arcytophyllum aristatum, Gentianella* sp. [316] and *Oritrophium peruvianum. Calamagrostis* sp. [251] tussocks were also present, sometimes co-dominant with the bamboo tussocks.

A number of species were common to this community and the *Calamagrostis* sp. [251] tussock grassland with *Oreomyrrhis andicola* and *Gnaphalium pensylvanicum* described above: *Lachemilla orbiculata, Satureja nubigena, Senecio chionageton, Sisyrinchium jamesoni, Bartsia laticrenata* and *Eryngium humile.*

The stands belonging to this community were located on slopes of 20° to 35°. The mean slope was 26°. Exposure was fair to high (3 or 4) with a mean of 3.4. The vegetation was moderately disturbed (2 or 3). The mean index score for disturbance was 2.4. Finally, pH was only measured for the single Volcán Cotacachi plot, which was 4.9.

Calamagrostis sp. [251] and *Espeletia pycnophylla* Tussock Grassland with *Paspalum tuberosum* (PCE, 6 Stands)

In the north, on the Colombian border between 3,600 and 3,700 m on Volcán Chiles, *Calamagrostis* sp. [251] tussocks covered 50-75% of the ground, but were themselves covered by a 5-50% cover of *Espeletia pycnophylla* stem rosettes. *Paspalum tuberosum* was a key floristic element, as were *Blechnum loxense, Pentacalia stuebellii, Gnaphalium pensylvanicum, Gynoxys fulaginosa, Hypochaeris sessiliflora, Oritrophium hieracioides, Rhynchospora ruiziana, Gentiana sedifolia, Eryngium humile, Hypericum* sp. [161], *Bartsia* sp. [165], *Agrostis* sp. [241], *Hypericum* sp. [275] *and Lycopodium clavatum.* Other important constituents of the vegetation of these stands were *Oritrophium peruvianum, Werneria humilis, Carex tristicha, Oreobolus goeppingeri, Halenia weddelliana, Geranium sibbaldioides, Lachemilla rupestris, Lachemilla nivalis, Agrostis* sp. [240], *Pernettya* sp. [185], *Sibthorpia reptans, Lupinus sarmentosus* and *Nertera granadensis.*

The slope of the plots in this group varied from 7° to 21°, exposure was rated as 3 on the scale from 0 to 5 and disturbance was high at 4. The pH of the plots at 3,700 m was found to be 4.7, whilst at 3,600 m the soil was the most acidic encountered in the study with a pH of 4.3.

Calamagrostis sp. [251] and *Espeletia pycnophylla* Tussock Grassland with *Viola* sp. [192] (VCE, 6 Stands)

At 3,800 and 3,900 m on Volcán Chiles, *Espeletia pycnophylla* was again co-dominant with tussock grass. At 3,800 m the tussock grass species was *Calamagrostis* sp. [251] with 50-100% cover. At 3,900 m, however, the *Calamagrostis* sp. [251] was replaced by tussocks of *Agrostis* sp. [240] with slightly less cover (50-75%). The distinctive floristic elements of this community were *Viola* sp. [192], *Rhynchospora macrochaeta, Sisyrinchium* aff. *alatum, Senecio chionageton, Bartsia laticrenata, Azorella aretoides, Diplostephium* sp. [233], *Agrostis nigritella, Poa* sp. [262], *Jamesonia pulchra,* and *Arcytophyllum* sp. [305]. Other species were present in this community in common with the similar stands lower on Volcán Chiles: *Lupinus sarmentosus, Oritrophium peruvianum, Carex tristicha, Oreobolus goeppingeri, Halenia weddelliana, Geranium sibbaldioides, Lachemilla rupestris and Pernettya* sp. [185].

Once again, slopes were very variable. One of the plots was located on completely level ground whereas the others were found on slopes between 12° and 20°. Exposure was moderately high with a mean of 3.5 and all of the plots were heavily disturbed (4). As with the páramo below this community, the soils were highly acidic with values of 4.4 and 4.7.

Calamagrostis sp. [251] Tussock Grassland with *Paspalum tuberosum* and *Chrysactinium acaule*(PCCT, 24 Stands)

In southern areas, a more open tussock grassland existed, with *Calamagrostis* sp. [251] tussocks less dominant with a cover of 25-75%. *Paspalum tuberosum* (often with a cover of greater than 25%) was indicative of such vegetation, along with *Chrysactinium acaule, Orthrosanthus chimboracensis, Oreobolus goeppingeri, Valeriana* *bonplandiana, Halenia* sp. [188], *Agrostis* sp. [240] and *Lycopodium clavatum.* Other members of the community were *Hypochaeris sessiliflora, Oritrophium peruvianum* forma intermedium, *Geranium sibbaldioides, Eryngium humile, Hypericum* sp. [161] and *Pernettya* sp. [185].

All of the plots in the páramos of Zapote Naida, Cumbe and Oña were assigned to this group by the TWINSPAN analysis, in addition to the three quadrats from 3,700 m in Cajas.

This was the largest grouping of stands from the analysis and the slopes of the 24 plots varied considerably from 4° to 42°. The index of exposure was between 2 and 4 (mean, 3.0) and disturbance was low in some plots but high in others, the mean was 3.0. Unfortunately, the soil samples from the plots in this community were amongst those stolen and no pH values are available.

Calamagrostis sp. [251] and *Poa* sp. [262] Tussock Grassland (PCT, 4 Stands)

This grouping consisted of the three plots from the highest altitude sampled in the páramo of Cajas (4,000 m), plus one plot from 3,800 m in the same area. The vegetation was dominated by *Calamagrostis* sp. [251] tussocks (cover 50-75%). This community was set apart by the presence of *Poa* sp. [262]. Other consistent species in the community which were of indicative value included *Carex pichinchensis, Halenia weddelliana, Baccharis alpinum, Diplostephium hartwegii, Ranunculus peruvianum, Eryngium humile, Valeriana bracteata, Bartsia* sp. [165] and *Jamesonia alstonii.* Other members of the community were *Arcytophyllum filiforme, Pernettya* sp. [185], *Lupinus sarmentosus, Oritrophium peruvianum forma intermedium, Hypochaeris sessiliflora, Werneria humilis* and *Hypericum* sp. [161].

One of the four stands was found on almost level ground, while the remainder occurred on a slope of 31°. Exposure was quite high with a mean of 3.8 and disturbance scored 2 for three of the sites, but 4 for the remaining plot. No pH measurements were made.

Calamagrostis sp. [251] and *Agrostis* sp. [243] Tussock Grassland (ACT, 2 Stands)

The remaining two stands at 3,800 m in the páramo of Cajas were quite similar to the community classified above as *Calamagrostis* sp. [251] and *Poa* sp. [262] tussock grassland. Approximately half the area was covered by *Calamagrostis* sp. [251]. This community differs in that *Poa* sp. [262] was absent, and a variety of other species were present: *Agrostis* sp. [243], *Valeriana bonplandiana, Lachemilla rupestris, Geranium sibbaldioides, Paspalum tuberosum, Carex tristicha, Gentiana sedifolia, Gentianella hirculus* and *Oreobolus goeppingeri.* However, *Arcytophyllum filiforme, Pernettya* sp. [185], *Werneria humilis, Hypericum* sp. [161], *Lupinus sarmentosus* and *Oritrophium peruvianum* forma intermedium were still important elements of the community.

The slope of these two plots was 5°, the exposure score moderate at 3 and disturbance high at 4. No pH values were available.

Calamagrostis sp. [251] and *Rhynchospora macrochaeta* Tussock Grassland (RCT, 4 Stands)

The plant community at 3,900 m in the páramo of Cajas and one plot from 4,100 m on Volcán Chimborazo were linked in the TWINSPAN analysis. Dominated by *Calamagrostis* sp. [251] tussocks (cover 50%), the community contained *Festuca* sp. [256] (cover 25-50%), *Rhynchospora macrochaeta* and *Senecio chionageton, Gynoxys miniphylla, Disterigma empetrifolium, Culcitium* sp. [232], *Pernettya* sp. [185], *Poa* sp. [262], *Jamesonia alstonii* and *Diplostephium hartwegii.*

The slope of three of the four plots was 37° (the remaining plot was on an incline of just 5°). Exposure was low at 2 and disturbance was moderate (3) to low (1) with a mean of 2.5. A single pH reading of 5.5 was available for the Chimborazo plot.

Calamagrostis sp. [251] and *Chuquiraga jussieui* Desert Páramo (CCD, 7 Stands)

A sparse, low-diversity vegetation was found at 4,200 m (and less extensively at 4,100, 4,300 and 4,600 m) on Volcán Chimborazo. Consisting of *Calamagrostis* sp. [251] tussocks and *Chuquiraga jussieui* shrubs, very few other species were found, and in any case were non-selective to this community. Most prominent amongst these species were *Baccharis genistelloides* and *Geranium* sp. [157].

These plots were located on the flanks of Volcán Chimborazo, some of which were on fairly level ground (5°) whilst others were on steep slopes of 19° to 30°. Exposure was highly variable: the plot at 4,600 m was rated as very highly exposed with a score of 5, but as altitude decreased the remaining plots scored 3 or 2. Overall, the mean was 2.7. Disturbance of these sites was assessed as minimal (mean, 0.9). The mean pH for this community was 5.5, with a variation from 5.3 to 5.7.

Calamagrostis sp. [251] and *Chuquiraga jussieui* Desert Páramo with *Nototriche jamesonia* (NCCD, 3 Stands)

The basic *Calamagrostis* sp. [251], *Chuquiraga jussieui, Baccharis genistelloides* and *Geranium* sp. [157] community on Volcán Chimborazo just described was enhanced at 4,300 and 4,400 m by the presence of *Nototriche jamesonia, Valeriana microphylla, Culcitium adscendens, Hypochaeris sessiliflora, Gentianella cernua,* Cruciferae sp. [206], *Agrostis* sp. [242] and *Plantago* sp. [302].

The mean slope of these plots was 20°. Exposure was high, averaging 3.7 and disturbance was low with a score of 1. pH was 5.4 or 5.7 (mean, 5.5).

Calamagrostis sp. [251] and *Chuquiraga jussieui* Desert Páramo, with *Agrostis nigritella* (ACCD, 1 Stand)

In one plot at 4,600 m on Volcán Chimborazo, a community was found consisting of a 25-50% cover of *Calamagrostis* sp. [251] tussocks with *Chuquiraga jussieui* shrubs, cushions of *Geranium* sp. [157] and the herbs *Baccharis alpinum, Valeriana hartwegii* and *Hypochaeris sessiliflora.* It differed from similar vegetation 100-200 m below in the presence of *Agrostis nigritella, Culcitium ovatum, Cerastium* sp. [200] and *Eryngium humile.*

This single plot community was found on a slope of 19°, in a very highly exposed location (5) with no signs of disturbance. The soil pH was measured at 5.7.

Calamagrostis sp. [251], *Chuquiraga jussieui* and *Geranium* sp. [157] Desert Páramo (GCCD, 4 Stands)

At 4,500 m, and one plot at 4,400 m, on Volcán Chimborazo the vegetation was variable in composition. *Calamagrostis* sp. [251] tussocks covered less than 50% of the area (and in two of the plots, less than 25%), with *Chuquiraga jussieui* shrubs, cushions of *Geranium* sp. [157], *Baccharis genistelloides, Baccharis alpinum, Valeriana hartwegii* and *Hypochaeris sessiliflora* between them. *Relbunium croceum, Castilleja* sp. [168], *Gentianella cernua, Lupinus smithianus, Erigeron pinnatus, Nototriche jamesonii, Agrostis* sp. [242] and *Lucilia radians* were additional constituents of this group.

The mean slope of these four plots was 19°. Exposure was high (4) and disturbance low (1). The mean pH was 5.3, with little variability.

Stipa sp. [253] and *Senecio teretifolius* Desert Páramo (SD, 3 Stands)

Tussocks of *Stipa* sp. [253] covering 25-50% of the ground, interspersed by small shrubs of *Senecio teretifolius* and acaulescent rosettes of *Plantago* sp. [301], characterised the vegetation at 4,000 m on Volcán Chimborazo. *Lucilia radians* was the only other species found in these plots, but was not as common as it was higher up the mountain.

At this location, the terrain was relatively flat, inclined at 5° in an area of reasonable shelter (exposure index score of 2). Few indications of disturbance were noted and these plots received a score of 1 on the disturbance scale. The pH at this altitude was found to be 5.6.

Discussion

In total, twelve sites were used to gather the data for this study. These mountain areas were well distributed throughout the country, and covered all of the major phytogeographical regions of Ecuador. However, owing to the isolated nature of many páramo areas, some regions were somewhat under-represented (in particular, the far south of Ecuador near the border with Perú, and the outer slopes of the eastern Andes).

The vegetation of the Ecuadorian páramos was described by means of stratified random sampling. This is a somewhat different approach to that used by Cleef (1981) to describe the páramo vegetation of the Colombian Cordillera Oriental. He recorded data from stands which were subjectively chosen as representative of a particular community: vegetation sampling according to the classical method of the Zurich-Montpellier school. The random approach employed in this study provided a more objective method for classifying different plant communities. Although it is less effective at sampling the entire range of vegetation types, a randomised selection of vegetation samples permits a statistical treatment of the data. However, a totally random procedure would have been impractical over such a large area which included variable terrain. Therefore, a stratified approach was adopted as a compromise. At regular 100 m intervals of altitude, a 100 m transect was established perpendicular to the slope and the location of the samples determined from random coordinates generated previously. This worked well in most cases, though at higher altitudes rocky outcrops and cliffs often demanded that the transect be shortened.

Sampling was conducted by means of square quadrats covering an area of 25 m2. This corresponds well with the minimal areas of 25-35 m2 advocated by Vareschi (1970) for Venezuelan páramo vegetation and Cleef (1981) for the páramo of the Colombian Cordillera Oriental. Fariñas & Monasterio (1980) sampled Venezuelan páramo vegetation with 5 m by 2 m rectangular quadrats which they believed gave "sufficient floristic information". However, in Ecuador at least, the tussocky nature of much of the vegetation required a larger sampling area to eliminate variability of composition resulting from the distribution of tussocks.

The Ecuadorian páramo flora is very similar to that recorded by Cleef (1981), but with fewer families and genera. This may be accountable to Cleef's wider interpretation of 'zonal páramo' and his additional sampling of azonal bogs and thickets. Despite this, the proportions of families and genera in the Ecuadorian páramos reflect those found in Colombia. The Compositae is the most important family by far, with over one-fifth of the recorded genera. The Gramineae family is also highly significant, responsible for 13% of the genera and with a strong influence on the remainder by virtue of the dominance of some of its members throughout the country. At the family level, and also to a lesser degree at genus level, the páramo flora described in this study is similar to that of other mountainous regions: the puna of Perú (Cabrera, 1958), and the mountains of East Africa (Hedberg, 1964) and New Guinea (J.M.B. Smith, 1977).

It is interesting to note the origins of the Ecuadorian páramo flora and compare them with the data presented for neighbouring páramo regions. Van der Hammen & Cleef (1986) provided a check-list of genera of vascular plants for the Colombian Cordillera Oriental, and assigned each genus to seven geographical floral elements. Sturm & Rangel (1985) present a similar phytogeographical spectrum for the 130 most important species in the Colombian páramo flora as a whole. Using the same approach for the genera presented in Table 2.4, a similar spectrum of origin has been obtained for Ecuador. These data are summarised in Table 2.8.

Geographical Element	Percentage of all Genera		
	Ecuador	Cordillera Oriental, Colombia	130 species, Colombia
Páramo Element	9	7	8
Other Neotropical Element	21	34	30
Austral-Antarctic Element	10	9	5
Holarctic Element	14	11	12
Wide Temperate Element	26	20	7
Wide Tropical Element	3	10	28
Cosmopolitan Element	17	8	10
Unknown Affinity Element	-	1	-

Table 2.8.
Phytogeographical spectra of vascular plant genera for the zonal páramos of Ecuador (this study), the Colombian Cordillera Oriental (Van der Hammen & Cleef, 1986) and the 130 most important species for Colombian páramos as a whole (Sturm & Rangel, 1985). The latter values are estimated from a graphical source.

The data of both Sturm & Rangel (1985) and Van der Hammen & Cleef (1986) demonstrate that for Colombia, approximately half of the genera present in the páramos are of (Neo)tropical origin, the other half of temperate origin, with 7 or 8% endemic to the páramos . In Ecuador, the situation is different. Taxa of temperate origin dominate the Ecuadorian páramos: two-thirds of the genera occurring in the 192 sample stands were of this group. Only one-third were of (Neo)tropical origin. This is perhaps the consequence of the lower humidity of Ecuadorian páramos and the more extreme temperatures that are likely to result from this, especially cold temperatures. Both humidity and temperature regimes in the mountainous regions of Ecuador are likely to present more of a challenge to developing Neotropical elements of the flora and their range may be expected to be narrower than in Colombia and Venezuela.

Both Colombian and Ecuadorian páramo floras have been subjected to similar periods of isolation during glaciations and expansion during warmer periods, and it is not surprising that endemic genera make up a similar proportion of the flora (9%) in both regions.

Balslev (1988) looked at the distributions of some Ecuadorian páramo species by consulting available taxonomic monographs. He found that only 16% of the species studied were known to occur beyond Peru and Colombia. Of the remainder, almost half were endemic to Ecuador (40% of the total). However, this study was based on a limited sample of species and treated all species equally regardless of their rarity. Balslev also found that the majority of páramo species were trans-Andean and not confined to one Cordillera.

Despite some general similarities, the Ecuadorian páramos are substantially different from those of Colombia and Venezuela on a number of counts. First of all, in Ecuador *Espeletia* species are absent from all but a few páramo regions. These are restricted to the north of the country at the Colombian border, and to one valley in Central Ecuador (Cuatrecasas, 1986). This genus is a significant member of the páramo flora in Colombia and Venezuela. Fosberg (1944) thought *Espeletia* so important that he defined páramo vegetation in terms of its presence.

Secondly, bamboo páramos of *Chusquea* (formerly known as *Swallenchloa*) are generally absent in Ecuador. On the eastern slopes of the Ecuadorian Andes, bamboo grasslands do occur, but are dominated by *Neurolepis elata* tussocks. This genus does not dominate the páramo in the same way in Colombia (*Neurolepis aristata* belongs to the timberline vegetation and locally extends into the sub-páramo – Cleef, 1981). Black (1982) refers to localised areas, which he termed 'carrizales', dominated by 'espadaña' (=*Neurolepis*) and *Swalenoclea* (= ?*Chusquea*) on Volcán Antisana in the eastern Andes of Ecuador, but no further details are given. Elsewhere in Ecuador, thickets of *Chusquea* may be seen (for example, in the páramo of Cajas), but these are confined to small patches, presumably by topographic and microclimatic factors.

A further distinction between Ecuadorian páramos and those to the north is that cushion plants are more abundant in the zonal vegetation of Ecuador. Cleef (1981) noted the lack of cushion plants in the Colombian superpáramo, but it should be remembered that there is little high altitude vegetation in the Cordillera Oriental which he studied. Sturm & Rangel (1985) listed more cushion and mat plants for the Cordillera Central of southern Colombia, which is directly linked to the páramos of northern Ecuador.

Overall, there appears to be a distinct trend across the páramos of the northern Andes, noted by Monasterio (1980c). In the far south, the jalca and Ecuadorian páramos are dominated by tussock grasses with genera from temperate regions, whereas in the Venezuelan páramos the giant stem rosettes (like *Espeletia*) are dominant. Between these extremes, the páramos of Colombia are intermediate, with grasses and rosettes sharing dominance.

It is difficult to compare species diversity in the different páramo regions of the northern Andes because descriptions are based on vegetation samples of varying sizes. Species-area effects render direct comparisons impossible. However, in terms of species evenness (one measure of diversity), the Ecuadorian páramos may be less diverse than those of Colombia and Perú, since much of the vegetation is dominated by *Calamagrostis* tussocks. Elsewhere, co-dominance in páramo vegetation is usual, with a more open physiognomy. Until more quantitative information is available for all areas, it is not possible to confirm such speculation on differences or similarities in terms of species richness.

This study did not include azonal páramo vegetation, such as bogs, thickets or woodlands. Areas of this kind are common in the páramos of Ecuador, and tend to be restricted by topographic and possibly edaphic factors. Disturbance, especially burning also plays a role in their distribution.

Permanently wet areas were typically dominated by cushion and mat plants such as *Distichia muscoides* (Juncaceae), *Plantago rigida* (Plantaginaceae) and *Oreobolus obtusangulus* (Cyperaceae) and similar communities have been described for other páramo regions (Cleef, 1978, 1981; Black, 1982). These plants provided a substrate for the establishment of other species which grew amongst their close-fitting leaves. Such cushion bogs are an antarctic-montane-tropical type of vegetation and are not found in the Boreal Zone of the northern hemisphere (Troll, 1968).

In places, thickets of various types were encountered in the páramo (often known as 'chaparrales'). Such thickets were frequently dominated by a single species, most often *Chuquiraga jussieui* (Compositae), *Loricaria* spp. (Compositae), *Baccharis* spp. (Compositae), *Chusquea* spp. (Gramineae) or *Brachyotum* spp. (Melastomataceae).

Woodlands were found mostly in the more extensive páramos of Ecuador, and were typically not present on volcanic peaks. Furthermore, they tended to be confined to scree slopes, often beneath sheltering cliffs. They were almost always composed of trees belonging to the genus *Polylepis* (Rosaceae) in conjunction with *Gynoxys* (Compositae). The extent to which these woodlands have been modified by human influence is still a matter of debate, which will be discussed the final chapter.

The zonal páramo vegetation was found to show pronounced patterns, which appeared to be related as much to regional factors as they were to altitude. Indeed, Furrer & Graf (1978) noted that the lower limit of the páramo was often 300-500 m higher (and the snow-line some 300 m lower) in eastern páramos than those in the west. This was explained by the higher precipitation levels on eastern slopes.

In all, seven main types of páramo vegetation were recorded in this study.

Shrubby Sub-páramo

In Ecuador, shrubby páramo vegetation occurs in two distinct zones. The first zone lies just above the cloud forest where woody vegetation grades into grassland. This is the sub-páramo referred to by Cuatrecasas (1954, 1958, 1968) and Cleef (1981).

In the Ecuadorian study areas, the sub-páramo appeared little developed. This contrasts sharply with Lauer's (1979) view that drier páramos are likely to possess a greater extent of sub-páramo without the ameliorating effects of greater cloud cover. However, population pressure in Ecuador is greater than that found elsewhere in the northern Andes, and could be responsible for the absence of sub-páramo. Certainly, the cloud forest is only locally present in many parts of the Ecuadorian Andes. The loss of sub-páramo vegetation would probably have accompanied the destruction of these forests. In most areas, the lower limit of the grassy páramo coincides with more intensive agriculture, whether as improved pastures or land under cultivation, and the shrubby sub-páramo no longer exists.

Sub-páramo vegetation was only represented in one of the study areas. The three replicate stands of *Blechnum loxense* sub-páramo (BS) at 3,900 m on Volcán Tungurahua were clearly intermediate between the forest vegetation below and the short páramo vegetation above. However, the volcanic mineral substrate in this area has resulted in a sub-páramo which is not typical of most of Ecuador. There are, of course, other volcanoes in the country which provide a very similar substrate. Lojtnant & Molau (1982) described a community dominated by *Blechnum loxense* on the humid summit of Volcán Sumaco in Ecuador. However, the flora of this mountain was considered to be unusual as a result of its isolated nature. Nevertheless, it does share some species with the plots on Volcán Tungurahua.

None of the other study areas had a zone of sub-páramo, and as a result there are no quantitative descriptions of this kind of vegetation for other parts of the country. In general, sub-páramo vegetation elsewhere in Ecuador was found to be characterised by the presence of *Calamagrostis* tussocks and associated flora, intermingled with shrubs of *Baccharis, Senecio, Gynoxys, Brachyotum, Escallonia, Hesperomeles, Miconia, Buddleia, Monnina* and *Hypericum*. Acosta-Solís (1966) also regarded these genera as important members of the sub-páramo flora of Ecuador.

High-altitude Dwarfshrub Páramo

A second belt of shrubby vegetation occurs at much higher altitudes, usually above 4,000 m. Cleef (1981) noted this formation in his study of the Cordillera Oriental of Colombia and explained its existence in terms of a condensation belt at this altitude which permits the growth of woody vegetation. This zone of high altitude dwarfshrubs was present in most of the Ecuadorian study sites. However, it often inhabited a very narrow altitudinal range, and many of these communities were missed during the stratified sampling procedure, where they occurred between the 100 m sampling levels. However, a number of representative stands were recorded in this study.

Diplostephium rupestre and *Loricaria* spp. are consistent members of this vegetation type. The tussock and cushion páramo with *Diplostephium rupestre* recorded at 4,200 m in the Páramo de Guamaní appears to be the Ecuadorian equivalent of the high-altitude páramo dwarfshrub vegetation described by Cleef (1981) for Colombia. However, tussocks of *Calamagrostis*, which were largely absent from Cleef's community, are dominant here.

One hundred metres higher in the Páramo de Guamaní, the tussocks of *Calamagrostis* are absent, and in physiognomic terms the vegetation matches Cleef's description more closely.

A third high altitude dwarfshrub community was recorded on Volcán Chiles at 4,100 m and 4,200 m. The description corresponds roughly with the community described by Sturm & Rangel (1985) for the adjoining Colombian region of Cumbal-Chiles. However, *Loricaria* cf. *colombiana* is absent from the Ecuadorian plots and cushions of *Distichia* seem to be replaced by mats of *Aciachne*.

Tussock Páramo

The most extensive type of páramo vegetation was tussock grassland, almost exclusively dominated by *Calamagrostis* sp. [251]. In the majority of stands belonging to this type, the tussocks covered over half of the surface area. Essentially, such vegetation consisted of a patchwork of raised tussocks and the spaces between them. Most plants occupied the intertussock regions, though some species were more frequent within the tussocks themselves.

There were altitudinal differences within the tussock páramos, and some regional differences. The lower reaches of tussock grassland were represented in this study by a number of communities. *Calamagrostis* sp. [251] Tussock Grassland with *Oreomyrrhis andicola* and *Gnaphalium pensylvanicum* was described for 20 stands in the páramos of Guamaní, El Altar (west) and Cajas. This community occurred between 3,400 to 4,100 m in areas with relatively humid conditions: on the eastern Cordillera or just above the cloud forest treeline, where rainfall is high.

In central and southern páramos, where conditions were less humid, the *Calamagrostis* sp. [251] tussocks were accompanied by a slightly different association of species. Stands belonging to the *Calamagrostis* sp. [251] Tussock Grassland with *Viola humboldtii* community were representative of such vegetation, and were located in the páramos of Cajas and Daldal between 3,500 and 3,900 m.

On Volcán Cotacachi in the north, from 3,600 to 3,900 m, the lower tussock grass páramo was represented by *Calamagrostis* sp. [251] Tussock Grassland with *Hypochaeris sonchoides, Plantago linearis* and *Relbunium croceum.* Located on the western Cordillera, this community received relatively little rainfall. Bare ground covered approximately 10% of the surface area on average, and reached as high as 20% in some stands. It was similar to the páramo vegetation surrounding Laguna Mojanda described by Øllgaard & Balslev (1979, Location 35).

In the far south of the country, in the páramos of Oña, Cumbe, Zapote Naida and Cajas, a widespread community of lower tussock grassland was observed. This community of *Calamagrostis* sp. [251] Tussock Grassland with *Paspalum tuberosum* and *Chrysactinium acaule* was the least humid of all the lower tussock páramo representatives. The vegetation was shorter in stature than that of more humid areas and tussock cover was more variable, though usually between 25% and 75% of the total area.

The TWINSPAN classification separated those tussock grass communities just described from those higher up the altitudinal gradient. One community occupied an intermediate position between upper and lower tussock páramos on El Altar (west) and in Daldal: the *Calamagrostis* sp. [251] Tussock Grassland with *Sisyrinchium jamesonia* community was described between 3,800 and 4,200 m.

The upper tussock grass communities were less extensive and this was reflected in the smaller number of stands of this type which were recorded. In the north, on Volcán Cotacachi at an altitude of 4,000 m, this type of vegetation was represented by the *Calamagrostis* sp. [251] and *Culcitium ovatum* Humid Tussock Grassland community, and at 4,100 m by the broadly similar *Calamagrostis* sp. [251] and *Festuca* sp. [255] Tussock Grassland. The latter community differed mainly by virtue of the co-dominance of *Festuca* sp. [255] tussocks.

At 4,000 and 4,100 m on Volcán Cotacachi, above the lower tussock páramo described earlier, there exists a more humid grassland: *Calamagrostis* sp. [251] Tussock Grassland with *Hypochaeris sonchoides, Halenia* sp, [189] and *Satureja nubigena.* As with the lower community, bare ground averages about 10% of the surface area. This vegetation was very similar in composition to that described by Øllgaard & Balslev (1979) for the Páramo de Guamaní at 4,000-4,100 m (Location 77).

Finally, three communities in Cajas represent variants of southern upper tussock páramos. These were the *Calamagrostis* sp. [251] and *Poa* sp. [262] Tussock Grassland (3,800-4,000 m), the *Calamagrostis* sp. [251] and *Agrostis* sp. [243] Tussock Grassland (3,800 m), and the *Calamagrostis* sp. [251] and *Rhynchospora macrochaeta* Tussock Grassland (3,900 m in Cajas, plus one stand from 4,100 m on Volcán Chimborazo). All three communities were broadly similar in composition, but varied sufficiently to be separated by TWINSPAN.

Bamboo Páramo

On the eastern slopes of the eastern range of the Ecuadorian Andes, with very humid conditions and over 5 m of rainfall per year, places which would be dominated by *Calamagrostis* sp. [251] tussocks elsewhere in the country are instead covered by tussocks of bamboo grass. This type of vegetation was only encountered in one study site, between 3,800 and 4,000 m on the eastern slopes of El Altar. Thus, only one community of bamboo páramo has been described (*Neurolepis elata* Bamboo Páramo). However, similar vegetation was observed in many other sites on the outer slopes of the eastern Cordillera (Bromley, 1971; Black, 1982). It would appear, therefore, that this community occupies an equivalent niche to the bamboo-bunchgrass páramo (the community of *Chusquea* and *Oreobolus obtusangulus* ssp. *rubrovaginitus*) described by Cleef (1981) for the Colombian Cordillera Oriental.

It has been suggested that the presence of *Neurolepis elata* indicates a lack of disturbance (Bromley, 1971). While this may be true in some cases, an undisturbed habitat does not appear to be a prerequisite for the presence of *Neurolepis*, evidenced by the relatively high burning scores for the samples of this type in the páramo of eastern El Altar. However, human habitation and disturbance is much lower in these páramos, most likely the consequence of high rainfall and unpleasant living conditions. This same rainfall and humidity is undoubtedly a major factor in determining the success of *Neurolepis*. In the same way, bamboo species in Colombian páramos are confined to similar areas, and their presence has also been linked with high annual precipitation (Gradstein, Cleef & Fulford, 1977; Cleef, 1978) and with the higher night temperatures associated with permanent atmospheric humidity (Cleef, 1981).

Espeletia Páramo

In the northern part of the country, and also in one isolated region in central Ecuador, the *Calamagrostis* sp. [251] tussock vegetation is replaced by páramo communities similar to those of Colombia. They are dominated by *Espeletia pycnophylla* rosette plants in conjunction with *Calamagrostis* sp. [251] tussocks. In this study, vegetation samples from Volcán Chiles provided quantitative descriptions of such communities. This area is connected directly to the expansive páramo of El Angel, which is perhaps the most famous area of *Espeletia* Páramo in Ecuador.

The lower *Espeletia* Páramo community on Volcán Chiles occurred at 3,600 and 3,700 m (*Calamagrostis* sp. [251] and *Espeletia pycnophylla* Tussock Grassland with *Paspalum tuberosum*). It corresponds well with the community of *Calamagrostis effusa* and *Espeletia* cf. *pycnophylla* described by Sturm & Rangel (1985) for the Cumbal-Chiles region. *Calamagrostis* and *Espeletia* are codominant, with *Blechnum loxense* and *Paspalum bonplandianum* key elements of the flora. Sturm & Rangel (1985) report that this community was present on "very humid sites" and associated with the greater soil moisture and the protection offered by hollows. Franco, Rangel & Lozano (1986) described a similar community (Castratello-Calamagrostietum effusae) in the Colombian Cordillera Oriental and linked its distribution to soil moisture conditions. It is also similar in many respects to the *Calamagrostis effusa* and *Espeletia hartwegiana* ssp. *centroandina* community described for two neighbouring Colombian páramos by Rangel & Franco (1985) and Rangel & Lozano (1986).

Miller & Silander (1991) report a community from 3,415 m in the nearby Páramo del Angel dominated by tussocks and giant rosettes. *Espeletia hartwegiana* (= *E. pycnophylla*) covered approximately 15% of the area, whereas *Puya hamata* was responsible for roughly 30% cover. Tussocks of *Calamagrostis intermedium* (c. 30%) and *Carex pichinchensis* (c. 15%) were codominants. This community appears similar in many ways to that just described for Volcán Chiles and may represent a lower altitude equivalent of the *Espeletia* and *Calamagrostis* tussock grassland. It is notable, however, that *Paspalum* is absent.

At 3,800 and 3,900 m on Volcán Chiles, a community of *Calamagrostis* sp. [251] and *Espeletia pycnophylla* Tussock Grassland with *Viola* sp. [192] was described. Tussocks of *Agrostis* sp. [240] displaced those of *Calamagrostis* sp. [251] at the highest altitude. This vegetation may correspond in some way with Sturm & Rangel's (1985) *Loricaria* cf. *colombiana* and *Agrostis foliata* community. They describe a shift at higher altitudes: a decrease in *Calamagrostis* and *Espeletia* in favour of *Loricaria* and *Agrostis*. Although, *Loricaria* was not present in the Ecuadorian plots, there was certainly a change from *Calamagrostis* to *Agrostis* with increasing altitude.

Cushion Páramo

At the highest elevations, tussock vegetation gives way to cushion páramo. Often, the transition is very rapid, occurring over very short distances. The physiognomic effect of replacing tussocks with cushions results in a much more open vegetation, with increased species diversity. The cushion páramo communities, by virtue of their residence on the tops of mountains, have a rather localised and isolated distribution.

The stratified sampling technique employed in this study was prone to overlooking some examples of this vegetation. However, six representative communities were described.

In most regions, *Calamagrostis* sp. [251] tussocks begin to decrease in cover between 3,950 and 4,000 m, and their dominant position in the vegetation is assumed by *Plantago rigida* cushions. At 4,200 m on the western slopes of El Altar, three stands were described which were typical of the vegetation which develops above the tussock páramos. In this *Plantago rigida* Cushion Páramo, the dominant species' cushions covered 50-75% of the surface area. Some *Calamagrostis* sp. [251] tussocks persisted, with a cover of 25-50%. This type of vegetation was reported from Volcán Pichincha, Ecuador, by Benoist (1935).

At the same altitude on the more humid eastern slopes of the same mountain, *Plantago rigida* cushions were co-dominant with mats of *Aciachne flagellifera* and *Valeriana aretioides*. One hundred metres lower on this slope and *Plantago rigida* was completely absent. In its place, were cushions and mats of *Azorella corymbosa, Distichia muscoides* and *Werneria humilis.*

At 4,300 m, vegetation cover was thinner. Although cushion plants were present (*Werneria humilis, Azorella corymbosa*) they were not dominant. In fact, no species was able to assume a dominant position in the community.

On Volcán Cotacachi at 4,200 m, cushions of *Werneria humilis* and *Plantago rigida* were co-dominant with *Lycopodium* sp. [289]. A number of other cushion forming species were also present (*Aciachne flagellifera, Valeriana aretioides*) along with some dwarf shrubs (*Diplostephium rupestre* and *Loricaria* sp. [334]).

At 4,400 m in the Páramo de Guamaní a similar cushion páramo was sampled. *Werneria humilis* was again a significant element in the community, though this time co-dominant with *Azorella corymbosa.*

Although Harling (1979) noted the widespread existence of cushion páramos in Ecuador, there are few descriptions of them in the literature. In Colombia and Venezuela, cushion communities occur almost exclusively in wet azonal bogs and mires, and therefore Cleef (1981) did not find the type of zonal communities described here. Øllgaard & Balslev (1979) describe several cushion communities in general terms. Communities close to the *Werneria humilis & Plantago rigida* Cushion Páramo described here were found at Locations 15, 72, 78 and 79.

Rainshadow Desert Páramo

Two forms of desert páramo were present in the study sites: high altitude desert páramo (the result of consistently low temperatures) and rainshadow desert páramo (occupying a wide altitudinal range in certain areas). General classifications of Ecuadorian páramo vegetation have sometimes confused these two kinds of desert (for example, Harling, 1979), though the differences are pronounced and are reflected in the floristic composition of the vegetation.

A regional desert páramo was sampled on Volcán Chimborazo. The 'Grande Arenal' or Great Beach of Chimborazo was described by Acosta-Solís (1985) as an example of puna vegetation in Ecuador, very different from the páramo vegetation elsewhere in the country, but comparable to the puna of Peru, Bolivia and Argentina. This was confirmed by the analyses in this study: the stands from Chimborazo were consistently separated from the remainder.

Below 4,000 m on Volcán Chimborazo, the vegetation was dominated by *Stipa* sp. [253] and *Senecio teretifolius* with *Plantago* sp. [301]. The presence of *Stipa* tussocks symbolises the link between the vegetation of the Arenal and that of the puna, where *Stipa ichu* is predominant.

The arid nature of the north-western part of Volcán Chimborazo can be explained by two factors. Firstly, the area is in rainshadow, both from the volcano itself, and also from the eastern range of the Andes upon which most of the rain falls. Secondly, the sandy substrate found here does not support surface waters. Acosta-Solís (1985) reports that meltwater from the snow-cap of the mountain flows below ground only to emerge at an altitude of around 4,000 m.

There are a number of other sites in Ecuador which are subject to similar conditions. Acosta-Solís (1984, 1985) gives a number of examples including the slopes of Volcán Carihuayrazo and Volcán Iliniza, and the páramos of Palmira and Moyocancha. By virtue of the free-draining substrate, a number of other regions may support similar vegetation locally. For example, Miller & Silander (1991) describe communities dominated by *Stipa ichu* tussocks on Volcán Cotopaxi, though they were more diverse than those described here.

High Altitude Desert Páramo

At the limits of plant survival at high altitudes, a sparse vegetation cover of plants may exist amongst the rocks and scree which provide shelter from the harsh conditions. This is equivalent to the super-páramo defined by Cuatrecasas (1954, 1958, 1968). The super-páramo reaches its greatest extent the south-west of Ecuador where it is driest (Furrer & Graf, 1978).

The vegetation of the upper reaches of Volcán Chimborazo provided a good example of this kind of desert páramo, though the rainshadow effects mentioned above may have contributed to its formation. The majority of the region is dominated by three species: *Chuquiraga jussieui, Calamagrostis* sp. [251] and *Geranium* sp. [157]. One of Øllgaard & Balslev's (1979) collecting locations was in a similar area on Volcán Cotopaxi (Location 74), with *Chuquiraga jussieui* a conspicuous element of the vegetation, but lacking *Calamagrostis* tussocks and *Geranium* cushions.

At the highest altitudes, the vegetation was heavily dependent upon sheltered sites amongst the rocky substrate. Pfitsch (1988) demonstrated that significant thermal advantages (and thus benefits to survival) were experienced beside large rocks. On Chimborazo, this resulted in a very variable floristic composition, which is reflected by the complex community patterns produced by TWINSPAN at these altitudes. All of the communities were dominated by *Chuquiraga jussieui, Calamagrostis* sp. [251] and cushions of *Geranium* sp. [157], with an associated range of other species.

On the humid slopes of Volcán Tungurahua, another desert páramo community was recorded at altitudes of 4,000 m and above. Tussock grasses were absent, the vegetation consisting of a low carpet of plants. Many of the species in this community may also be found in the cushion páramos which have already been described.

The distributions of the páramo communities which have been described above are determined by a number of environmental factors. Many of these factors are interdependent, and altitude, in particular, proved to be correlated with almost all of the other environmental variables measured in this study. It was also strongly related to species and community distributions. Thus, altitude provides a useful overview of many of the elements which control the presence and extent of páramo vegetation. Baruch (1984), in a study of Venezuelan páramo vegetation, also found that altitude was the principal component of his first ordination axis, and that most of the environmental parameters he measured were statistically related to it.

Cleef (1981) proposed that the zonation found in the Colombian Cordillera Oriental was related to the incidence and frequency of sub-zero temperatures. The mechanisms involved may be related to tissue damage and early morning water stress, illustrated by studies such as that by Goldstein & Meinzer (1983) and Goldstein, Meinzer & Monasterio (1985). Unfortunately, it was not possible to collect representative climatic information during the field visits and no data was available from other sources.

Although the altitude of an area would indicate the general level of minimum temperatures, they are buffered by humidity. Páramos in humid, cloudy regions tend to be subject to fewer, less intense frosts than their counterparts in drier areas (Sarmiento, 1986). In a similar way, soil moisture may buffer temperatures close to the ground and around the roots. Thus, the drainage and water holding capacities of páramo soils may also be relevant to plant distribution.

It is not clear whether plant communities develop in response to soil pH, or *vice versa*. For example, the páramo soils of Sumapaz in Colombia are acidic despite overlying limestone (Fosberg, 1944). However, certain patterns of soil pH are evident from this study, despite the loss of some samples. Whilst cushion and tussock páramos occupy areas of relatively average pH (around 4.5-5.5), *Espeletia* páramos appear to inhabit more acidic areas (pH of about 4.5) and desert páramos are found largely on soils with higher pH values (5.5). Cleef (1981) also linked soil depth to plant distribution in the Colombian páramo. This is particularly important at higher altitudes where soil formation is slow.

In high altitude páramos, vegetation was restricted to sheltered sites next to rocks or other plants. Exposure was important in determining the presence or absence of species throughout the páramo vegetation studied. Smith (1978) clearly demonstrated that *Polylepis sericea* seedlings were unable to establish in open páramo in

Venezuela, and many other species may be similarly restricted in the Ecuadorian Andes.

Overall disturbance was rated for each sample on a six-point scale. This index proved a reliable estimator for three other indices used in this study: burning, trampling and grazing. These three variables are strongly linked with each other. Usually, páramo areas are burned because a farmer wishes to improve the nutritional value of the land for livestock. Implicitly, the same area must be subject to grazing pressure. Furthermore, cattle and horses with freedom to roam the páramo appear to favour recently burned areas (personal observation; Verweij & Kok, 1992). This will concentrate grazing activity in burned areas. Of course, wherever there is grazing pressure, there must also be trampling. On steep slopes throughout the Ecuadorian Andes, the effects of trampling can be clearly seen: the hillsides are minutely terraced along the contours by the movements of livestock. It might appear from the aforementioned that agricultural use of the páramos is intensive. In fact, the reverse is usually the case, cattle and horses are grazed over wide areas and at low density. However, in an environment such as the páramo, recovery from disturbance is slow. This leads to widespread indications of disturbance, though the rate of disturbance may be low. Schmidt & Verweij (1992) observed that cattle on the páramo graze for long hours and over large areas to meet their nutritional requirements. It was estimated that cattle walked an extra 5 km per day, with an estimated ascent of 50 m, when compared to the foraging behaviour of lowland animals.

Disturbance (both natural and human) was considered to be an important factor determining the distribution of Colombian and Venezuelan páramo species by Lozano & Schnetter (1976) and Baruch (1984), respectively. In Ecuador, disturbance was clearly correlated to species and community distributions. This will be discussed further in the final chapter.

Species diversity was found to rise with increasing altitude. Baruch (1984) observed the same phenomenon in a Venezuela páramo. This follows general observations that diversity tends to increase in places with relatively high environmental stress (Peet, 1978). In such places, stress tolerance is the main strategy and competitive exclusion is less influential on community composition (Grime, 1979). In the Ecuadorian páramos, the diminishing dominance of *Calamagrostis* tussocks and its eventual disappearance at the highest altitudes results in a much more even distribution of species abundance, which increases diversity. The cushions, which tend to dominate the higher altitudinal zones, are less able to exclude other species which grow upon them.

This study has described a number of páramo communities throughout Ecuador and covering a wide altitudinal range. The distributions of the plant species making up these communities were statistically related to environmental variables such as altitude, exposure and disturbance. Other factors seem to be involved which were not measured, like minimum temperatures and humidity. These factors have been linked to plant distributions in the páramos of Venezuela (Fariñas & Monasterio, 1980; Baruch, 1984) and Colombia (Lozano & Schnetter, 1976; Cleef, 1981).

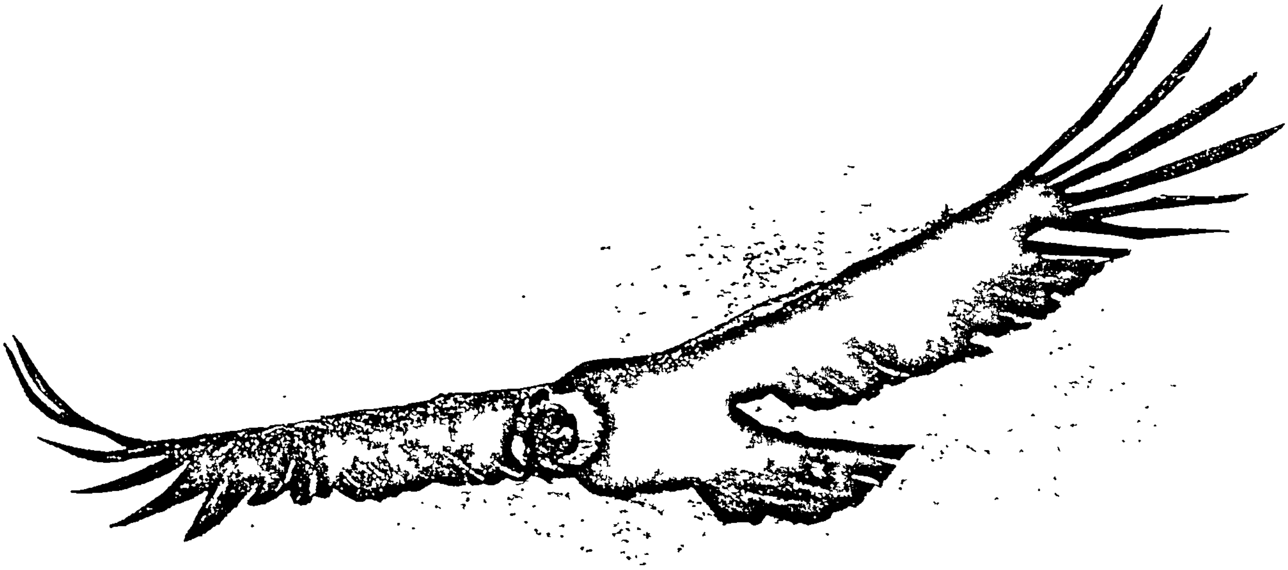
Three areas of research, in particular, warrant further study. First of all, more quantitative descriptions of páramo areas of Ecuador are needed, to determine the representativeness of the current study and to give a better picture of variability in composition. Páramos to the south and east were under-represented in this study and the understanding of Ecuadorian mountain vegetation would benefit from further attention to these regions.

Secondly, the mechanisms which limit plant species distribution require attention. This requires detailed study over a long period of time so that due consideration is given to climatic factors. A useful starting point for such research would be the transition zone between tussock and cushion páramo found so often at around 4,000 m, which is described in more detail in Chapter 4. Here, there are pronounced changes in physiognomy over a very short distance (both laterally and altitudinally) and an opportunity to conduct a detailed study of the processes involved.

Finally, a third avenue of study concerns the distribution and composition of azonal vegetation in the Ecuadorian páramos. Bogs, woodlands and thickets are frequently discovered amidst the more extensive zonal páramo dealt with here. Consideration of the adaptations evolved by plants in response to such environments may reward investigation.

Chapter 3

Plant Form In The Ecuadorian Páramos



I. A Growth Form Classification for the Ecuadorian Páramo

The form of plants has long been recognized as an important descriptive feature of both individual plants themselves and of the vegetation they comprise. Terms such as tree and herb for plants, and forest and grassland for plant communities are in general use and relate to particular forms of plant life. There are other, more specialized terms like xerophyte, which suggest particular adaptations to specific environmental conditions.

Not surprisingly, there exists a large body of literature on plant forms with varied applications. Throughout, there has been confusion over the use of the terms growth form and life form. In this work, the definitions of Clements (1920) in Schulze (1982) have been adopted – the growth form is the direct, quantifiable response made by a plant to different habitats and conditions, while the life form is a morphological feature of a species which is insensitive to environmental changes. This distinction is a useful one, and any temptation to use the terms synonymously should be resisted. However, it is difficult to establish which of these terms applies to a particular feature without first subjecting the plant to artificial environments. It is often impractical to determine whether particular plant forms are fixed regardless of the environment, and for this reason all plant forms will be referred to here as growth forms. Future research may yield the information necessary to distinguish between those features that have a plastic response to the environment and those which do not.

Von Humboldt (1806) offered the first widely recognized classification of *'Hauptformen'* (physiognomic types) following his travels in the Andes. His system grouped plants according to physiognomic similarities, rather than by conventional taxonomic comparison. He described nineteen distinctive plant forms, named and characterized by a genus or family in which that form was clearly represented (for example, palms, banana, lianas, lily, fern, grass). Later in the century, other authors advocated similar physiognomic systems of plant classification. For example, Grisebach (1872) described sixty vegetative forms and attempted to show their correlation with the climate in which they were found.

Warming (1884), Schimper (1898) and others, stressing the ecological significance of plant form, classified plants partly by an assessment of their response to water supply and transpiration.

A simpler system was proposed by Raunkiaer (1907, 1908, 1934): his life form divisions were based on the position of the buds or organs from which new shoots or foliage developed after an unfavourable season. Plant behaviour during the growing season was largely ignored. Ellenberg & Müller-Dombois (1967) found it necessary to modify the system to include more emphasis on structure and seasonality of the crown, foliage and shoot systems. Despite difficulties, the Raunkiaer system and its derivatives have enjoyed wide usage for comparing different vegetation types and their relationship to the environment.

Criticism of the Raunkiaer approach led to the development of other systems. Du Rietz (1931) concluded that it was impossible to formulate one, all-encompassing classification; rather, more was to be gained from the use of several parallel systems, emphasizing different features. He proposed six classifications including main life forms (based upon the general physiognomy of the plant in the growing season), bud height life forms (as in the Raunkiaer system) and leaf life forms (based upon the character of the leaves).

Most of the classification approaches have been devised in the temperate zone, with only a secondary incorporation of tropical regions. Hedberg (1964) points out the hopeless task of creating a system to incorporate all plants on earth for all climates. It is not surprising, therefore, that the applicability of general-use systems for classifying growth forms in the peculiar environments of the tropical alpine regions is limited. Many problems arise from the lack of climatic seasonality, which results in the absence of a growing season (and of "resting buds"). The "unfavourable season" required by a host of classifications occurs every night, invalidating such systems. In addition, it is impossible to distinguish annuals from perennials, monocarps from polycarps, or half-shrubs from herbs. Many plants are frutescent, but the younger shoots are herbaceous, only acquiring woodiness with age (irrespective of the time of year).

For these reasons, Hedberg (1964) found it necessary to establish his own system for grouping plant forms in the Afroalpine environment. His system consisted of five classes: giant rosette plants, tussock grasses, acaulescent rosette plants, cushion plants and sclerophyllous shrubs. Some 45% of the flora fitted these classes, the rest being ignored (showing "less conspicuous adaptations to this environment"). Vareschi (1970) referred to nine 'biotypes' of the Venezuelan Andes. Stem rosettes, cushion plants, 'trellis' plants, dense bunch plants, plants with clustered flowers, dwarf shrubs, rosette plants, geophytes and therophytes comprised his list. Troll (1975 – cited by Lauer, 1979) associated nine life forms with the páramo: páramo grasses, stem rosettes, basal rosettes, evergreen shrubs with dense scales or involuted leaves, macrophyllous evergreen shrubs, shrubs with pubescent leaves, cushion plants, dwarf rosette plants and dwarf semi-woody shrubs forming cushions.

Hedberg (1964) and Hedberg & Hedberg (1979) used their five classes of growth form to examine the adaptive significance of these plants to the environment. However, it is also of interest to compare regions on the basis of growth form and to describe communities by their growth form composition. For these to be accomplished, it is desirable to attempt to account for the 55% of the flora left out of Hedberg's system, though Mena & Balslev (1986) compared the páramo of El Angel with Afroalpine vegetation using only Hedberg's five growth forms. The categories proposed by Vareschi (1970) and Troll (1975) go some way to accounting for the omitted flora, though their classifications do produce further problems of undue complication, particularly with regard to shrubs.

Perhaps ideally, a classification system should indicate relationships between the various groups in a hierarchical manner. However, in practice, this is very hard to achieve with growth forms. Von Humboldt (1806) recognised that life forms are "by their nature not capable of strict classification". Warming (1909) considered it "an intricate task to arrange the life-forms of plants in a genetic system, because they exhibit an overwhelming diversity of forms, ... also because it is difficult to discover guiding principles that are really natural". Only small modifications to a growth pattern are required to change the growth form (the fact that certain taxa may have representatives in a number of growth form categories is evidence for this). A tussock can thus be viewed as an exploded cushion (Hodge, 1946), which in turn may be seen as a contracted shrub and so on. Therefore, an hierarchical classification has not been attempted since the end groups are all that is required.

Tansley & Chipp (1926) state that "the independent student of evolution will do well, however, to make his own classification of life-forms of the communities he actually studies". It is my intention to add to Hedberg's system in an attempt to include a larger portion of the flora than the five classes currently accommodate, and to apply it to the páramo flora of Ecuador.

Hedberg's classes are dealt with first, with examples from the Ecuadorian páramo flora and further afield. Then, additional types of growth form are defined and examples given.

Stem Rosettes (Figure 3.1)

Hedberg's classification (1964) included both stem rosettes and basal rosettes in a group termed 'Giant Rosettes'. These forms are differentiated in the present system.

Stem Rosettes are characterized by thick and unbranched stems covered by dense, dry leaves that remain attached to the plant when they die (marcescent). The single aerial meristem produces lateral inflorescences. It is polycarpic and growth is not determinate (that is, flowering does not halt the development of the axis). Cuatrecasas (1979) terms this growth form as a polycarpic, more or less tall, monocaul caulirosula. Vareschi (1970) and Troll (1975) both include this form in their systems.

A widely used concept of plant form is the architectural model (Hallé & Oldeman, 1970): an inherent growth strategy which defines both the manner in which a plant elaborates its form and the resulting architecture (Barthélémy, Edelin & Hallé, 1989). The architectural model of any plant is based on observations of the type of growth, branching pattern, morphological differentiation of axes and the position of sexuality (Barthélémy *et al.,* 1989). Therefore, the architectural model is entirely independent of taxonomic boundaries between plants. It may express both the phenotypic plasticity of plants (including branch ageing, die-back, release of dormant meristems and re-iteration) and the genetic control of metameric growth and iteration (Hallé, Oldeman & Tomlinson, 1978).

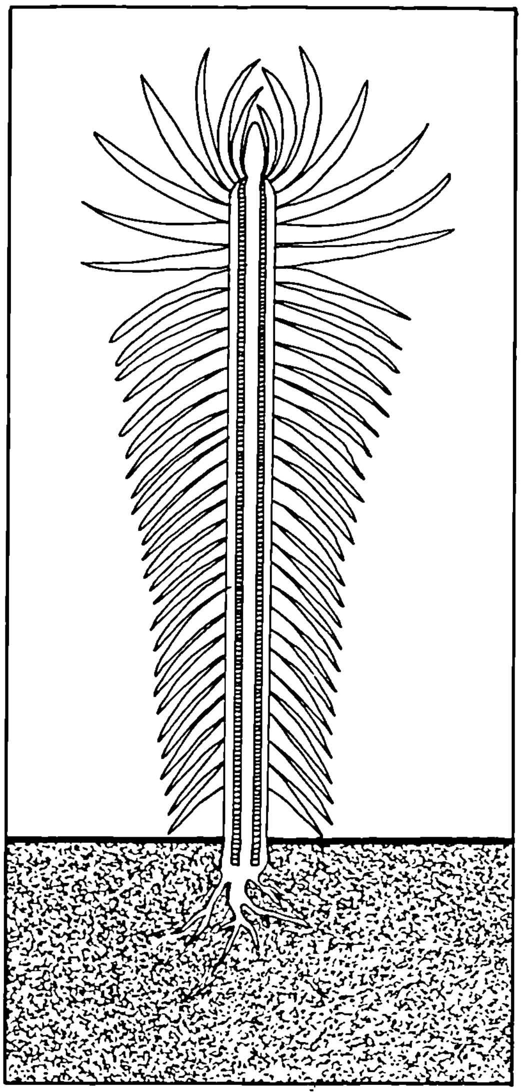


Figure 3.1.
The stem rosette growth form (for example, *Espeletia pycnophylla*).

The stem rosette form corresponds, in a wide sense, to Corner's model of tree architecture (Hallé *et al.*, 1978). However, there are differences—differentiated reproductive branches, spiral phyllotaxis in the stem but decussate phyllotaxis in the inflorescence—which strictly requires another architectural model (Cuatrecasas, 1986). In the Raunkiaer system (Ellenberg & Müller-Dombois, 1967) these plants would be classified as phanerophytes.

It is exemplified by *Espeletia pycnophylla* ssp. *angelensis* in the páramos of northern Ecuador (illustrated in Figure 3.1). Tree ferns also conform to this model, and so *Blechnum loxense* has been incorporated into this class.

Elsewhere in the northern Andes, *Espeletia* species are a more important element of the páramos (Cuatrecasas, 1979). Monasterio (1986) estimated that *Espeletia timotensis* in the Venezuelan Andes has a life-span of 170 years. In Venezuela, *Planta-*

go perrymondii and *Bulbostylis* sp. (Cyperaceae) also exhibit this form (Vareschi, 1970). In the puna vegetation of the Southern Andes, stem rosettes are not present. On a wider scale, stem rosettes are common in the afroalpine region: *Senecio, Dendrosenecio* and *Carduus* species (Mabberley, 1986). *Cyathea, Dicksonia* and *Cibotium* tree ferns occur in subalpine habitats in the grasslands of Malaysian mountains (Van Royen, 1967).

Basal Rosettes (Figure 3.2)

Holttum's model (Hallé *et al.*, 1978) is defined as a plant with a unique axis provided by a single aerial apical meristem which always remains unbranched. After a phase of

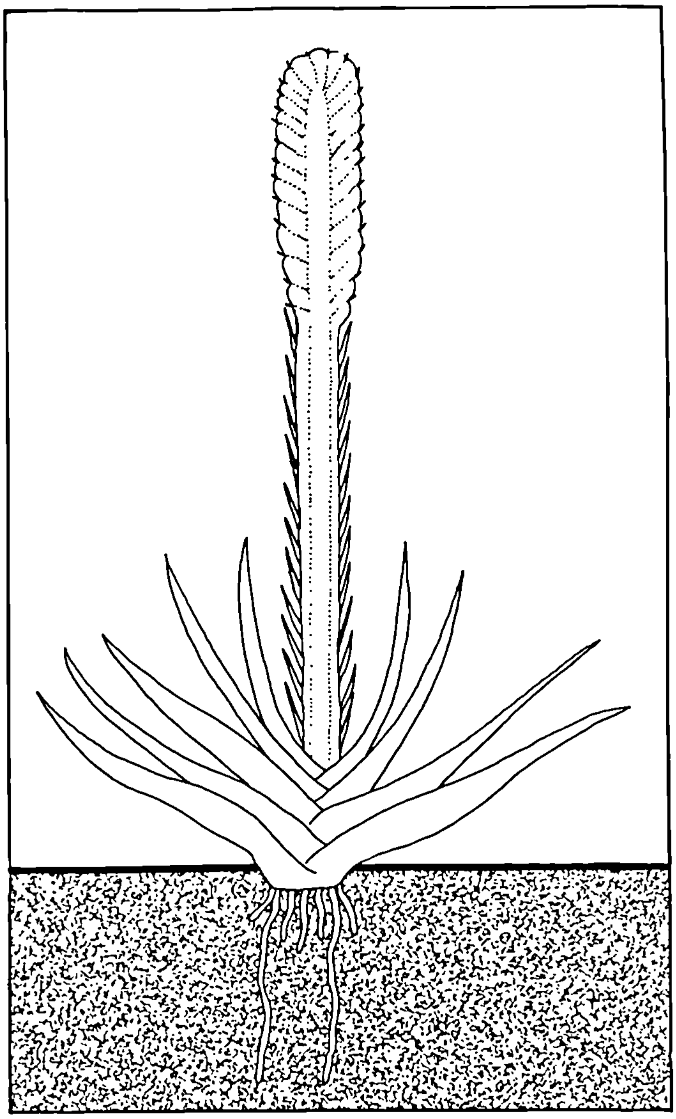


Figure 3.2.
The basal rosette growth form (for example, *Puya hamata*).

stem building, the terminal meristem differentiates completely into an inflorescence. It is, therefore, monocarpic. Sometimes they are referred to as 'candle plants'. These plants are rosulate phanerophytes according to the modified Raunkiaer system of Ellenberg & Müller-Dombois (1967).

Hedberg (1964) failed to differentiate this group from the stem rosettes, though Troll (1975) did make the distinction. The basal rosette growth form is more commonly represented in the Ecuadorian páramos than the stem rosettes. Several species of *Puya* (for example, *P. hamata*, shown in Figure 3.2) conform to this growth model. Several other species in Ecuador have a similar overall appearance, and belong to this category but, unlike *Puya*, are neither woody nor monocarpic: *Rumex tolimensis, Valeriana plantaginea, Lupinus alopecuroides* and *Culcitium* sp. A number of fern species can also demonstrate this form, for example, *Thelypteris* sp.

Basal rosettes are present, but are not as important in Colombia and Venezuela – representatives of this growth form, such as *Draba* spp. and *Senecio* spp., were reported in several studies of the Colombian páramos (for example, Sturm & Rangel, 1985); and Vareschi (1970) fails to mention them at all in his study of Venezuelan páramo vegetation. In the puna of Perú, however, they are much more conspicuous (for example, the impressive *Puya raimondii*). In East Africa, *Lobelia* spp. (Campanulaceae) are very significant basal rosettes. *Rheum nobile* (Polygonaceae), *Lobelia* (Campanulaceae), *Eremurus himalaicus* (Liliaceae), *Arnebia* (Boraginaceae) and *Saussurea* (Compositae) in the Himalayas, Silverswords (*Argyroxiphium* spp., *Haleakala* spp. – Compositae) in Hawaii and *Echium* spp. (Boraginaceae) in the Canary Islands are all examples of 'candle plants' in mountain areas.

Tussock Plants (Figure 3.3)

In tussock or bunch grasses, erect tillers are produced from tightly packed culms at the soil surface (though often growth of the tussock raises this region of dense culm-bases above ground level). Dead leaves are retained and decay while still attached to the plant. The scleromorphic leaves tend to be filiform, either tightly folded or inrolled. This growth form would classify as a caespitose hemicryptophyte in Raunkiaer's system. It is often difficult to distinguish between true tussock-formers and those plants which are only loosely tufted (Hedberg, 1964).

In the Ecuadorian páramos, tussock grasses most commonly belong to the genera *Calamagrostis, Cortaderia, Festuca* and *Stipa*. Non-graminoids also belong to this group, in particular a number of sedges (*Carex, Rhynchospora, Uncinia*) and *Sisyrinchium* spp.

Tussock grasses are common elsewhere in the páramos of the northern Andes, though their prominence declines northwards as the giant rosettes become increasingly significant. Vareschi (1970) notes that bunch grasses (particularly *Agrostis haenkeana* and *Helleria fragilis*) occur at the highest altitudes in Venezuela. Yet further north, in the Mexican zacatal, large stands of tussock grasses occur, the genera *Briza, Bromus, Calamagrostis, Festuca, Muhlenbergia* and *Stipa* well-represented (Breed-

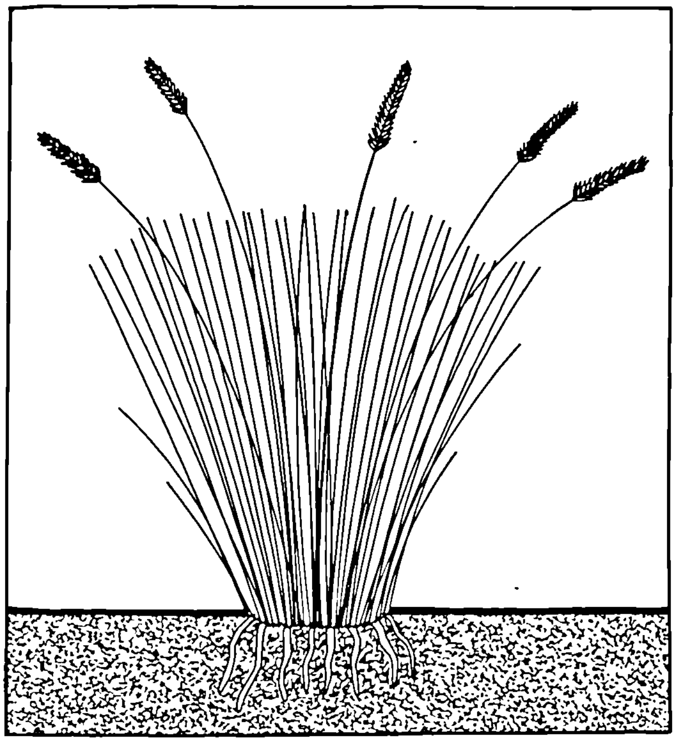


Figure 3.3.
The tussock growth form (for example, *Calamagrostis effusa*).

love, 1973). In the puna of the Altiplano, tussock grasses (*Stipa*, *Calamagrostis* and *Festuca*) represent an important growth form element (Ruthsatz, 1977; Seibert, 1983). In the afroalpine zone of East Africa tussock grasses are equally significant in community physiognomy. Hedberg (1964) cites *Festuca*, *Poa*, *Agrostis*, *Pentaschistis* and *Carex* as the main tussock-forming genera. Van Royen (1967) cites the main tussock grasses of New Guinea as *Danthonia*, *Agrostis*, *Anthoxanthum* and *Festuca*. This growth form is also highly characteristic of Sub-Antarctic regions, exemplified by *Poa* and *Stipa* (Sewell, 1954), and *Chionochloa*, *Poa*, *Festuca* and *Notodanthonia* for New Zealand (Mark & Adams, 1973).

Acaulescent Rosettes (Figure 3.4)

The basal rosette of these forms is initiated at or below ground level, the leaves being attached at virtually the same level. An overground stem is absent (though in some members the flowers are not sessile, but borne on more or less leafless flowering stems). These plants commonly possess a large tap root. They are usually small (up to 30cm across, but generally smaller), though some of the larger species may be viewed as small versions of the giant basal rosette form. Rosette or semi-rosette hemicryptophyte approximates to this growth form in the Raunkiaer system (Ellenberg & Müller-Dombois, 1967).

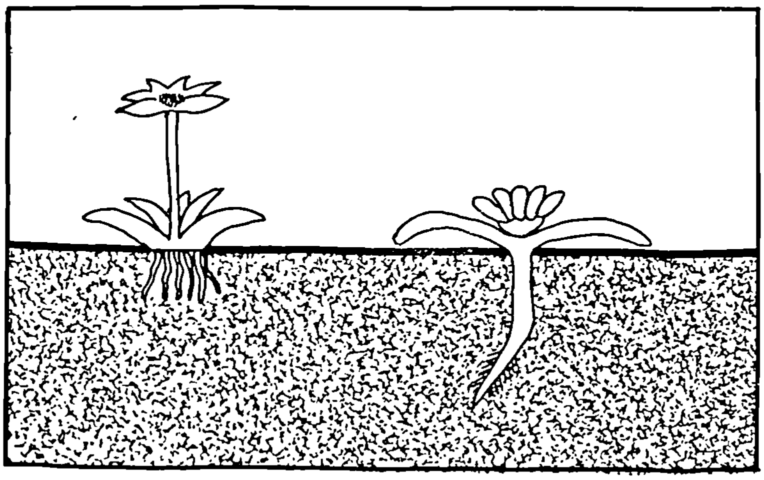


Figure 3.4.
The acaulescent rosette growth form, for example, *Eryngium humile* (left) and *Hypochaeris sessiliflora* (right).

The páramo flora of Ecuador contains many representatives of this growth form. The commonest include *Hypochaeris sessiliflora, Oritrophium peruvianum, Hieracium frigidum, Senecio pimpinellifolius, Senecio repens* and *Plantago major. Werneria nubigena* is a variation on the rosette form, the leaves stacked on top of each other. *Luzula* spp. and a number of sedges are included here. Less well-defined acaulescent rosettes are *Lachemilla hispidula* (and other similar members of the same genus), *Oreomyrrhis andicola* and *Niphogeton dissecta. Isoëtes* is also placed in this category, though perhaps it merits a group of its own.

Acaulescent rosettes are common elsewhere in the páramo; for example, *Rhizocephalum candollei* Wedd. in the Venezuelan páramo (Hedberg & Hedberg, 1979). Cleef (1978) includes *Acaena cylindristachya, Valeriana* spp., *Castratella* spp. and *Oritrophium* spp. among the Colombian páramo acaulescent rosettes. The form is well-represented in the puna (Hedberg & Hedberg, 1979). Wilcox *et al.* (1986) list a number of acaulescent rosette species in their bofedal communities in the highlands of Central Perú. Cabrera (1968) lists a number of species occurring in the puna, including *Chaptalia similis, Trechonaetes lanigera, Plantago monticola* and *Northoscordum sessile*.

In East Africa, there are several notable examples, including *Ranunculus cryptanthus, Oreophyton falcatum, Haplocarpha rueppellii* and *Carduus chamaecephalus* (Hedberg, 1964). In New Zealand, there are a large number of species belonging to this growth form, notably *Aciphylla congesta, Celmisia* spp. (*C.major* var. *brevis* appears remarkably similar to the Andean *Oritrophium peruvianum* – Solbrig (1960) considered *Oritrophium* a section of the genus *Celmisia* but Cuatrecasas (1968) treated them as separate genera) and *Craspedia* spp. (Mark & Adams, 1973). Himalayan rosette species (Polunin & Stainton, 1987) include *Pycnoplinthopsis bhutanica* (Cruciferae) and *Astragalus rhizanthus* (Leguminosae).

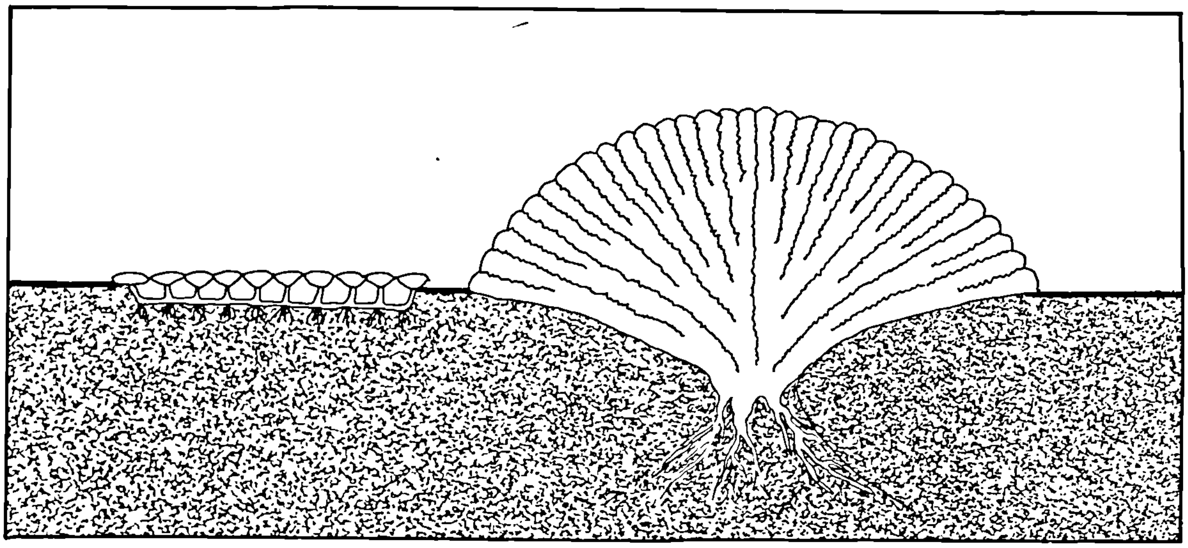


Figure 3.5.
The cushion and mat growth form, for example, *Plantago rigida* (right) and *Azorella pedunculata* (left).

Cushion Plants (Figure 3.5)

The term cushion is used here in its widest sense, to include soft mat-cushions and hard, compact bolster plants.

The plants in this class show a variety of shapes, ranging from semi-spherical through hummock to flat mat. Rauh (1939) distinguished a number of morphological types of which rosette cushions, creeping cushions and ball cushions are commonest in the Ecuadorian páramos. All have profusely branched stems with short internodes, the branches terminated by imbricate leaves in more or less evident rosettes, forming a dense layer covering the peaty interior (formed by the decay of the remains of leaves, branches and roots). As the older branches die and decay, the younger parts become isolated from the original plant (Heilborn, 1926; Hedberg, 1964). It is difficult to establish whether cushions or mats are composed of one individual or more; the complete fusion of cushions of different species has been observed (Heilborn, 1926). In the Raunkiaer system, cushion plants would be classified as semi-woody dwarf shrubs, more specifically as "suffrescent" pulvinate chamaephytes. The classification of mat or hummock plants is less precise.

Cushion plants are very conspicuous in the Ecuadorian páramos, particularly above 4,000m. Harling (1979) recognized an entire vegetation type as "cushion páramo". Notable examples of cushion-formers are *Plantago rigida, Valeriana rigida, Nototriche jamesonii, Geranium* sp., *Azorella diapensioides, Arcytophyllum* spp., *Werneria humilis, Viola* sp. and *Distichia muscoides*. Mat-formers include *Oreobolus obtusangulus, Distichia muscoides, Plantago rigida, Aciachne flagellifera* and *Azorella pedunculata*.

According to Cleef (1978) six taxa constitute common vegetation types in the Colombian páramos: *Plantago rigida, Distichia muscoides, Distichia tolimensis, Oreobolus* sp., *Azorella multifida* and *Aciachne pulvinata*. In the Venezuelan páramo around Mucubají, Hedberg & Hedberg (1979) classified *Aciachne pulvinata, Paepalanthus karstenii, Calandrinia acaulis, Arenaria venezuelana* f. *caespitosa, Azorella crenata* and *Plantago rigida* as cushion plants.

The cushion growth form reaches its height of supremacy in the puna vegetation where desert conditions produce the so-called puna mat vegetation (Hodge, 1946). Notable puna species with a cushion or mat form include *Azorella compacta, Adesmia erinacea, Adesmia patacana, Pycnophyllum* spp., *Anthobryum tetragonum* and *Opuntia atacamensis* (Cabrera, 1968). Hodge (1946, 1960) lists a number of cushion plants for the Peruvian puna and emphasises the use of 'llareta' (*Azorella* spp.) for fuel. Ruthsatz (1978) identified some thirty species of cushion plants in North-west Argentina including several which occur in Ecuador (for example, *Distichia muscoides, Werneria pygmaea*). In Northern Chile, Quintanilla (1983) reports *Pycnophyllum bryoides, Azorella* sp. and *Adesmia* sp., whilst Armesto, Arroyo & Villagran (1980) studied cushions of *Laretia acaulis, Azorella monantha* and *Azorella madreporica* in Central Chile.

In East Africa only five species were found by Hedberg (1964) to belong to this class: *Agrostis sclerophylla, Sagina afroalpina, Swertia subnivalis, Myosotis keniensis* and *Haplocarpha ruppellii*. In Malaysia cushions are also very rare (Van Steenis, 1935 p.346, 1939 p.448). Van Royen (1967) describes mats of *Eurya brasii* and *Oreobolus* sp. in Papua New Guinea. In the alpine zone of New Zealand mats and cushions are a very conspicuous group, with *Colobanthus canaliculatus* (and other species), *Drapetes lyallii, Dracophyllum muscoides, Celmisia sessiliflora, Haastia pulvinaris, Raoulia* spp., *Phyllachne* spp. and *Pygmaea* spp. good examples (Mark & Adams, 1973; Godley, 1978). Reference to Polunin & Stainton (1987) shows that cushion and mat plants are represented in the Himalayas, notably by *Thylacospermum caespitosum* (Caryophyllaceae), *Arenaria bryophylla* and *A.densissima* (Caryophyllaceae), *Saxifraga saginoides* and *S.pulvinaria* (Saxifragaceae) and *Androsace delarayis* and *A.tapete* (Primulaceae).

Upright Shrubs (Figure 3.6)

The sclerophyllous (tough-leaved) and dwarf shrubs of Hedberg's (1964) classificatory system are characterized by thin and distinctly woody branches with thin bark. The leaves are rigid, more or less coriaceous (leathery), often small, folded or revolute. The leaf surface is sometimes covered by dense, white pubescence, often mixed with gland hairs. The shrubs vary in height from 50cm to 2m or more. Not all shrubs in Hedberg's classification were sclerophyllous and likewise, there are a number of different leaf forms in the páramo species forming this group. Troll (1975) divided upright shrubs into three classes: those with dense scales or involuted leaves (like *Loricaria*), those with large leaves (such as *Befaria*) and shrubs with pubescent leaves (for example, *Helichrysum*).

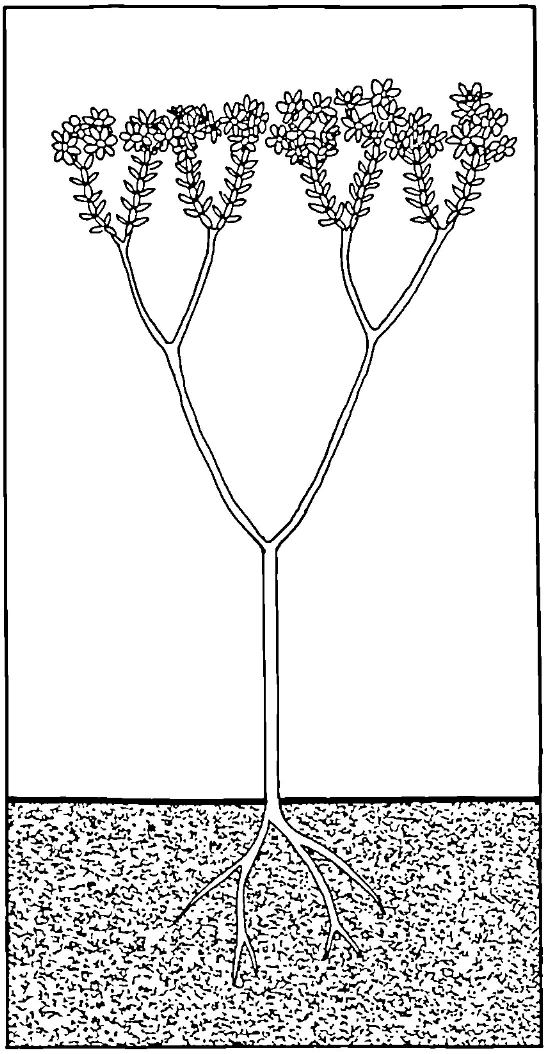


Figure 3.6.
The upright shrub growth form (for example, *Valeriana microphylla*).

The group is continuous with suffrescent herbs and borderline cases are difficult to distinguish. The absence of a resting season makes the classification of this growth form according to the system of Raunkiaer impossible. Perhaps evergreen nanophanerophytes without bud protection is close, but so too is suffruticose/frutescent chamaephytes (Ellenberg & Müller-Dombois, 1967). Sturm (1978) found this to be a problem too – many of his dwarf shrubs were denoted as "chamaephyte or nanophanerophyte".

Dwarf shrubs occur quite frequently in the Ecuadorian páramos, particularly in its lowest reaches. *Valeriana, Gynoxys, Diplostephium, Pentacalia* (= *Senecio*), *Chuquiraga, Berberis, Hypericum, Gnaphalium, Lupinus, Loricaria, Calceolaria* and *Hesperomeles* are all genera with representatives of this growth form.

Cleef (1981) referred to a dwarfshrub páramo and a number of azonal dwarfshrub comunities in the Colombian Cordillera Oreintal. Sclerophyllous shrubs constitute

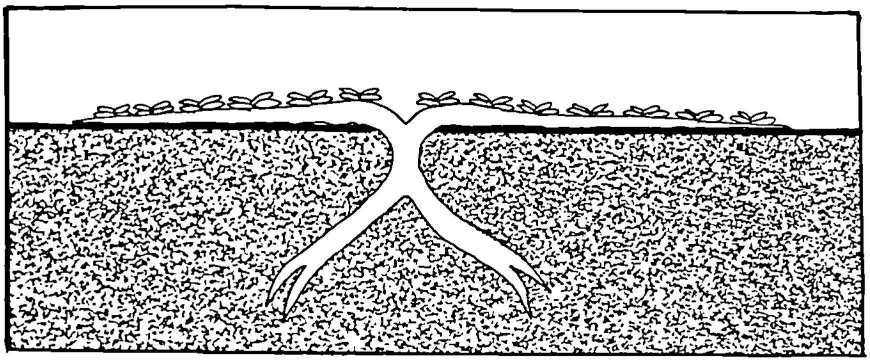


Figure 3.7.
The prostrate shrub growth form (for example, *Pernettya prostrata*).

one of the most frequent growth forms of the Venezuelan páramo, including *Hesperomeles pernettyoides, Lachemilla verticillata, Polylepis sericea, Draba* cf. *funckiana, Hypericum laricifolium, Valeriana parviflora* and *Baccharis prunifolia* (Hedberg & Hedberg, 1979).

In the remainder of páramo regions, dwarf shrubs are common in the lower portions, the subpáramo of Cuatrecasas (1958, 1968). In the puna of the Central Andes, tola (*Parastrephia lepidophylla*) plays a major role in the plant community, in conjunction with other composite shrubs (Seibert, 1983). Quintanilla (1983) describes *Chuquiraga kuschelli* and *Chuquiraga spinosa* for the Chilean puna. 'Sclerophyllous' shrubs are a common element of the afroalpine flora: according to Hedberg (1964) about fifty taxa belong to this group, including *Protea kilimandscharica, Thesium kilimandscharicum, Alchemilla* spp., *Adenocarpus mannii, Hypericum* spp., all afroalpine Ericaceae, *Bartsia* spp., *Helichrysum* spp., *Senecio* spp. and *Euryops* spp. J.M.B. Smith (1975) notes the importance of shrubs in the tropicalpine zone of New Guinea (for example, *Hypericum*). In New Zealand, a number of species belonging to the genera *Drapetes, Hebe* and *Helichrysum* are similar in general appearance to *Loricaria* spp. in the páramo. Some *Hebe* spp. are also like the páramo shrubs of *Valeriana* (Mark & Adams, 1973).

Prostrate Shrubs (Figure 3.7)

Woody plants which form a dense covering on the ground have already been dealt with in the cushion and mat section. However, certain creeping dwarf shrubs have a more open cover and these are the plants which belong to this class. Vareschi (1970) termed them 'trellis' plants.

It is possible to view these prostrate shrubs as dwarf shrubs or as mats in a loose sense. For example, when dealing with the tropicalpine species *Eurya brasii*, J.M.B.

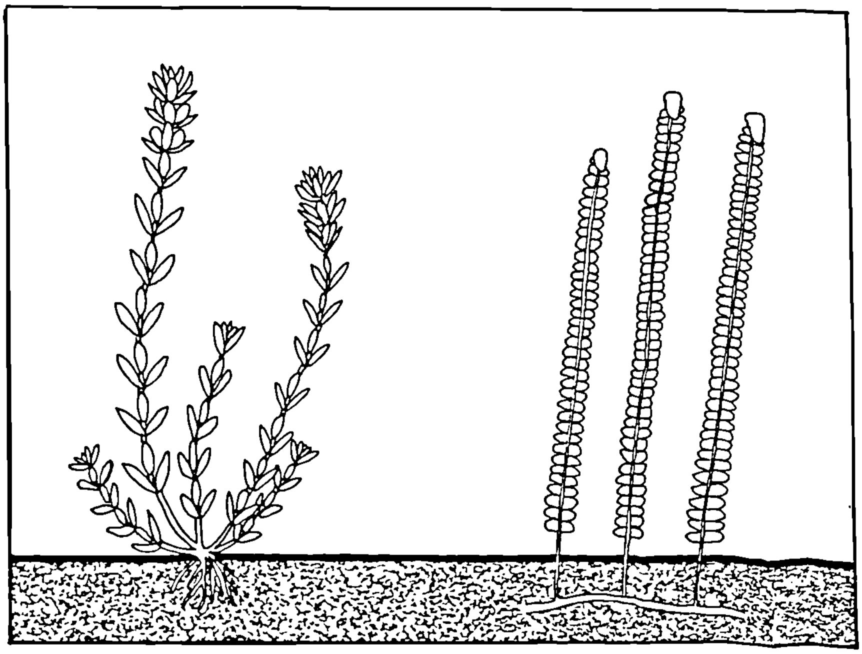


Figure 3.8.
The erect herb growth form, for example, *Bartsia laticrenata* (left) and *Jamesonia alstonii* (right).

Smith (1975) talks of a shrub, while Van Royen (1967) terms it a mat. These plants would classify as frutescent chamaephytes under the Raunkiaer system.

Pernettya prostrata, Disterigma empetrifolium, Baccharis alpina and *Arcytophyllum aristatum* are common representatives of this growth form in the Ecuadorian páramo. These and similar species occur elsewhere in the páramos of the northern Andes (Cleef, 1978, 1981). Vareschi (1970) offers *Pernettya prostrata, Cyrilla racemiflora, Eugenia triquetra* and *Hesperomeles pernettyoides* as Venezuelan representatives. *Adesmia horrida, A.atamensis* and *Nardophylum* sp. are cited by Quintanilla (1983) as prostrate shrubs of the Chilean puna. In New Zealand examples of prostrate shrubs are found in the alpine zone, such as *Pernettya nana, P.alpina, Gaultheria depressa* and *Coprosma petriei* (Mark & Adams, 1973). *Salix cayculata* (Salicaceae) is a good example of a Himalayan prostrate shrub (Polunin & Stainton, 1987).

Erect Herbs (Figure 3.8)

Since the 'herbaceous stems' grade continuous into small shrubs through varying degrees of woodiness, it is difficult to distinguish the larger members of this class from the smaller ones of the 'dwarf shrubs' group.

In the Raunkiaer system, plants from this group can be included in the phanerophytes, particularly phanerophytic grasses (maybe lignified as in the bamboos) and

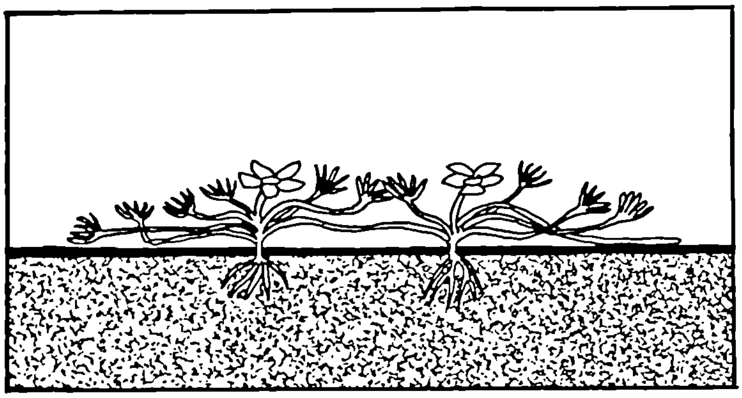


Figure 3.9.
The prostrate herb growth form (for example, *Geranium multipartitum*).

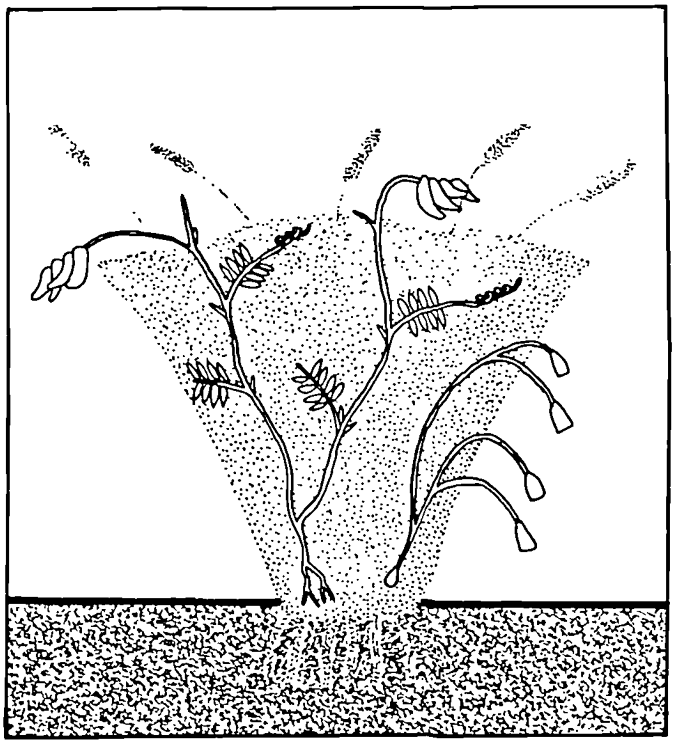


Figure 3.10.
The trailing Herb growth form (for example, *Vicia setifolia*).

herbaceous phanerophytes. Several hemicryptophytes, which do not form tussocks, are also included here. Some members may even be assigned to the geophytes. A number of forms included here were termed 'plants with clustered flowers' by Vareschi (1970).

Common elements of the Ecuadorian páramo flora in this group include: *Bartsia, Castilleja, Draba, Jamesonia, Gentianella, Lobelia, Lycopodium, Bomarea, Lupinus* and a variety of genera from the Gramineae; similarly for the páramo vegetation elsewhere in the northern Andes.

This growth form is prominent in other high altitude tropical vegetation types, along with most plant communities throughout the world.

Reptant and Prostrate Herbs (Figure 3.9)

These plants lack erect, leafy stems and possess stolons or other means of spreading vegetatively, along the soil surface or just underneath it. Reptant hemicryptophytes or reptant herbaceous chamaephytes defined in Raunkiaer system belong to this growth form and are common throughout the world.

Lachemilla, Geranium, Satureja, Bidens, Gentiana, Gentianella, Halenia and *Ranunculus* are all extremely common genera with a reptant herb growth form in the Ecuadorian páramos.

Trailing Herbs (Figure 3.10)

With weak ascending stems, some with tendrils or minutely toothed stems aiding their support among other plants, this growth form is relatively common in the grassy páramo. The tussock grasses provide an ideal framework for these plants. The Raunkiaer system would classify Ecuadorian páramo climbers into various categories: spreading, climbing, hemicryptophytic lianas (*Galium*); tendril-climbing, hemicryptophytic lianas (*Vicia*); or spreading, climbing, geophytic lianas (*Oxalis*). Other climbers include *Stellaria* (on tussocks) and *Bomarea* (on shrubs). Here they are all grouped together.

Cryptogams

Clothing the surface of soil or rocks in a close mantle, mosses and lichens are particularly common in undisturbed humid páramos. Though not of the same character as the mats of the earlier section, bryophyte mats can be the dominant growth form, especially at high altitudes on ashy soils. In the Raunkiaer system, these plants are termed adnate thallophytes. This category includes leafy and thalloid cryptogams (mosses, leafy and thallose liverworts, filmy ferns) and foliose, fruticose and thallose lichen mats. One lichen species, *Thamnolia* sp., is a solifluction floater (according to the definition of Lind & Morrison, 1974), which merely lies, unattached to the substrate, on the surface of the ground.

Owing to the loss of voucher specimens for a number of sites, it was not possible to include this growth form category in later analyses.

Other Growth Forms

There are a number of species not strictly classifiable into the above growth forms, though dealt with by Raunkiaer's system. These include trees (for example, *Polylepis, Gynoxys*) which are occasionally found in the páramo, and several geophytes such as *Stenomesson aurantiacum* (Amaryllidaceae).

None of these plants was present in the following studies described in Sections II and III of this chapter.

II. The Growth Form Composition of the Ecuadorian Páramos

Introduction

In Chapter 2, a number of vegetation samples from the páramo vegetation of Ecuador were classified according to their species composition. Many of the resulting communities were assigned to various physiognomic groups (for example, cushion páramo, tussock páramo), with the same dominant growth forms but not necessarily the same species present.

Given that all characters of an organism are likely to reflect the action of selection (Fisher, 1930), differences in plant form can be thought of as visible indications of niche differentiation. Thus, selection gives rise to organisms that are ecologically equivalent, a process known as convergent evolution (Johnson, 1973). It is often the case that where the dominant growth form is the same, there is a similar degree of convergence in the subordinate units of vegetation (Mooney, 1974).

The vegetation of high tropical mountains has often been cited as support for the concept of convergent evolution (for example, Hedberg, 1964; Troll, 1968; Hedberg & Hedberg, 1979; Halloy, 1983). Such reports are based on qualitative observations of physiognomic parallelism between, for example, the mountains of East Africa and the Andes. To test the extent of convergent evolution, more quantitative approaches are required. However, before different mountain systems are compared, it is necessary to determine the degree of variability of the vegetation within single mountain regions.

Mena & Balslev (1986) used Hedberg's (1964) growth form classification and applied it to three 10 x 10 m plots in the páramo of El Angel in northern Ecuador, where they estimated the percentage cover of each of five growth forms. However, the majority of their work related to a floristic comparison with the Afroalpine vegetation.

In this study, using ten of the eleven growth forms defined in the first section of this chapter (bryophytes and lichens were not used here, because a large number of voucher specimens were stolen in Ecuador), the growth form composition of Ecuadorian páramo vegetation is described in detail. Comparisons between the samples are made and growth forms are related to environmental variables which may be responsible for variations in their distribution.

Methods

In Chapter 2, the vascular plant composition of 192 páramo quadrats was described. Using these same data, collected from twelve sites, each vascular plant species was assigned to one of the ten growth form categories described in the previous section. Appendix 1 indicates the growth form category of each of the 348 taxa.

Where several species in a quadrat belonged to the same growth form category, their Braun-Blanquet abundance scores were summed (by converting the individual scores to their mid-point percentage cover, summing and converting the resultant cover value back to a Braun-Blanquet score). In this way, the growth form composition of the 192 quadrats was determined.

Environmental data for each quadrat were also collected (described in Chapter 2). Altitude, aspect and slope were measured, and exposure, burning intensity, grazing intensity, trampling intensity and overall disturbance were estimated using subjective, semi-quantitative scales. The coverage (as a percentage) of bare ground and rock cover (including scree) were also noted for each sample.

The 192 páramo stands and the ten growth forms were classified using the TWINSPAN algorithm (Hill, 1979), part of the VESPAN-II package (Malloch, 1988).

In order to explore the relationship between the growth form composition of the stands and the environmental variables measured in the study, direct gradient analysis was performed using the CANOCO programme (ter Braak, 1988). The TWINSPAN classes were later superimposed as centroids upon the resulting ordination. The first axis of the ordination and the trace statistic (the sum of all axes) were tested for statistical significance by means of a Monte Carlo permutation test (Hope, 1968), also part of the CANOCO package.

Results

The summary statistics on the growth form composition of the sample stands in the twelve regions is presented in Table 3.1. In total, the growth form composition of 192 samples was recorded. The only site to have all ten growth forms was Volcán Tungurahua, but the remaining sites all had eight or nine of the ten present, with the exception of the páramo near Oña which had only seven.

Overall, the mean number of growth forms in a 25 m^2 sample was just under seven. Notably different from this value was the mean for the samples from Volcán Chimborazo, at 4.38.

Combining the three plots at each altitude level resulted in a mean growth form complement of 7.25 for all of the sites. Again, Volcán Chimborazo had fewer growth

Site	No of Altitude Levels	No of Quadrats	No of Forms in all Quadrats	Mean No Forms per Quadrat	Mean No Forms per Altitude (3 Quadrats)
Volcán Chiles	7	21	9	7.67	8.14
Volcán Cotacachi	7	21	8	7.38	7.57
Páramo de Guamaní	7	21	8	6.33	6.86
Volcán Tungurahua	5	15	10	6.87	7.40
El Altar (west)	5	15	8	6.73	7.20
El Altar (east)	6	18	8	6.06	6.33
Daldal	6	18	9	7.67	8.00
Volcán Chimborazo	7	21	8	4.38	5.43
Páramo de Zapote Naida	3	9	8	7.33	8.00
Cajas	7	21	8	6.95	7.57
Cumbe	3	9	9	7.67	8.33
Oña	1	3	7	6.33	7.00
Overall	64	192	10	6.73	7.25

Table 3.1.
The location and summarised growth form composition of 192 páramo quadrats. For each locality the number of altitude levels sampled and the number of quadrats used are stated. The total number of growth forms found in the stands at each locality are given. The mean number of growth forms found in each stand and at each altitude level (three quadrats combined) are shown.

forms on average (6.33). The altitude levels in the páramo of Cumbe had the highest mean with over eight growth forms on average.

Figure 3.11 indicates the frequency of occurrence of the ten growth forms in the sample quadrats. Erect herbs, acaulescent rosettes and prostrate herbs were recorded in over 90% of the stands. Seven of the ten forms occurred in over three-quarters of the vegetation samples (tussocks, acaulescent rosettes, cushions, upright shrubs, prostrate shrubs, erect herbs, prostrate herbs). The remaining three forms were much less frequent: trailing herbs and basal rosettes were present in approximately one-quarter of the stands, and stem rosettes were observed in just over 10% of the samples.

The four most dominant growth forms were tussocks, acaulescent rosettes, erect herbs and prostrate herbs, each of which accounted for more than 5% of the area of about three-quarters of the plots. Only tussocks and acaulescent rosettes achieved a cover of greater than 50% (in 65 and 8 plots, respectively).

The CANOCO analysis produced only two useful axes, due in part to the overall similarity of the samples in terms of growth form composition. Subsequent axes were unable to explain sufficient variation in the dataset to merit interpretation, demonstrated by low eigenvalues ($\lambda < 0.2$). Another possible cause for such low eigenvalues could be that the environmental variables recorded in this study were not sufficient to ordinate the growth forms beyond the first two axes. However, the relationship between the distribution of the growth forms and the ordination axes was tested using a Monte Carlo permutation test and was found to be statistically significant ($p < 0.001$).

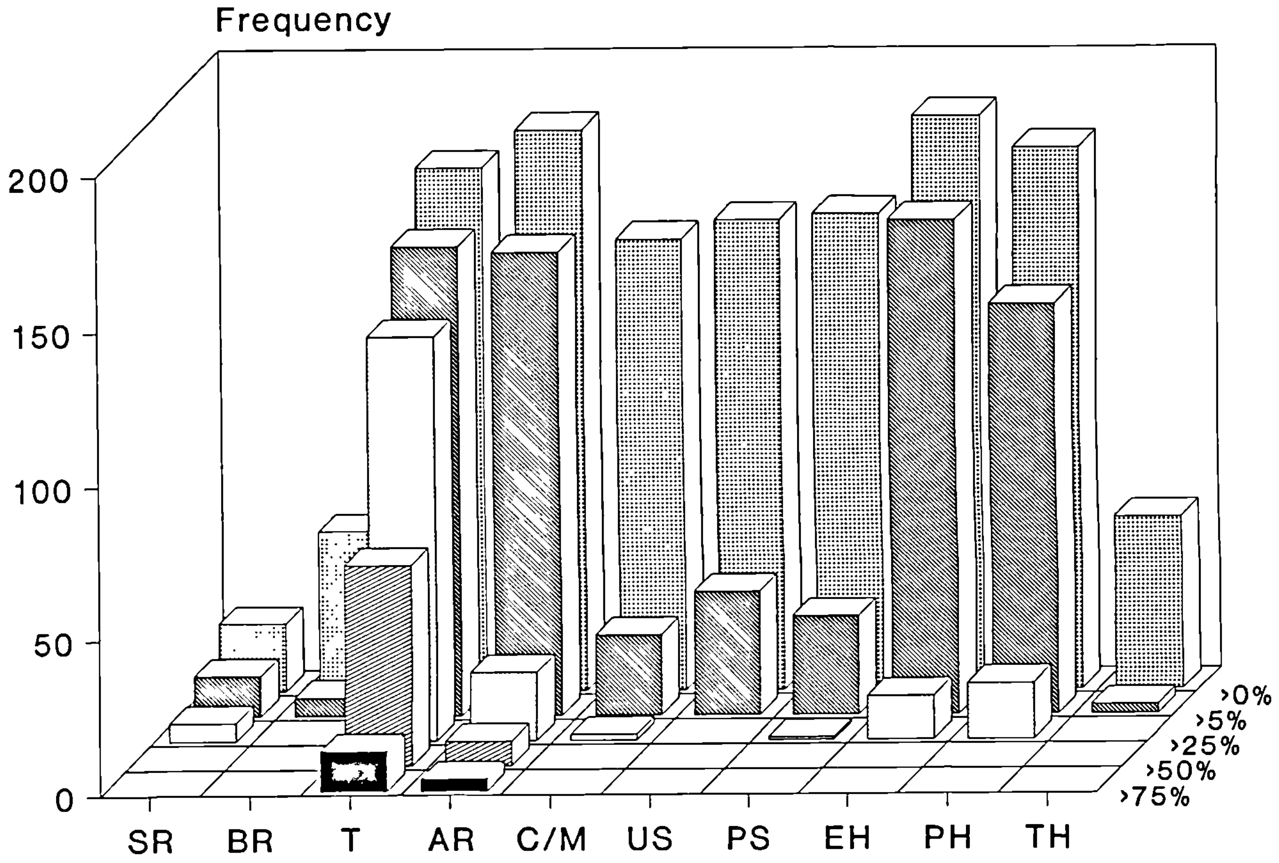


Figure 3.11.
The growth form composition of in 192 samples of Ecuadorian páramo vegetation. The frequency of each growth form is shown cumulatively for five cover values. [SR, Stem Rosettes; BR, Basal Rosettes; T, Tussocks; AR, Acaulescent Rosettes; C/M, Cushions; US, Upright Shrubs; PS, Prostrate Shrubs; EH, Erect Herbs; PH, Prostrate Herbs; TH, Trailing Herbs]

Figure 3.12 shows the CANOCO biplot for the ten growth forms with the environmental variables superimposed on the ordination. The growth forms are well separated in the ordination space along a number of planes, which demonstrates a complex relationship with the environmental variables.

Stem rosettes and basal rosettes have their optima in the lower right portion of the ordination. This area can be partially characterised by relatively high exposure scores and low bare ground coverage. Disturbance, altitude and rock cover appear to be poorly correlated to their presence. However, none of the environmental variables

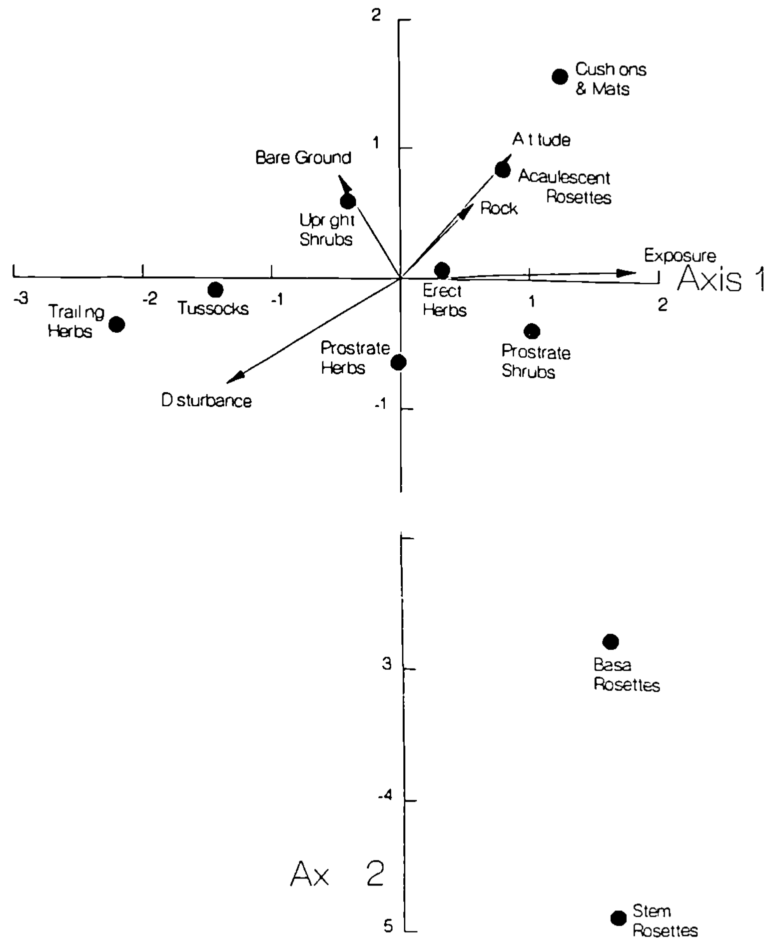


Figure 3.12.
CANOCO biplot ordination of the ten growth forms recorded in 192 samples of páramo vegetation. Environmental variables are depicted as solid arrows. The axes are divided into standard deviation units ($\lambda_1 = 0.057$, $\lambda_2 = 0.026$). To the left-hand side of the ordination, trailing herbs and tussocks are located, characterised by lower altitudes, higher disturbance levels, less rock cover and lower exposure scores. By contrast, cushions, and to a lesser extent acaulescent rosettes have their optima at higher altitudes, with higher exposure levels, more rock cover and less disturbance.

measured in this study explains the distribution of stem and basal rosettes satisfactorily.

Tussocks and trailing herbs are found on the left-hand side of the ordinaton and are associated with plots of low exposure and relatively high disturbance. High altitude with comparitively high rock cover characterises the plots containing acaulesent rosettes, and cushions and mats.

Erect herbs, prostrate herbs, prostrate shrubs and upright shrubs are located around the origin of the ordination and are not, therefore, associated with extremes of any of the studied environmental variables.

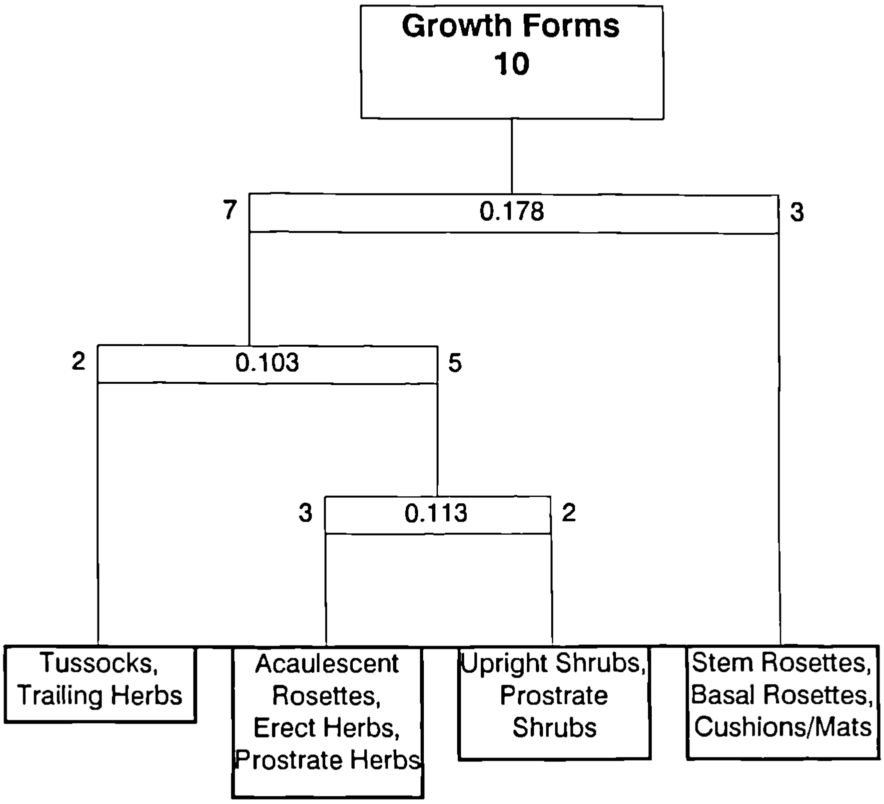


Figure 3.13.
TWINSPAN classification of the ten growth forms recorded in 192 páramo vegetation samples. Those growth forms which show similar distributions in these samples are grouped together. Four groups resulted from the classification. The eigenvalue, which gives an indication of the importance of each division, is shown directly beneath each division. The number of growth forms in each group is provided either side of a division.

Using TWINSPAN, the growth forms were grouped together according to their similarity of distribution throughout the 192 páramo samples. The results of this analysis are depicted in Figure 3.13.

The first division of the ten growth forms separates a group containing the stem rosettes, basal rosettes and cushions from the remainder. Of the remaining seven forms, tussocks and trailing herbs showed a linkage in distribution, as did the upright shrubs and prostrate shrubs. The final association consisted of the acaulescent rosettes, erect herbs and prostrate herbs.

The páramo samples were analysed by virtue of their growth form composition, both with TWINSPAN and CANOCO. The TWINSPAN classification of the 192 páramo quadrats in terms of growth form is shown in Figure 3.14. Twelve groups resulted from the TWINSPAN classification. Each class contained at least six of the ten growth forms, while two had the full complement of ten. The usual number (and mean) was eight growth forms. It is clear from this that the differences in composi-

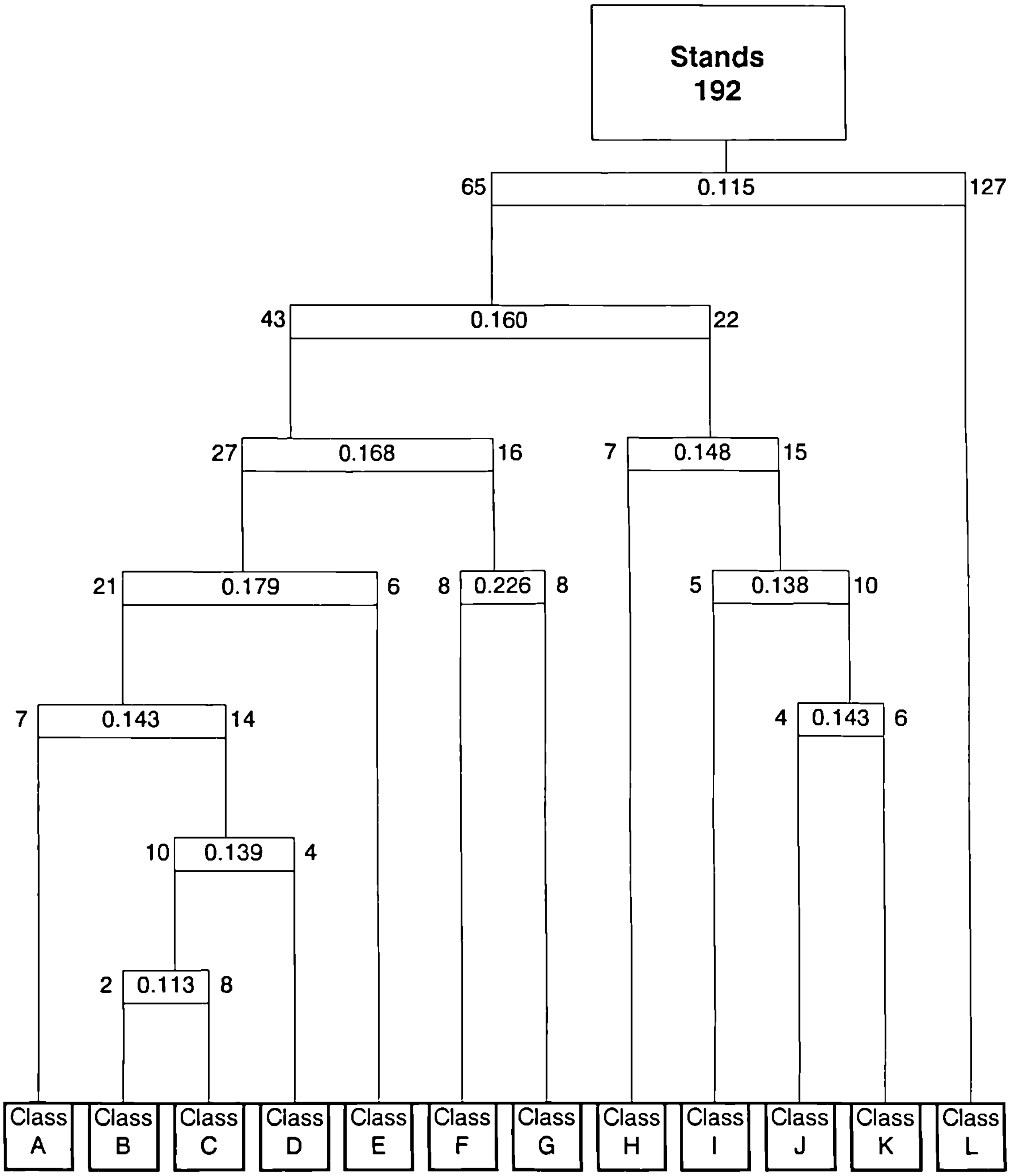
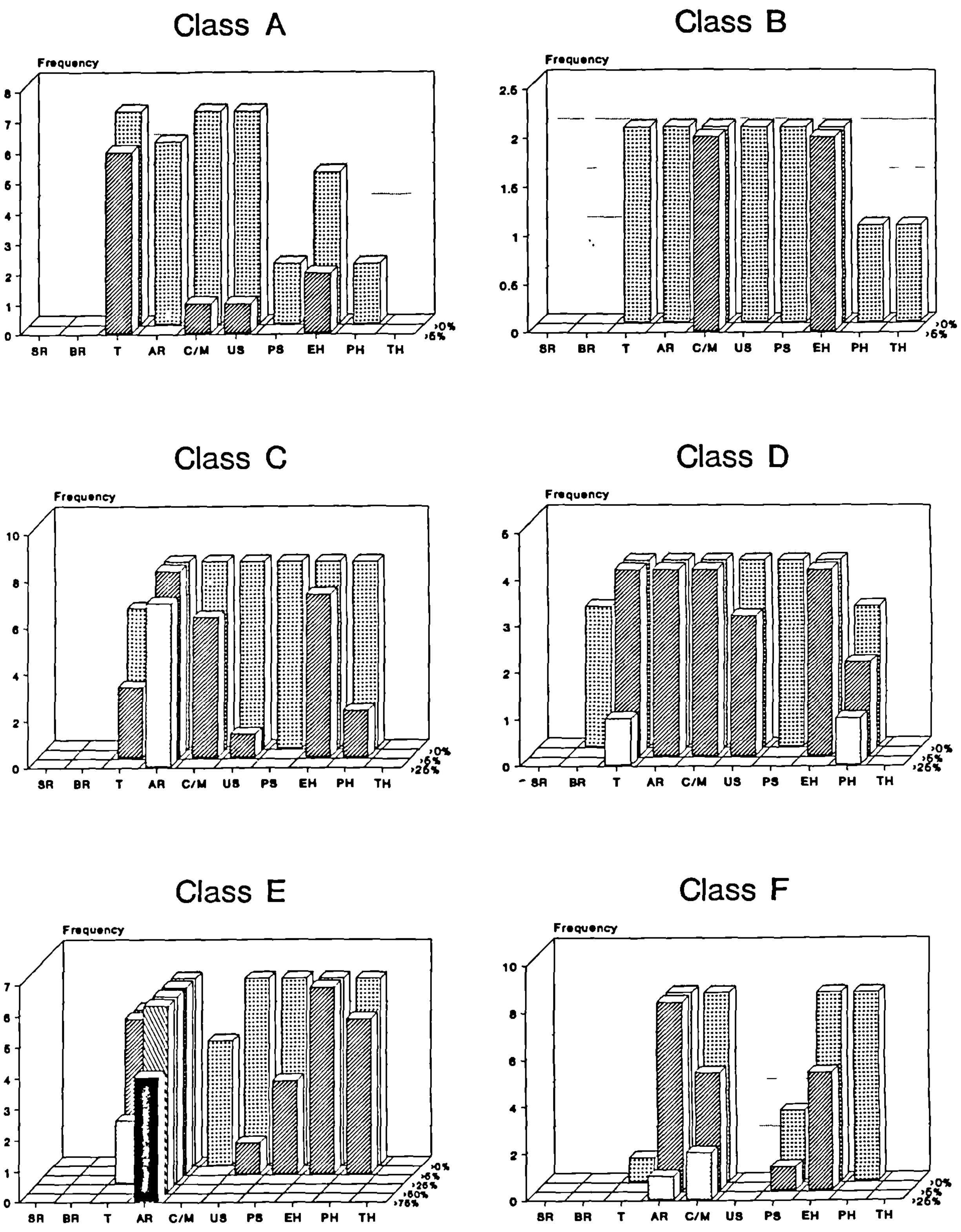


Figure 3.14.

TWINSPAN classification of 192 samples of páramo vegetation according to growth form composition. The composition of each of the twelve end groups is described in detail in the text. The eigenvalue, which gives an indication of the importance of each division, is shown directly beneath each division. The number of stands in each group is provided either side of a division.



Class A

Class B

Class C

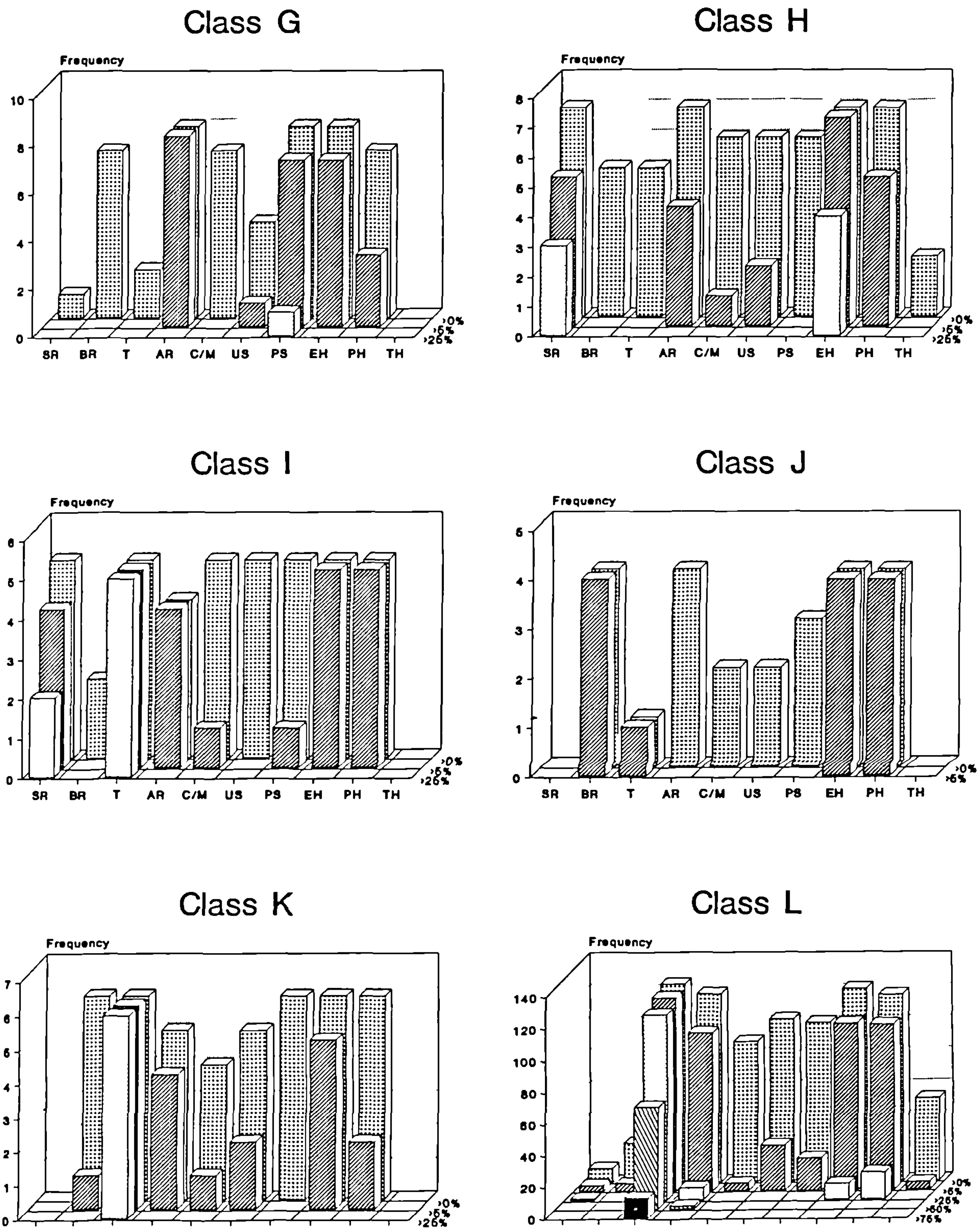
Class D

Class E

Class F

Figure 3.15.

The growth form composition of the twelve groups defined by TWINSPAN from 192 samples of páramo vegetation. KEY: SR Stem Rosettes; BR Basal Rosettes; T Tussocks; AR Acaulescent Rosettes; CM Cushions/Mats; US Upright Shrubs; PS Prostrate Shrubs; EH Erect Herbs; PH Prostrate Herbs; TH Trailing Herbs.


Class G

Class H

Class I

Class J

Class K

Class L

Figure 3.15. (Continued)
The growth form composition of the twelve groups defined by TWINSPAN from 192 samples of páramo vegetation.

tion were largely in terms of the relative abundances of the growth forms rather than their presence or absence from the stands.

The growth form composition of each of the twelve TWINSPAN classes is shown in detail in Figure 3.15, and their distribution throughout the study areas indicated in Figure 3.16.

Class A (7 stands)

The plots belonging to this group were all located on Volcán Chimborazo (two at 4,600 m, one at 4,500 m, two at 4,400 m, one at 4,300 m and another at 4,000 m). All of the plots had a sparse cover of vegetation, consisting of tussocks (5-25% cover) with cushions, and upright shrubs (both growth forms with up to 25% cover). Acaulescent rosettes were present in six stands (<5% cover), erect herbs in five (<25% cover), with a sparse cover of prostrate shrubs and prostrate herbs (each <5% cover).

Class B (2 stands)

One stand at 4,200 m on Volcán Chiles and another at 4,400 m on Volcán Chimborazo were grouped by the TWINSPAN analysis. Cushions, and erect herbs were recorded in both plots with a cover of more than 5%. Accounting for less than 5% cover, tussocks, acaulescent rosettes, upright shrubs and prostrate shrubs were found in both stands, whilst prostrate herbs and trailing herbs were only present in one stand each.

Class C (8 stands)

This group comprised three plots from 4,200 m on Volcán Cotacachi, one from 4,200 m and another from 4,100 m on Volcán Chiles, and one plot from 4,200 m and another two from 4,100 m on the eastern slopes of El Altar. Acaulescent rosettes were dominant, with a cover of greater than 25% in most cases. Prostrate herbs and erect herbs occurred in all of the stands, sometimes with more than 5% cover. Prostrate shrubs and upright shrubs were also present in all of the stands, though responsible for less than 5% of the ground cover in most cases. Cushions frequently accounted for 5-25% cover. Tussocks were found in the majority of the samples, with a cover of up to 25%.

Class D (4 stands)

One plot at 3,400 m in the páramo of Cumbe, one at 4,200 m in the páramo of Guamaní, one at 4,200 m and another at 4,100 m on Volcán Chiles made up Class D. All of the plots had a cover of 5-25% tussocks, and in one quadrat, tussocks were responsible for 25-50% cover. All four stands were vegetated by acaulescent rosettes, cushions, and erect herbs (5-25% cover each), with lesser coverage by upright shrubs and prostrate shrubs. Prostrate herbs were present in three of the samples and reached more than 25% cover in one. Basal rosettes were also recorded in three of the plots, but with less than 5% cover.

Class E (6 stands)

Three plots at 4,200 m on the western side of El Altar, two plots at 4,000 m in the páramo of Daldal and one quadrat at 4,300 m in the páramo of Guamaní were dominated by acaulescent rosettes. In all of the stands, they covered over 50% of the ground, and in two-thirds of cases more than 75%. Erect herbs were present in all of the stands and covered 5-25% of the area in three plots. Prostrate herbs, prostrate shrubs and upright shrubs were also found in all of the stands, each with a cover of up to 25%. The majority of the plots had a cover of tussock plants, sometimes in excess of 25%.

Class F (8 stands)

Eight stands were grouped together by TWINSPAN in this growth form class (three at 4,400 m in the páramo of Guamaní, three at 4,300 m and two at 4,200 m on the eastern flank of El Altar). Cushions were present in all of the stands, and in over half of them covered 5-25% of the ground surface and in a quarter covered more than 25%. Acaulescent rosettes (5-50% cover), erect herbs (up to 25% cover) and prostrate herbs (< 5% cover) formed the remainder of the vegetation cover. Prostrate shrubs were recorded in three samples with up to 25% cover. Tussocks were present in only one plot, with a cover of less than 5%. Upright shrubs were completely absent.

Class G (8 stands)

On Volcán Tungurahua, in all three quadrats at 4,000 and at 4,100 m, one at 4,200 and another at 4,300 m, the vegetation was similar in many ways to that described for Class F: acaulescent rosettes covered 5-25% of the ground, erect herbs up to 25% and prostrate herbs less than 5%. Cushions were less conspicuous, responsible for less than 5% cover. Prostrate shrubs were present in all of the stands and accounted for more than 5% cover in all but one. Prostrate herbs were also present in three of the quadrats. Basal rosette plants were recorded in seven of the eight plots, but covered less than 5% in every case. Upright shrubs, contributing up to 25% cover, were recorded in half the samples belonging to this class. Again, tussocks were rare members of the community.

Class H (7 stands)

Four stands on Volcán Tungurahua (three at 3,900 m and one at 4,200 m) and three on Volcán Chiles (all at 3,900 m) had a similar growth form composition. Stem rosettes and erect herbs were present in all of the samples, sometimes covering more than 25% each of the plot's area. The other growth forms, present in the majority of samples, were basal rosettes (< 5% cover), tussocks (< 5% cover), acaulescent rosettes (< 25% cover), cushions (< 25% cover), upright shrubs (< 25% cover), prostrate shrubs (< 5% cover) and prostrate herbs (< 25% cover). Trailing herbs were recorded in two of the plots with minimal cover.

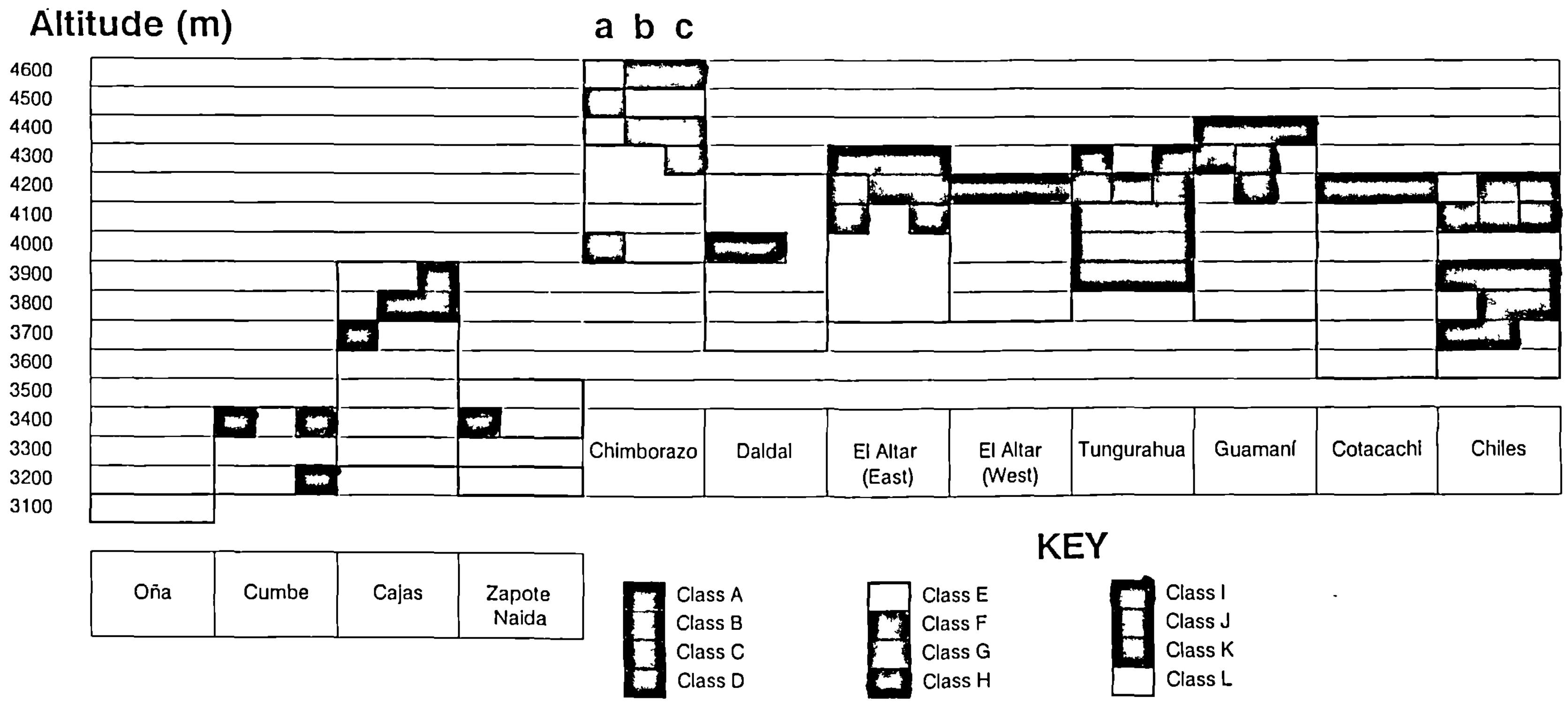


Figure 3.16.
The distribution of the 12 TWINSPAN growth form classes which are defined and described in detail in the text (cross-referenced by the letter code). All 192 vegetation samples are colour-coded.

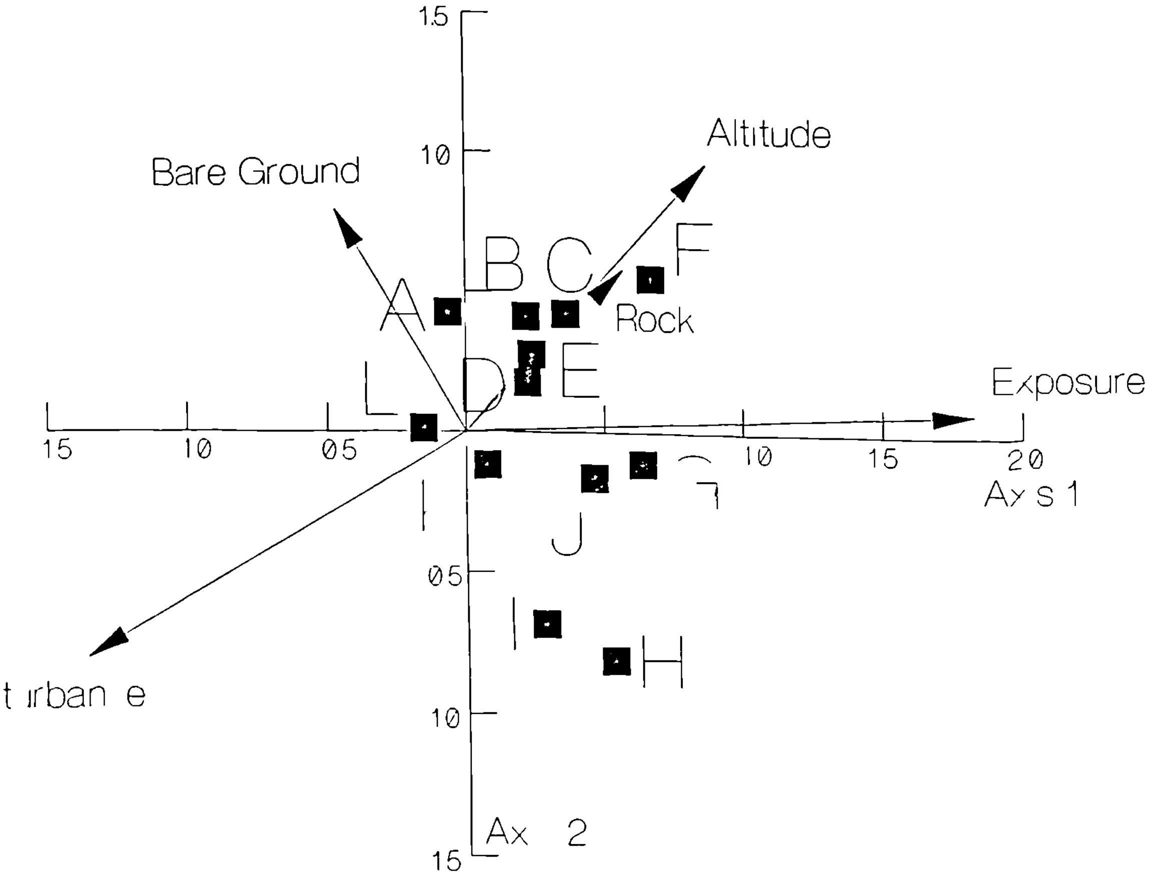


Figure 3.17.
CANOCO biplot ordination of the twelve growth form classes defined by TWINSPAN from 192 samples of páramo vegetation. The axes are divided into standard deviation units ($\lambda_1 = 0.057$, $\lambda_2 = 0.026$).

Class I (5 stands)

Four samples from Volcán Chiles (two from 3,700 m and two from 3,800 m) and a fifth from 3,400 m in the páramo of Zapote Naida, were notable for the presence of stem rosettes (with a cover up to 50%). Co-dominant were tussocks (25-50% cover), and the other growth forms recorded were prostrate shrubs (up to 25% cover), cushions (up to 25% cover), erect herbs (5-25% cover), prostrate herbs (5-25% cover) and upright shrubs (< 5% cover). Acaulescent rosettes (5-25% cover) and basal rosettes (< 5% cover) were found in four and two of the five stands, respectively.

Class J (4 stands)

Two plots on Volcán Tungurahua (one at 4,300 m, the other at 4,200 m), one plot at 4,300 m in the páramo of Guamaní, and a fourth plot at 4,100 m on Volcán Chiles comprised another TWINSPAN group. Prostrate herbs, erect herbs and basal rosettes each covered more than 5% of the area of all plots. Acaulescent rosettes were also recorded in all of the samples, but with a cover of less than 5%. In addition, cushions, upright shrubs and prostrate shrubs were all present in at least half of the plots, with a cover of less than 5%.

Class K (6 stands)

Six plots were dominated by tussocks (25-50% cover). They were located at 4,000 m, 3,900 m (two) and 3,800 m in the páramo of Cajas, and at 3,400 m and 3,200 m in the páramo of Cumbe. Basal rosettes (<5% cover), prostrate shrubs (<5% cover), erect herbs (<25% cover) and prostrate herbs (<25% cover) were present in all samples, and acaulescent rosettes, cushions and upright shrubs were recorded in the majority of the plots, each with up to 25% cover each.

Class L (127 stands)

The remaining 127 stands were included in the largest TWINSPAN group, representing two-thirds of the samples. All ten growth forms were present in this class, though stem rosettes, with up to 50% cover, were found in only nine plots. The most notable feature of this group was the dominance of tussocks, occurring in all but two of the plots and covering over 75% in some samples. Acaulescent rosettes, erect herbs and prostrate herbs were also strongly represented, each accounting for up to 50% cover in the majority of plots. Responsible for up to 25% cover in most samples in this group, upright shrubs, prostrate shrubs and cushions formed a significant part of the growth form community. Basal rosettes were only present in 25 stands, exceeding 5% cover in some of these. Finally, trailing herbs were recorded in 53 plots (only three plots outside this class were found to have this growth form). In the majority of cases, the coverage of trailing herbs was less than 5%, though this was surpassed in three plots.

The twelve classes described above were super-imposed on the CANOCO biplot (Figure 3.17). Most of the classes were clustered around the origin of the ordination, confirming their overall similarity of composition. However, Classes I and H were located away from the main cluster, towards the position occupied by the stem rosettes and basal rosettes. This indicates the importance of these forms in Classes I and H. In the same way, Classes F, C, B and E were situated in the upper right sector of the plot, indicating the predominance of cushions & mats and acaulescent rosettes. Class L was sited close to the origin (as expected for the group representing two-thirds of the samples), but towards the left-hand side, dominated by tussocks and trailing herbs.

Discussion

In Hedberg's (1964) growth form classification, 55% of the flora were not classified. Hedberg (1992) maintains that although many páramo plants cannot be assigned to one of the five forms in his system, all of the dominant plants can. Mena & Balslev (1986), using the Hedberg classification, concluded that those species which did not fit amounted to very little cover. It is interesting to find, therefore, that the additional growth form categories used in this study do account for a significant part of the vegetation cover. In particular, erect herbs and prostrate herbs covered 5-25% of the sample area in the majority of plots. By comparison, stem rosettes and basal rosettes were much less frequent and abundant members of the Ecuadorian páramo communities.

It may be that this shift of emphasis in growth forms accompanies the change from stem rosette-dominated páramos in the north to the grassy páramos of Ecuador and northern Perú in the south. However, erect and prostrate herbs were significant elements of even the stem rosette communities (Classes H & I) of Volcán Chiles.

Clearly, for a full and illuminating comparison of páramo regions within the Andes (and more so for inter-continental comparisons), the full growth form spectrum should be investigated. Merely because certain growth forms do not appear to be adapted to the high altitude environment does not mean that they are not so. In fact, their very presence must mean that they are successfully tackling the problems of such environments. Furthermore, by omitting a large part of the flora from a growth form classification system, important differences may be overlooked.

According to Mooney (1974), there is an optimal dominant growth form for a given climatic-substrate-successional combination. Further, he suggests a similar degree of convergence in the subordinate units of vegetation. On this assumption, one would expect to find a high degree of growth form similarity in the 192 páramo stands sampled in this study. This is indeed the case, as evidenced in Table 3.1. In most of the study areas, the average number of growth forms per plot was found to be between 6 and 7, with the overall average 6.73. Examination of Figure 3.11 reveals that stem rosettes, basal rosettes and trailing herbs were generally absent. The dominant growth form was the tussock. It was responsible for more than 50% of the vegetative cover in one-third of the samples, and more than 25% in two-thirds.

The similarity of composition of the samples was also demonstrated by the TWINSPAN and CANOCO analyses, with low eigenvalues indicating little variation between plots.

However, some differences were evident. The TWINSPAN classification resulted in twelve groups of stands according to growth form composition. One group, Class L, contained about two-thirds of the samples and represented the most widespread growth form composition. Tussock grasses were clearly dominant and associated with them were trailing herbs present in 53 plots. Acaulescent rosettes, erect herbs, prostrate herbs, upright shrubs, prostrate shrubs and cushion plants were all strongly represented in this group.

A group of six stands, all found in the southern páramo regions (Class K), was very similar to the large group just described. It differed in that tussocks, though still dominant, were less abundant and trailing herbs were absent. Basal rosettes were present in all of the plots but accounted for less than 5% of the cover.

In four samples from the humid northern páramo of Volcán Chiles and one from Zapote Naida in the south (Class I), tussocks were co-dominant with stem rosettes.

In other parts of Volcán Chiles and on Volcán Tungurahua, stem rosettes were dominant in their own right, with tussocks accounting for less than 5% cover (Class H).

The remaining eight groups of samples were typically from plots with extreme conditions where tussock grasses were less abundant, generally at higher altitudes.

In places where such extremes restricted plants to microhabitats which permitted establishment and growth, dominance of a single growth form was rare. In the arid conditions of the Grande Arenal de Chimborazo, a number of samples showed co-dominance of tussocks, cushions and upright shrubs (Class A). Another plot from Volcán Chimborazo was similar to a sample of vegetation from the highest altitude sampled on Volcán Chiles (Class B). Although eight growth forms were present, only erect herbs and cushions were able to exceed 5% cover.

Where a more continuous vegetative cover existed at high altitudes, the dominant growth form was often the acaulescent rosette. In Class D, which consisted of plots from the páramos of Cumbe, Guamaní and Volcán Chiles, acaulescent rosettes were co-dominant with tussocks, cushions and erect herbs. Class C was more clearly dominated by acaulescent rosettes with tussocks, cushions and erect herbs subordinate members of the community. In the six samples of Class E from the páramos of El Altar (west), Daldal and Guamaní, acaulescent rosettes accounted for over 50% of the vegetative cover (more than 75% in half of these plots).

In some páramo regions, above the vegetation dominated by acaulescent rosettes, cushion plants became co-dominant (Class F). Upright shrubs which were present in the lower altitude vegetation were not found and tussocks were rare. This vegetation consisted of only six growth forms, the fewest of all the TWINSPAN groups.

On Volcán Tungurahua, much of the vegetation (Class G) showed a similar composition to that of higher altitudes elsewhere. Acaulescent rosettes were once again co-dominant, this time with erect herbs and prostrate herbs. Basal rosette plants were present in almost all samples in this group.

The co-dominance of basal rosettes, erect herbs and prostrate herbs characterised the vegetation of plots from Volcán Tungurahua, Volcán Chiles and the páramo of Guamaní (Class J).

From the CANOCO analysis, it is evident that altitude, and environmental variables closely correlated to it (for example, rock cover and disturbance), were related to the distribution of acaulescent rosettes and cushions. These low stature plants are probably confined to high-altitude, rocky sites by competition from other species for light. *Plantago rigida* has been grown in a more favourable greenhouse environment in the absence of competition from other species (personal observation). A later chapter will examine the nature of the relationship between this species and *Calamagrostis* tussocks.

Tussocks and trailing herbs (which relied heavily on the tussocks for physical support) tended to occur more frequently in stands at lower altitudes, subjected to higher disturbance.

According to Bliss (1971), cushions and mats increase and tussocks and acaulescent rosettes decrease as the environment becomes more severe. This supports the results of the current study.

To summarise , the growth form composition of the Ecuadorian páramos can be described as follows:

- The majority of páramo vegetation is dominated by tussocks. The accompanying growth forms are mostly acaulescent rosettes, cushions, upright shrubs, prostrate shrubs, erect herbs and prostrate herbs, sometimes with stem rosettes, basal rosettes or trailing herbs.
- At higher altitudes, the dominance of tussocks is reduced. At first, acaulescent rosettes become dominant, but at yet higher altitudes their dominance is shared with cushions. At the highest altitudes of all, where plant cover is thin, no single growth form is dominant.
- In other locations where plant cover is sparse, once again no single growth form is dominant.
- In humid páramos, stem rosettes may be co-dominant with tussocks or erect herbs. Basal rosettes, erect herbs and prostrate herbs may be locally co-dominant at higher altitudes.

In terms of percentage cover, prostrate shrubs, erect herbs and prostrate herbs are as important as upright shrubs and giant rosettes, but less conspicuously so. They also account for a large proportion of the species present in the páramo. Their persistence in the páramo environment implies that strategies other than those of Hedberg's five forms are successful and deserve attention. Therefore, it is suggested that all growth forms are considered in future páramo studies, at least in Ecuador.

Both basal and stem rosettes were present in stands with the least bare ground. Miller (1987b) reports that establishment of *Puya clava-herculis* (a basal rosette species) in the Ecuadorian páramo was reduced on bare, exposed soil, and even more so in vegetation dominated by cushions and mats.

However, the environmental variables which were measured did not explain the distribution of stem and basal rosettes satisfactorily. Miller & Sillander (1991) suggest that the upper elevational limit of *Puya clava-herculis* (a basal rosette species) in the páramo of Virgen, Ecuador, is due to the combined effects of physiological drought and low temperatures. Similar explanations have been offered to explain the distribution of *Espeletia* species (stem rosettes) in other páramo regions of the Northern Andes (Fariñas & Monasterio, 1980; Perez, 1987).

Billings (1973) linked the local distribution of growth forms in the equatorial alpine region to the availability of soil moisture: graminoids in the wetter sites, acaulescent rosettes and cushions in drier sites (and ridges, rocky places and disturbed sites) and prostrate shrubs along the whole moisture gradient.

According to Barkman (1988), plant forms which grow together can be expected to have some similarity in their physiology. In the Ecuadorian páramo, four groups of such forms were determined (Figure 3.13), such as that containing acaulescent rosettes, erect herbs and prostrate herbs. The CANOCO analysis did not place members of the same group close together in the ordination. This provides more evidence that additional environmental factors are important in determining the distribution of growth forms in the páramo.

In particular, soil characteristics, climatic features (especially measures of temperature and atmospheric humidity) and studies of plant water balance may yield interesting relationships with plant forms in the Andes. The next section in this chapter looks at morphological adaptations to temperature in the páramos of Ecuador.

III. Temperature Characteristics of Major Growth Forms in the Ecuadorian Páramos

Introduction

High elevation tropical grasslands have often been used as an example of convergent evolution (for example, Monasterio, 1986). Accepting Fisher's (1930) view that "no character is likely to remain immune from selection for very long", the structure and form of tropicalpine plants can be considered to be adapted to the prevailing environment. Similar selective agents in East Africa and the Andes, for example, will give rise to plants that are ecologically equivalent and therefore alike in form and function.

One striking aspect of the tropicalpine environment which differentiates it from other alpine and arctic regions is the diurnal temperature climate. "Summer every day and winter every night" (Hedberg, 1964) present unique problems to tropicalpine plants. Temperature and its effects on water balance have been repeatedly used to explain convergent evolution (Walter, 1973; Carlquist, 1974; Hedberg, 1964; Hedberg & Hedberg, 1979; Monasterio, 1986).

Wind induced cooling and water stress has been implicated in delayed flowering in *Hypericum laricifolium* (Smith, 1972). Differences in the responses of plants to wind in the páramo are closely correlated with differences in their growth form (Smith, 1972).

It is usually the reproductive organs of a plant that are most sensitive to chilling and frost (Larcher & Bauer, 1981). Miller (1987a) carried out detailed observations of the temperature relations of *Puya* inflorescences.

Hedberg & Hedberg (1979) presented temperature records for five species, each representing one of Hedberg's (1964) growth forms, in the Venezuelan páramo in Mucubají, Mérida. The evidence was seen to support the hypothesis that the various growth forms represent different strategies to maintain the water balance in the tropicalpine environment. Pfitsch (1988) stated that of Hedberg's five growth forms that characterise the páramos, only sclerophyllous shrubs have no morphological means of moderating the temperature extremes experienced by growing plant tissues.

Similar temperature measurements to those collected by Hedberg & Hedberg (1979) were carried out in an Ecuadorian páramo over a 24 hour period.

Methods

Study Site

This study was carried out in the páramo on the slopes of Volcán Chiles, about 38km from Tulcán (0°47'N 77°57'W), near or in a boggy depression just below 4,000m. Øllgaard & Balslev (1979) visited the site during the third Danish botanical expedition to Ecuador in 1976 (Location 23) and described it floristically.

The area was not far from the three quadrats used to sample the vegetation at 4,000m in the phytosociological study of Volcán Chiles (one of the sites used in Chapter 2 and the previous section of this chapter).

Temperature Measurements

A Comark 2007 digital thermometer equipped with thermocouples (wire and probe attachments) were used to record temperatures of the plants at various positions within their structure. Measurements were also carried out to provide contemporaneous records of air and soil temperature near the plants involved in the study.

The measurements taken were as follows (a wire thermocouple was used unless stated otherwise):

Ambient Air	Measured at 1.5 m above ground surface, shielded from the sun.
Ambient Soil	Measured at 100 mm below ground surface using a probe thermocouple.
Giant Stem Rosettes	*Espeletia pycnophylla* ssp. *angelensis* Centre of flowers Surface of stem beneath marcescent leaves Surface of stem lacking marcescent leaves Surface of living leaf
Tussock Plants	*Calamagrostis* sp. [251] Air between leaves at base of tussock Air between leaves in upper part of tussock *Cortaderia sericantha* Air between leaves at base of tussock Surface of inflorescence

Acaulescent Rosettes

- *Valeriana bracteata*
  - Surface of basal leaf
  - Surface of flower
- *Senecio* sp
  - [voucher no. 847 in Ramsay & Merrow-Smith 1987 collection, corresponding to the "pretty Senecio with large solitary nodding heads" (no. 8450) in Øllgaard & Balslev, 1979.]
  - Surface of basal leaf
  - Surface of flower
- *Oritrophium peruvianum*
  - Surface of basal leaf
  - Surface of flower

Cushion Plants

- *Werneria humilis*
  - Surface of rosette
  - Cushion at 100 mm depth (using probe)
- *Oreobolus obtusangulus*
  - Surface of mat
- *Plantago rigida*
  - Surface of rosette
  - Cushion at 100 mm depth (using probe)

Upright Shrubs

- *Loricaria ilinissae*
  - Tip of branch
- *Pentacalia stuebellii*
  - Tip of branch
- *Hypericum* sp. [coll no. 915]
  - Tip of branch
  - Centre of flower
- *Pentacalia andicola*
  - Tip of branch
  - Air within interior of shrub

Erect Herbs

- *Jamesonia* sp [coll no 861]
  - Apex of stalk
- *Lycopodium* sp [coll no. 859]
  - Apex of stalk
- *Perezia pungens*
  - Surface of stem
  - Centre of flower
  - Centre of unopened flower bud
- *Castilleja* sp [coll no. 946]
  - Centre of flower
- *Culcitium ovatum*
  - Surface of stem
  - Centre of flower

The measurements were taken on the 20th and 21st of October 1987, with five records over the 24 hour period: on the first day at 14.30 and just after sunset at 18.30, then on the second day at 01.30, 05.30 (just before sunrise) and finally at 13.30. It was clearly impossible to measure all plants simultaneously and so these times mark the start of the temperature recording sessions. These sessions followed a precise sequence from plant to plant.

Over the course of this study, the sky was overcast during the day and for most of the night, with intermittent drizzle, though occasional patches of clear sky appeared during darkness hours.

Results

The ambient air temperature reached a maximum of 8.9°C at 14.30 hrs on the first day. This temperature fell quickly after sunset (approximately 18.00 hrs) to 5.0°C and reached a minimum of 3.7°C at 05.30 hrs on the following day (approximately half an hour before sunrise). Air temperature rose quickly after sunrise, and by 13.30 hrs had reached 7.3°C.

The temperature of the soil 100 mm beneath the surface showed little variation. The maximum temperature was 6.9°C in the early hours of the second day, and the minimum temperature was 6.4°C at 13.30 hrs later the same day. Clearly, there is a considerable delay in warming up and cooling down at this depth.

The temperature measurements for the plants are described below.

Giant Stem Rosette

Espeletia pycnophylla spp. *angelensis* was the only species examined which belonged to this growth form. Unlike some of the other species of *Espeletia*, *E.pycnophylla* spp. *angelensis* does not appear to exhibit nyctinasty (the closure of the leaves around the leaf buds at night). The thermocouple measurements relating to this plant are presented in Figure 3.15.

In general plant parts were found to follow the ambient air temperature closely at night. During the day, however, their temperatures were at times more than 10°C above the air temperature.

Flower temperatures were high during the day (about 14°C) but dropped considerably at night, to below the ambient air temperature at 01.30 hrs. The flower temperatures showed oscillations of up to 11.2°C over the 24-hour period.

The leaves of *Espeletia* remain fixed to the stem after death (marcescence). The majority of specimens in this area lacked marcescent leaves on the lower portion of their stems as a direct consequence of burning. The insulating effect of marcescent leaves was demonstrated by the reduced amplitude of the stem temperature beneath the mantle of dead leaves (9.9°C) compared to the temperature of part of the stem which lacked them (18.8°C). This was largely the result of the higher daytime temperatures of the bare stem (which was black because of charring). The marcescence did maintain the stem temperature slightly above the ambient air temperature during the night.

Examination of the temperatures for the living leaves revealed a similar pattern to that exhibited by the stem clothed by dead leaves, namely, a reduction of extreme, high temperatures in the daytime and the maintenance of a slightly higher temperature than the air at night.

Tussock Plants

Two species of tussock grasses were represented in this study, *Calamagrostis effusa* and *Cortaderia sericantha* (Figure 3.16). The former species is found as the co-dominant over most of the area, the latter is a common element of the flora in boggy areas.

The upper portion of the *Calamagrostis* tussock was found to maintain a high temperature (close to 15°C) in the trapped air between the leaves. The amplitude of the measurements taken was 10.6°C. Lower down the tussock in the dense base, the amplitude was half this range (5.3°C). The air between the basal parts of the leaves cooled more slowly after darkness fell and was not subjected to temperatures above 10°C over the entire 24-hour period.

Even the extremes of temperature of the ground surface between the tussocks were reduced, remaining slightly above the ambient air temperature throughout the night.

Cortaderia sericantha has a more open tussock structure. In some respects, the basal portion of the *Cortaderia tussock* is most similar to the upper (rather than the lower) portion of the *Calamagrostis* tussock; sunlight penetration and air circulation are greater. Thus, daytime temperatures are in excess of 15°C in the bases of the *Cortaderia tussock.* At night the leaf bases were found to be approximately 1.5-2.0°C higher than the corresponding air temperature. The inflorescence temperatures follow closely the air temperature.

Acaulescent Rosettes

Three species inhabiting the boggy area were used as representatives of the acaulescent rosette form: *Oritrophium peruvianum, Valeriana bracteata* and *Senecio* sp. [847]. The flower temperatures of the former two species were observed to be approximately 0.5-1.0°C higher than the air temperature at night (Figure 3.17). The taller flower of *Senecio* sp. followed the air temperature closely for most of the study period, falling below it at one time during the night.

The basal rosettes of the three species were higher than the ambient air temperature at all times over the course of the 24-hour study. In particular, the basal rosette of *Senecio* sp. was strikingly higher than the air temperature at night, by some 2-3°C.

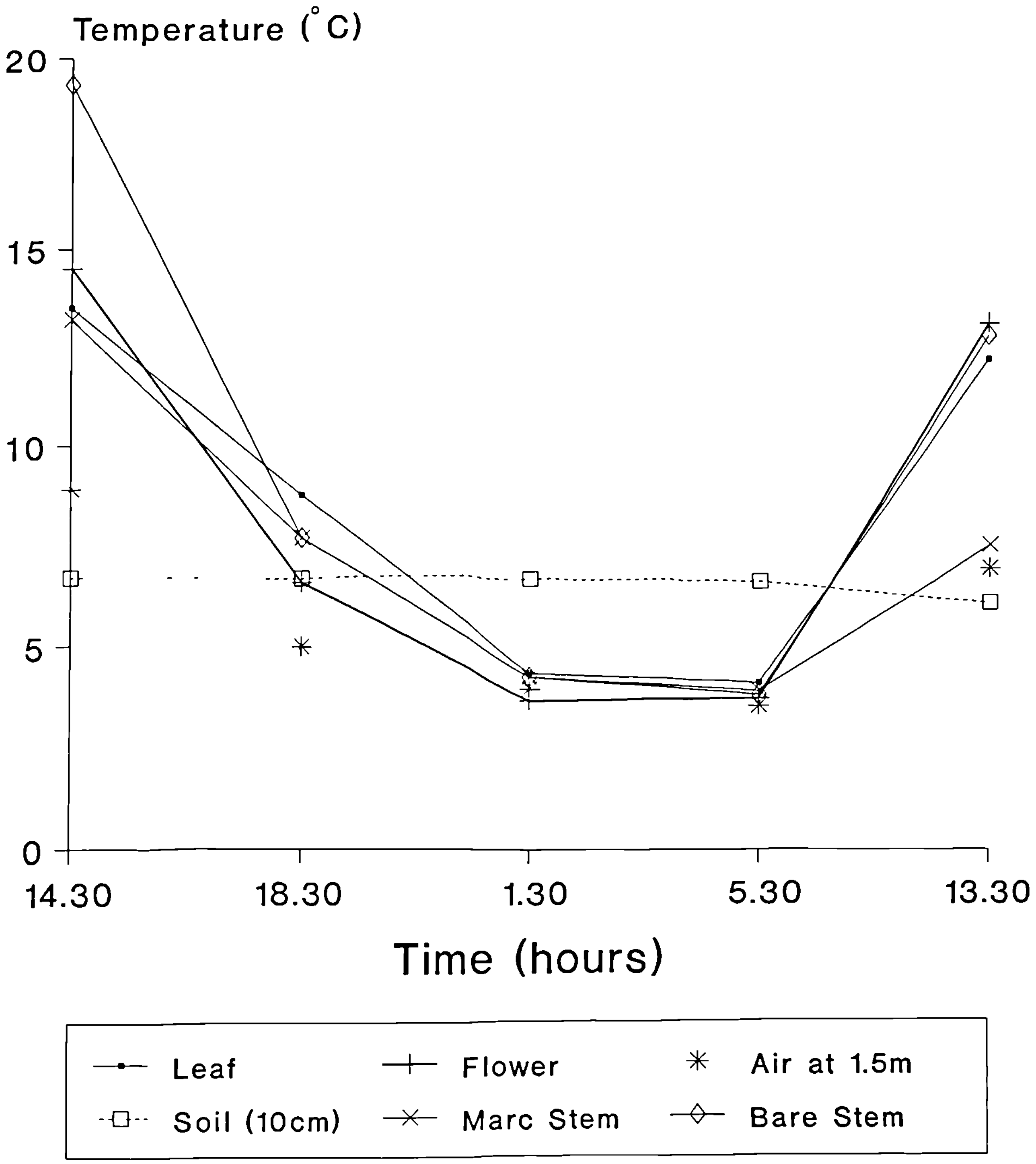


Figure 3.18.
Temperature variation over 24 hours at a number of measuring points on *Espeletia pycnophylla* ssp. *angelensis* at 4,050m in the páramo of Volcán Chiles. The points measured were the flower disc, upper leaf surface, the surface of the stem clothed in dead leaves ('Marc Stem') and the surface of the bare stem. Air and soil temperatures are also shown.

Cushion/Mat Plants

Two species of cushion plant (*Werneria humilis* and *Plantago rigida*) and one mat species (*Oreobolus obtusangulus*) formed the basis for the examination of these growth forms (Figure 3.18).

The surfaces of all the cushion and mat species follow roughly the same pattern. During the day, temperatures were high, in some cases in excess of 20°C. At night, temperatures were higher than the surrounding air temperature by about 0.5-3.0°C.

At 10cm depth in the two cushion species, temperatures were conspicuously constant at about 9°C, less variable than that of the waterlogged soil surrounding them.

Upright Shrubs

Figure 3.19 presents the temperature data collected for four species of shrub: *Loricaria ilinissae, Pentacalia stuebellii, Hypericum ? strictum* and *Pentacalia andicola.* A similar pattern of temperature variation was observed for all four species. At night, the tips of the branches were almost always slightly above the air temperature, while by day they were often 5-10°C higher than the ambient temperature.

The dense branches of *Pentacalia andicola* formed an effective screen against light and air circulation, but the temperature within this space did not demonstrate an amelioration of the temperature extremes; in fact, it deviated little from the ambient air temperature.

The flowers of *Hypericum ? strictum* showed similar temperature patterns over the course of the study period to this species' branch tips.

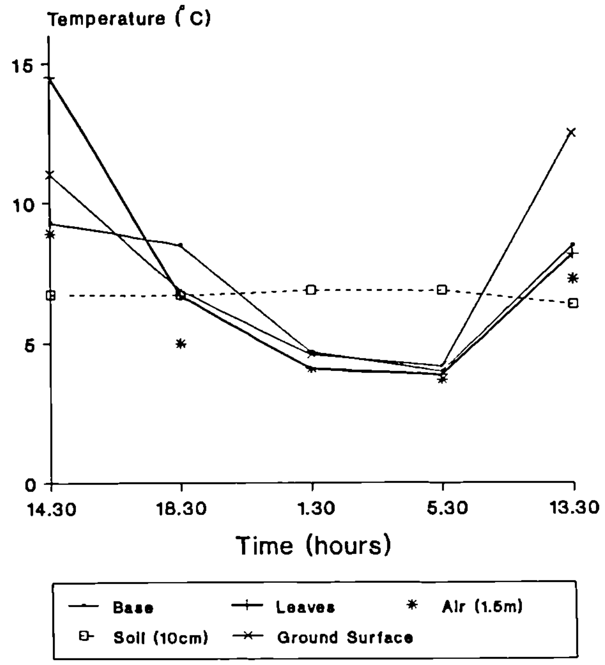
Erect Herbs

This growth form was found to experience similar fluctuations in diurnal temperature to those observed in other plants in this study: temperatures close to air temperatures at night complemented by daytime temperatures well in excess of the ambient conditions (Figure 3.20). Stem, bud and flower temperatures did not vary markedly from this pattern in the five species studied: *Lycopodium ? crassum, Castilleja* sp., *Perezia pungens, Culcitium ovatum* and *Jamesonia ? goudotii.*

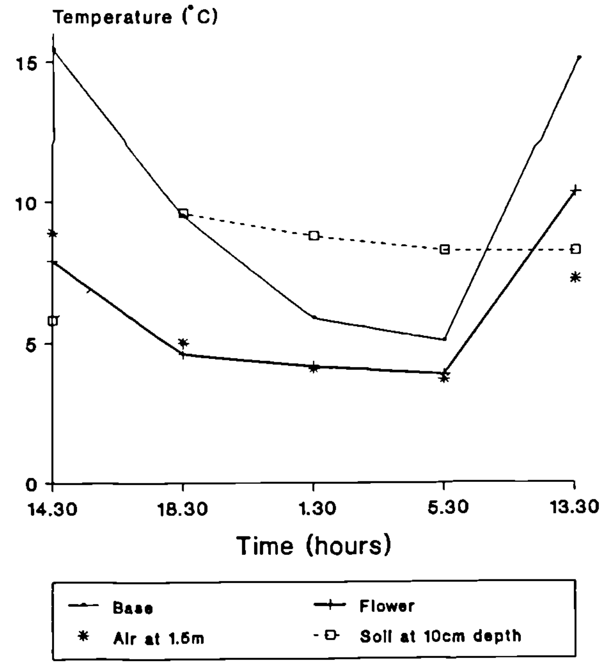
The most interesting observation in this group concerns the higher night-time temperatures of the hairy stalk apex of *Jamesonia*, which did not reflect the corresponding ambient air temperatures as faithfully as the remaining erect herbs.

Discussion

Unfortunately, the night-time temperatures experienced on the study dates were not particularly low. In 1976, Øllgaard & Balslev (1979) had measured a night-time



Calamagrostis



Cotaderia sericantha

Figure 3.19.

Temperature variation over 24 hours at a number of measuring points on two species with a tussock growthform (*Calamagrostis* sp. and *Cortaderia sericantha*) at 4,050m in the páramo of Volcán Chiles. The temperature was measured at the base of the tussock, the upper leaf region (*Calamagrostis* only), the surface of the inflorescence (*Cortaderia* only) and the ground surface at the edge of the tussock. Air and soil temperatures are also shown.

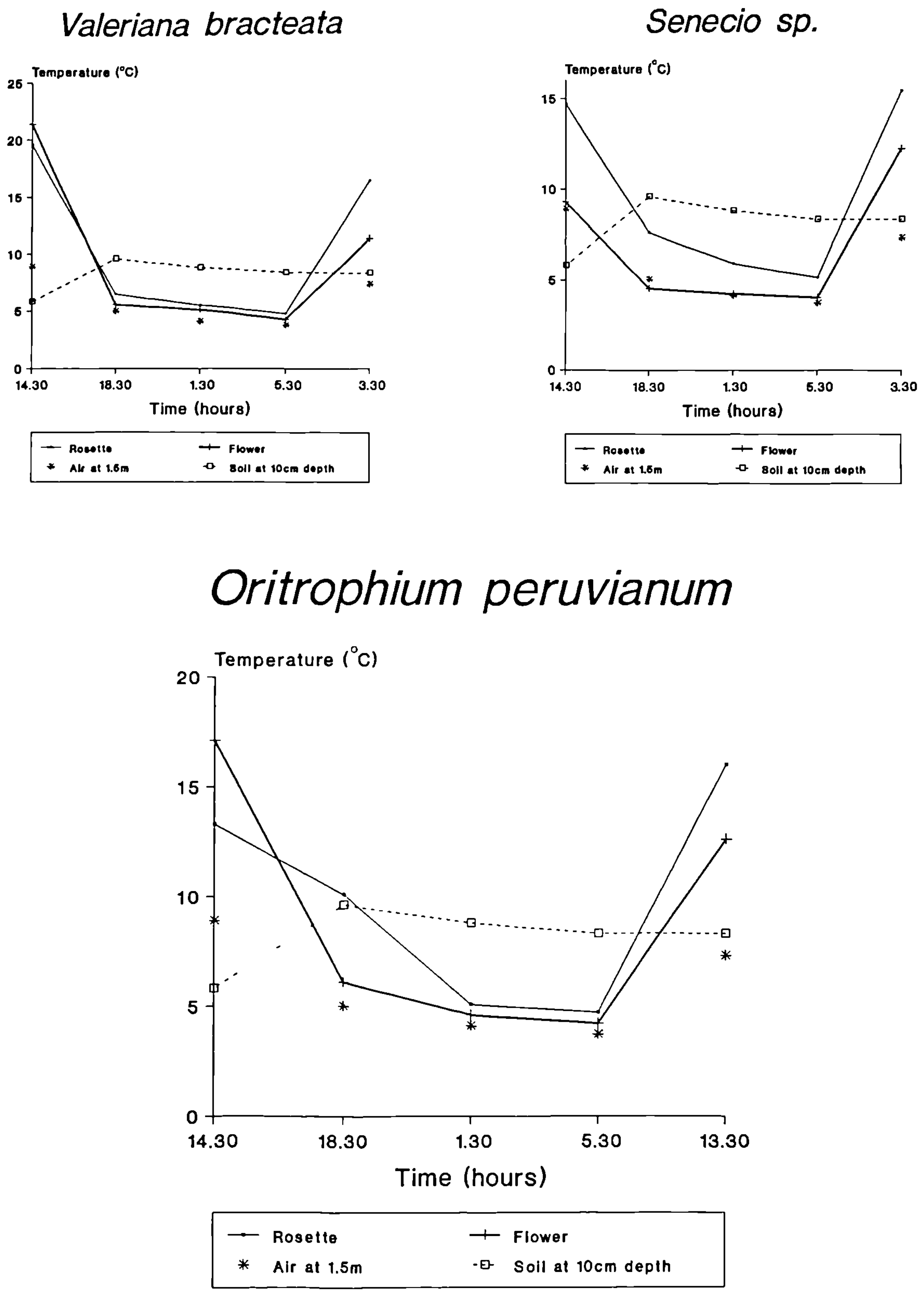


Figure 3.20.

Temperature variation over 24 hours at a number of measuring points on three species with an acaulescent rosette growthform (*Oritrophium peruvianum, Valeriana bracteata* and *Senecio* sp.) at 4,050m in the páramo of Volcán Chiles. Basal leaf surface and flower temperature were measured. Air and soil temperatures are also shown.

minimum of about + 1°C a few hundred metres away from the location of this present study (where the minimum temperature was 3.7°C). Examination of Hedberg & Hedberg's (1979) figures reveals that much of the evidence used to support their hypotheses was derived from one of the three nights for which they had recorded data, when temperatures dropped to around + 1°C. On the remaining two nights, minimum temperatures were about 7-9°C, and the thermoregulatory properties of their study plants were not so pronounced, if apparent at all. Clearly, better insights into plant strategies can be gained when the nights are cold, preferably with a frost.

Figures 3.16-3.20 give the impression that a sharp temperature decline takes place between 1430 and 1830, as a consequence of the intervals between measuring times. It should be noted, however, that the majority of the temperatures decline occurred between 1800 and 1830. After sunrise, however, air temperatures increased more steadily, taking several hours to achieve values similar to those indicated at 1330; though as a result of insolation, some surface temperatures may have risen considerably immediately after sunrise.

Radiation frost – the loss of radiated heat from surfaces – is an important consideration in interpreting these results. Surfaces of vegetation or ground cool down several degrees more than air at 2m. Usually, minimum plant temperatures on clear nights are 1-3°C below the minimum air temperature (Larcher & Bauer, 1981). According to Grace (1988), short vegetation would be expected to be cooler than tall vegetation because mixing of air is reduced closer to the ground and therefore radiated losses are more important.

Stem Rosettes

The stems of giant rosette plants in Africa and South America contain voluminous, parenchymatous pith that acts as a water source during periods of low water availability (Hedberg, 1964; Goldstein, Meinzer & Monasterio, 1984). Many of these giant rosette plants exhibit nyctinasty: the leaves close around the single apical bud at night and open during the day (Smith, 1974), damping diurnal temperature fluctuations. Thus they avoid freezing stress on cold nights and overheating (and resultant water stress in young leaves) early in the morning. Smith (1974) has demonstrated that leaf wilting and death results from the prevention of nyctinastic leaf movements in such species. Mabberley (1986) attributed damped heating and cooling of stem rosettes to their massive construction, a view that is supported by the findings of Smith (1980) that *Espeletia schultzii* plants were larger at higher altitudes. *Coespeletia lutescens* was found to modify the microclimate beneath the plant (air temperatures 4.7-7.0°C higher than in the open; soil at 20 cm depth 2.4-4.2°C higher), and was linked to better seedling survival and greater water uptake.

The species observed in this study, *Espeletia pycnophylla* ssp. *angelensis,* did not exhibit nyctinasty. However, the living leaves making up the apical rosette were densely pubescent (Acosta-Solís, 1984, refers to them as "donkey's ears"). This fur-like covering may explain why these leaves cooled down more slowly and remained slightly warmer than the other parts of the plant throughout the night. Meinzer & Goldstein (1985) found that the thickness of pubescence in a Venezuelan species of *Espeletia* increased by 1.5 mm along a 1,600 m gradient of increasing altitude. Hed-

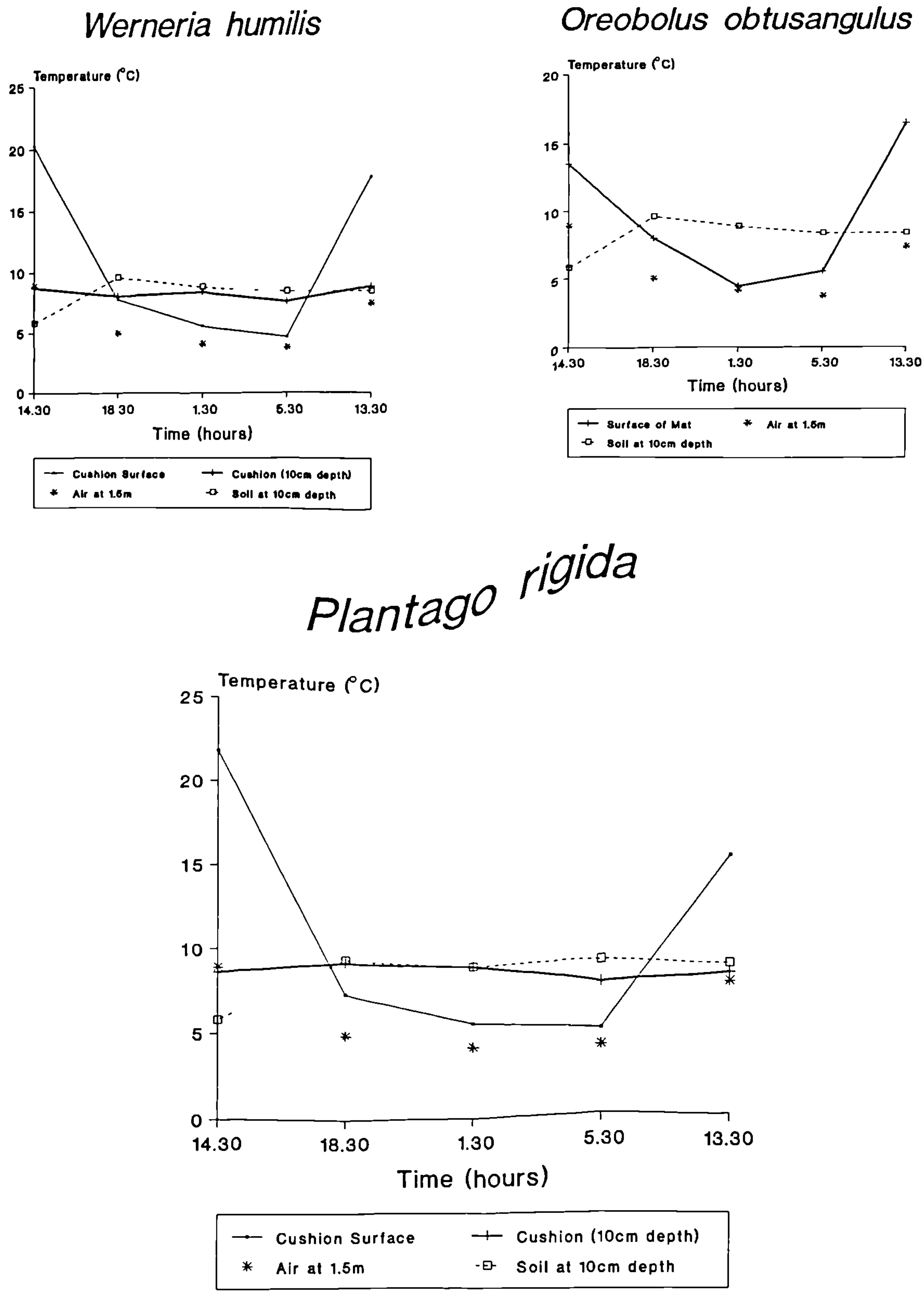
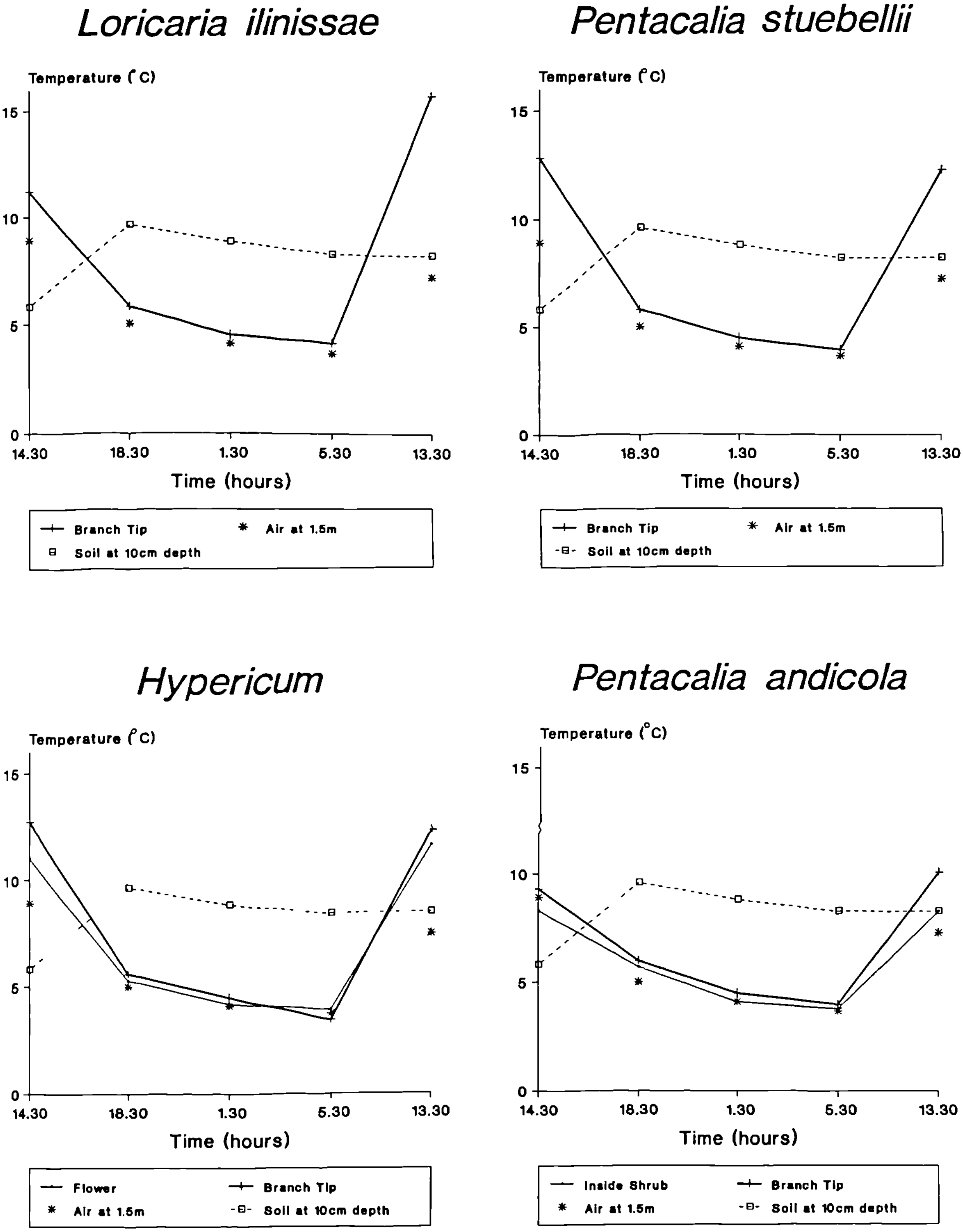


Figure 3.21.

Temperature variation over 24 hours at a number of measuring points on three species with a cushion or mat growthform (*Werneria humilis, Plantago rigida* and *Oreobolus goeppingeri*) at 4,050m in the páramo of Volcán Chiles. Cushion or mat surface temperature and that 10cm below the surface were measured. Air and soil temperatures are also shown.



Loricaria ilinissae

Pentacalia stuebellii

Hypericum

Pentacalia andicola

Figure 3.22.

Temperature variation over 24 hours at a number of measuring points on four species with a shrubby growthform (*Loricaria ilinissae, Pentacalia stuebellii, Hypericum* sp. and *Pentacalia andicola*) at 4,050m in the páramo of Volcán Chiles. The temperature of the branch tip, flower and the inside of the shrub were measured. Air and soil temperatures are also shown.

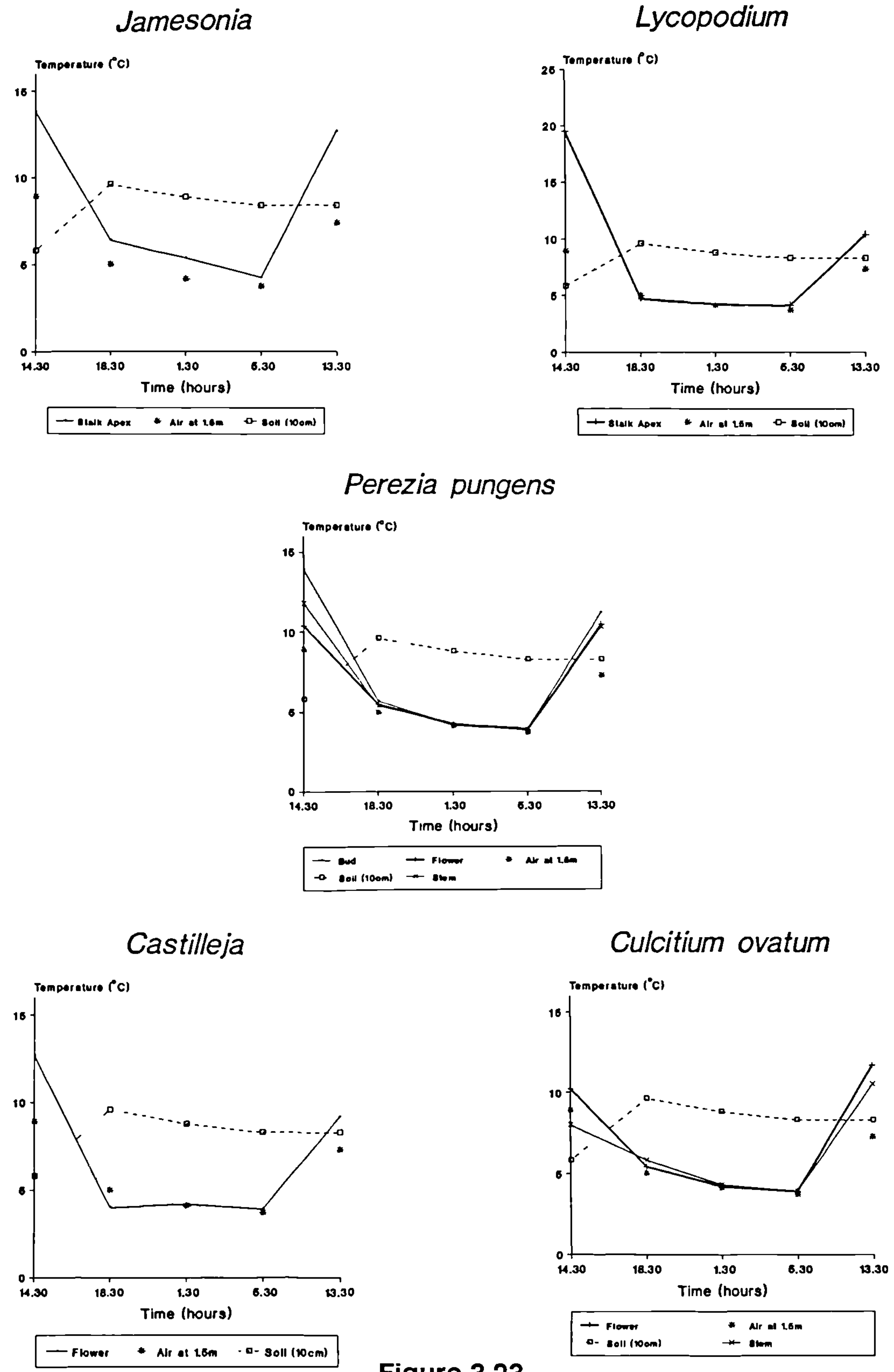


Figure 3.23.

Temperature variation over 24 hours at a number of measuring points on five species with an erect herb growthform (*Jamesonia* sp., *Lycopodium* sp., *Castilleja* sp., *Perezia pungens* and *Culcitium ovatum*) at 4,050m in the páramo of Volcán Chiles. The temperature of the branch tip, flower, bud and halfway up the stem were measured. Air and soil temperatures are also shown.

berg (1964) and Baruch & Smith (1979) hypothesised that the adaptive significance of leaf pubescence in tropical alpine giant rosette species lay in reduced radiation absorption, leading to reduced leaf temperature and lower rates of transpiration. Meinzer & Goldstein (1985), however, suggest that prevailing air temperatures indicate that latent and convective heat loss are more critical in determining the thermal balance of the leaf. They predict that leaf pubescence could result in up to 5°C higher leaf temperature. Similar pubescence on the inflorescence of *Puya hamata* was shown to increase tissue temperature significantly and thus increase seed production (Miller, 1987a).

A clear effect of the marcescent leaves on the surface temperature of the stem was observed. The diurnal range of temperature was reduced from 18.8°C to 9.9°C by this covering of dead leaves. Minimum surface temperatures on the stem were approximately the same regardless of the presence of marcescent leaves. The buffering effect of the marcescent layer was, therefore, largely in the prevention of extreme high temperatures. Hedberg & Hedberg (1979) demonstrated the good insulating capacity of the mantle of marcescent leaves in *Espeletia schultzii*, which remained remarkably constant at around 7.5°C, regardless of the temperature outside the mantle. The mean temperature of the stem beneath the dead leaves of *E.pycnophylla* ssp. *angelensis* over the course of the present study was also 7.5°C.

The marcescent leaf mantle was incomplete – the lower portion having been destroyed by fire – and this may have resulted in some loss of insulatory protection. Goldstein & Meinzer (1983) removed the dead leaf layer of *Espeletia timotensis* and showed that stem temperature was altered, resulting in transient and permanent effects on water balance. Smith (1979) and Goldstein, Meinzer & Monasterio (1984) report similar conclusions. The mechanism attributed to this effect by Goldstein & Meinzer (1983) was considered to be one or more of the following: the inhibition of pith recharge by subfreezing stem temperatures, the formation of embolisms in the stem xylem and freezing injury to pith tissue.

Flower temperatures were close to ambient air temperatures for most of the 24-hour period. This indicates that the inflorescences possess little ability to modify temperature from that of the surrounding air and rely on tolerance of low temperatures rather than avoidance. Smith (1974) reported that the parabolic form of *Espeletia schultzii* leaves concentrated the sun's rays, raising the temperature of the bud. Based on the evidence of this study, *E.pycnophylla* ssp. *angelensis* does not function in the same way, since flower temperatures were not found to be greater than the air. As mentioned earlier, high inflorescence temperature was linked to increased seed production in *Puya hamata* (Miller, 1987a). Fewer numbers of flowers were found on the windward sides of the *Espeletia* plants by Smith (1974). These are clear illustrations of how temperature stress can effect reproductive potential.

Tussock Grasses

Tussocks provide a well-defined boundary layer of dead air (Geiger, 1966; Jones, 1983). The outer leaves of the *Calamagrostis* tussock are subject to greater temperature variability than the basal leaves, but the trapping of air within the tussock allows the temperature to rise more than 5°C above that of the ambient air during daylight hours. At night the temperature does not deviate greatly from the ambient air temperature, but since these leaves are old and hardy, low temperatures may not be damaging.

The dense bases of *Calamagrostis* sp. are well insulated against extremes of temperature, cooling slowly after dark and not exceeding 10°C during the day. It would appear likely that during severe frosts the developing tillers of *Calamagrostis* are protected by the surrounding leaves. The retention of dead leaves within the tussock structure may enhance this shielding effect. Hedberg (1964) observed that the dense base of a tussock of *Festuca pilgeri* ssp. *pilgeri* on Mount Kenya, East Africa, was 7.5°C warmer than the -5°C temperature in the outermost leaves of the tussock. Coe (1967) presented similar findings for the same species. In the Venezuelan Andes, Hedberg & Hedberg (1979) showed a similar phenomenon in *Stipa* sp.

The insulatory properties are similar with respect to factors other than climate. During a fire, for example, this portion of the tussock is shielded against radiated heat in much the same way as it is protected from intense cold (Chapter 4).

The hairy basal leaves of *Cortaderia sericantha* serve a similar function to the pubescence on the marcescent *Espeletia* leaves, with the same result. The protection from frosts afforded by these hairs allows newer leaves to develop undamaged.

The flowers of *C.sericantha* project beyond the vegetative leaves of the tussock. Although this results in lower night-time temperatures and thus lower seed production, the flowerheads serve the function of pollen and seed dispersal which requires good air circulation to be effective. The benefits of increased pollination and dispersal might outweigh the disadvantages of low seed production.

According to Nishikawa (1990), tussock formation provides stable growth conditions against fluctuations in water level, air temperature and other factors. Tussock formation changes a plant from a competitor in an unformed tussock to a stress tolerator in maturity.

Acaulescent Rosettes

The higher night rosette temperatures of the three acaulescent rosette species compared with the air temperature corroborate the findings of Hedberg & Hedberg (1979) with *Hypochaeris sessiliflora* in Venezuela. In particular, *Senecio* sp. showed the same degree of difference between these temperatures.

Hedberg & Hedberg (1979) suggest that the position of these plants at the air/soil interface enables them to buffer temperature variation, but they do not offer a mechanism for this, nor explain their results, which show the rosette temperature above both air and soil surface temperature over the three day period. Possible explanations include the protective properties of the outermost leaves and the beneficial heat output of groundwater during cold nights (Carlquist, 1974). Hedberg (1964) noted that water is more viscous at low temperatures and that the short internodes of acaulescent rosettes mitigate this problem, and perhaps explains their success.

The three species covered in the present study are found on soil which is heavily waterlogged. The temperature of this wet soil is several degrees higher than that of neighbouring areas. These higher soil temperatures may help plants considerably in buffering extreme cold. Heat transfer from lower in the soil profile would clearly be advantageous. In Hedberg & Hedberg's (1979) study, the soil temperature 10cm below ground is 10-14°C, several degrees higher than the soil temperature found in the boggy areas of the Volcán Chiles study location. It is likely that the soil temperature will remain several degrees above the night-time air minimum throughout the páramo, and acaulescent rosettes can therefore, exploit the soil/air interface over a wide range of temperatures.

The flower temperatures of *Valeriana bracteata* and *Oritrophium peruvianum* were observed to be 0.5-1.0°C higher than the air temperature at night. It is difficult to establish an external morphological explanation for this. One possible explanation may be that these structures are able to exploit the heat release associated with condensation of water vapour on the flower surface. By encouraging condensation, the flowers may sustain a higher temperature than the surrounding air through the night.

Cushions

The surfaces of the cushions followed a similar diurnal pattern to that found by Hedberg & Hedberg (1979) for *Plantago rigida* in Venezuela. By day, temperatures reached in excess of 20°C, while at night these surfaces fell to within a few degrees of the air temperature. Ruthsatz (1978) observed the diurnal temperature regimes of five cushion species in the puna of North-west Argentina and reported similarly wide thermal fluctuations just beneath the cushion surface.

Hedberg & Hedberg (1979) point out that cushions merely represent an aggregate of acaulescent rosettes and they may be viewed as adopting a similar approach to thermoregulation, that is, taking advantage of the soil/air interface (Rauh, 1939; Hedberg, 1964; Billings & Mooney, 1968; Billings, 1973; Armesto, Arroyo & Villagran, 1980).

The inside of the cushions (10cm below the surface) remained markedly constant – more so than the soil at the same depth – at around 9°C in both *Plantago rigida* and *Werneria humilis*. In support of these observations, Ruthsatz (1978) found that temperature measurements 10 cm deep within five cushion species in Argentina had much smaller oscillations than the ambient conditions.

Therefore, the cushion form may enjoy the advantages of an enhanced soil/air interface situation while the increased height which the domed shape provides for some species may reduce waterlogging and increase the competitive ability of the plant with regard to light. In addition, the grouping of rosettes may provide mutual protection against strong winds and desiccation. Therefore, it does seem plausible that the cushions can effectively raise the soil/air interface to their rosettes by means of the cushion structure. Alliende & Hoffmann (1985) demonstrated that for some puna species cushions provide an ideal substrate for germination; indeed, some species were found almost exclusively on cushion plants. This indicates that the physical characteristics of cushions ameliorate the extremes of environment in such cases.

Shrubs

These plants showed little adaptation towards temperature regulation, relying heavily on low temperature tolerance. By day they were warmed by insolation and by night they cooled with the air temperature. Hedberg & Hedberg (1979) proposed that these plants do not possess morphological features to avoid low temperatures; instead, their morphology enables these plants to withstand them. Thus the scale-like leaves of *Loricaria ilinissae*, the needle-like leaves of *Hypericum* sp., the waxy leaves of *Pentacalia stuebellii*, and the leathery leaves of *Pentacalia andicola* all serve to reduce transpiration during low temperatures, and by these means prevent water stress. If this were so, then one would expect to see increasing xeromorphy as conditions become more severe: Hedberg (1957) found this to be the case in East Africa.

Carlquist (1974) affirmed the frost resistant function of the 'cupressoid' habit of *Loricaria* and added the functions of minimising transpiration and withstanding the effects of alpine light conditions. He also pointed out that *Loricaria* has ultraspecialised wood with an abundance of vascular tracheids which is related to cold tissue temperatures.

Erect Herbs

Like the shrubs, it would appear that four of the five erect herbs in this study do not possess morphological features to ameliorate their temperatures. *Lycopodium* sp. appears to rely on low temperature tolerance and was found to show significant altitudinal trends in leaf and plant size for Central Ecuador (Buckland & Ramsay, in press), which may be a response to temperature and water stress.

Culcitium ovatum has leaves covered with downy hairs, but does not appear to gain thermal benefit from this pubescence at the temperatures encountered in this study. These hairs may instead serve to reduce transpiration during periods of water stress.

Unlike *Culcitium*, *Jamesonia goudotii* was found to stay approximately 0.5-1.0°C above the air temperature overnight. Dense pubescence around the developing frond tip and along the midrib characterises this species, and may explain the slightly higher temperatures.

Essentially, there are three major problems associated with low temperatures in the páramo:

- direct damage to tissues by low temperatures.
- reduction in rates of growth and development
- water stress caused by transpiration demand when cold temperatures restrict the rate of water uptake.

Minor thermal differences can have a significant effect on plant water balance (Goldstein & Meinzer, 1983) and survival (Smith, 1979). These problems are particularly pronounced when temperatures fall below zero. In a cold environment, there is strong selective pressure for the evolution of freezing avoidance and/or tolerance mechanisms (Azocâr, Rada & Goldstein, 1988). In habitats where temperatures at night do not fall far below zero and remain there only for short periods of time, the main resistance mechanism should be freezing avoidance (Larcher, 1981; Sakai & Larcher, 1987). On the other hand, if temperatures drop well below freezing at night and stay there for several hours, tolerance should be the selected resistance mechanism (Larcher, 1981; Rada *et al.*, 1985; Sakai & Larcher, 1987). In the study area, a combination of both avoidance and tolerance would be expected, since the plants there must endure both short and more long-lasting periods of freezing stress, according to the season (Sarmiento, 1986).

In the case of tolerance, physiological adaptations are most important permitting tropical alpine plants to recover their full photosynthetic capacity after a night frost (Schulze *et al.*, 1985). Azócar *et al.* (1988) studied *Draba chionophila* in the Venezuelan páramo. This rosette plant was not insulated from low night-time temperatures and leaves, pith and roots were observed to freeze without causing injury to the plant.

Morphological features may be important in reducing transpiration (for example, by means of xeromorphy or pubescence) or in maintaining the water balance in some other way (such as the water-storing pith of *Espeletia* spp. – Goldstein *et al.*, 1984).

A number of avoidance strategies have been adopted by páramo plant species. One approach is the shielding of delicate parts with dead, hardy or expendable parts: as in the case of the marcescent leaf mantle clothing the *Espeletia* stem, or the protection of developing tillers and leaves by the outer leaves in tussock grasses. Many rosette plants protect their inner developing leaves with outer ones (for example, *Puya hamata*, *Werneria nubigena*). Trees of the genus *Polylepis* buffer temperatures by means of many thin layers of exfoliating bark (Simpson, 1979) – a significant reduction in the extremes of high and low temperatures beneath the bark was measured by Liley (1986). As mentioned earlier, insulatory functions of a plant can increase its survival rate after a fire by shielding part of the plant from intense radiated heat.

Pubescence is another common strategy for low temperature avoidance. Meinzer & Goldstein (1985) demonstrated by model simulation that leaf pubescence works by increasing the thickness of the boundary layer of still air and reducing convective heat transfer from leaf to air. This is particularly pronounced when many pubescent layers lie together (as in a developing bud).

In this study, *Espeletia pycnophylla*, *Cortaderia sericantha* and *Jamesonia goudotii* maintained higher temperatures than that of the air by means of hairiness. Miller (1987a) reported an increase in inflorescence pubescence for various species of *Puya*, and with a combination of temperature measurements and pubescence removal demonstrated that the layer of hairs was responsible for up to 80% of the difference between flower and air temperature. He then linked this higher thermal regime with increased success in seed production.

Finally, by inhabiting the boundary between soil and air, some smaller plants are able to benefit from the warmer soil temperatures at night just below the surface.

The acaulescent rosette growth form adopts this strategy, as do mat-forming species. Taken one stage further, cushion plants are able to artificially raise the soil surface, perhaps increasing their competitive abilities or reducing the effects of waterlogging. In addition, by retaining a smooth surface, the individuals of a cushion or mat are able to offer mutual protection from desiccation and wind action.

In some cases, both avoidance and tolerance strategies occur in combination. For instance, nyctinasty was found to enhance the avoidance of low temperatures in young leaves at night in *Espeletia semiglobulata*, whilst the outer leaves undergo regular freezing and appear to be undamaged (Larcher, 1975). The acaulescent rosette, *Senecio* sp., and the tussock, *Cortaderia sericantha*, both employ avoidance in their vegetative parts (by means of the soil/air interface and pubescence/mutual shelter, respectively) and tolerance in the floral parts.

According to Dobzhansky (1950), any organism that lives in a temperate or cold climate is exposed at different periods of its life cycle or in different generations to sharply different climates. To survive and reproduce, any species must be at least tolerably well adapted to every one of the environments which it regularly meets. Changeable environments put the highest premium on versatility rather than perfection in adaptation. This view is supported by Tomlinson (1987) who suggests that plasticity is more significant in adaptive terms than initial architecture.

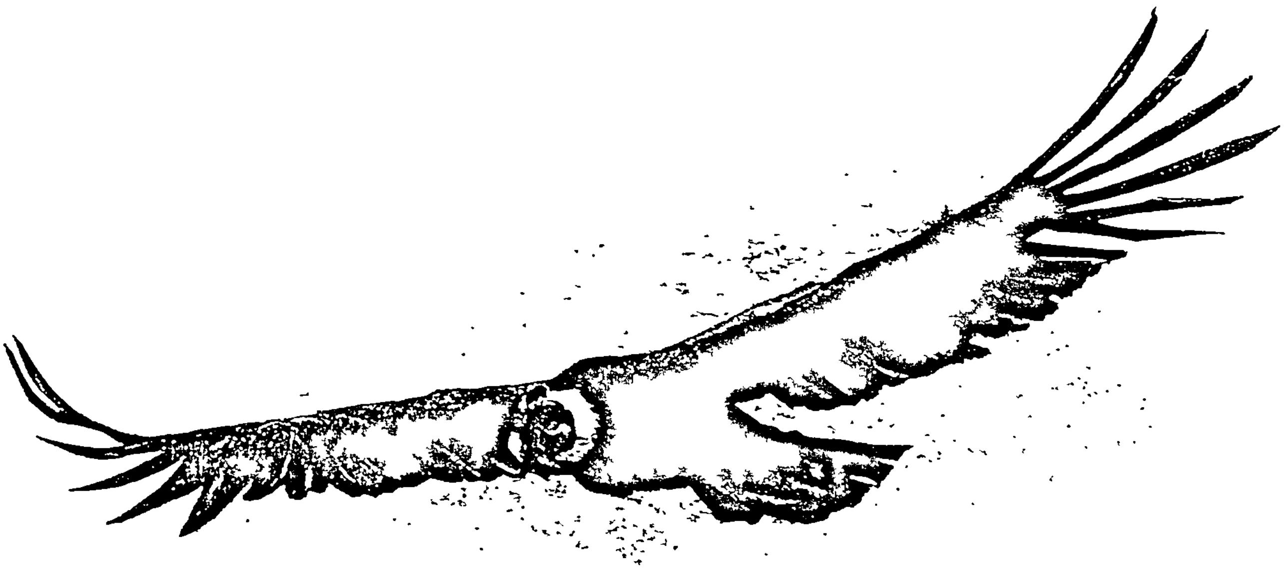
The thermal regime is just one of the elements of the environment addressed by growth form. It has already been mentioned that resistance to fire, protection from solar radiation, transpiration, reproduction and competition are rival considerations for inclusion in the overall form of a páramo plant. Therefore, the form of a plant represents the outcome of many selection pressures, some weightier than others. The form is a structural and functional compromise which allows for the optimization of cost-benefit relationships (Baruch, 1982). As long as a plant gains more carbon than it pays for its architecture and physiology it may survive (Küppers, 1989).

So, the inflorescence may suffer reduced seed production in an exposed position, but the fewer seeds that are produced may be dispersed more efficiently. Such forces are not necessarily antagonistic: it has already been cited that morphological features which insulate sensitive tissues from extremes of climatic temperature can also serve to protect against the high temperatures experienced during a páramo fire. Givnish, McDiarmid & Buck (1986) suggest that the evolution of a stem rosette species in the Venezuelan tepuis has been driven by fire rather than low temperatures and were able to demonstrate that fire survival was correlated with rosette height. Beck, Scheibe & Schulze (1986) found that tussock grasses were increased after an East African alpine fire, suggesting that fire favours the tussock form.

Despite competition for morphological adaptations from other considerations, it is clear from the results of this study that resistance to low night-time temperatures has been evolved by a number of plants and the growth form plays a major role in this. A study of this kind, performed on a very cold night, would provide further and possibly more conclusive evidence for thermoregulation by growth form and other morphological features.

Chapter 4

Aspects of Plant Community Dynamics in the Ecuadorian Páramos



Introduction

Páramo plant species are not randomly scattered throughout the vegetation; they exist in repeated patterns of particular species – as plant communities. Chapter 2 provided a descriptive treatment of páramo communities and correlated species composition with a number of environmental variables.

This century has seen a productive and well-documented difference of opinion between those who believed, like Clements (1916), that communities were 'super-organisms' (and succession an entirely deterministic process) and those who saw the vegetation as merely the resultant of two factors, the fluctuating and fortuitous immigration of plants and an equally fortuitous and fluctuating environment (Gleason, 1917, 1976). The debate between the Clementsian holists and the Gleasonian individualists resulted in the rejection of the holist approach and the application of Darwinian reductionist thinking to the development of plant communities. Plant communities are therefore viewed as the result of three influences:

- the response of plants to variation in external factors in their environment.
- the response of plants to each other through competitive interactions between individuals.
- historical chance events, reflecting both colonisation and extinction.

Emphasis has shifted away from the abstract of plant communities to the components of the vegetation, the individual plants themselves. Although particular communities may appear static in composition, these communities are longer-lived than their component parts (the plants) and they are maintained by a dynamic process of death and replacement of individual plants. Two main approaches have been used to examine the dynamic nature of plant communities. One involves piecing together a picture of the processes involved by comparing contemporaneous plots at different stages of development. This means of investigation is somewhat subjective, but as Watt (1947) points out: "the formulation of laws and their expression in mathematical terms will be facilitated if an acceptable qualitative statement of the nature of relations between the components of the vegetation is first presented."

The second, and perhaps more satisfying approach examines the actual changes in plant communities over time, looking at individual plants or plants falling into categories (patches involving dominant growth forms or smaller associations within the community). The advantage of this quantitative approach is that it is open to statistical interpretation. In its simplest form, each individual or category has a certain probability of being replaced by another of its kind or by an individual or category of another kind. This approach has been used widely and has led to the development of Markov modelling where these probabilities of replacement are used to predict succession in vegetation (Horn, 1975; Usher, 1979, 1981; Hobbs & Legg, 1983; Lough *et al.*, 1987).

These approaches can be used to investigate not only the dynamic nature of the maintenance of community composition in climax vegetation, but also to examine succession or recovery from disturbance. It has been proposed by a number of authors that much of today's grassy páramos (and other Andean high elevation grasslands) are secondary vegetation types, maintained artificially by man via burning (Ellenberg, 1979; Laegaard, 1992), though other authors disagree (for example, Simpson, 1979). In Chapter 2, burning (an element of disturbance) was found to be at the very least correlated with species distributions.

Fire is commonplace in the páramo, a tool used by farmers to improve their pastures. If fire is a very rare (catastrophic) event then it is unlikely to exert a selective influence on the vegetation, but if (as is the case in the páramo) burning is frequent, the vegetation might be expected to show some kind of fire adaption. Although the páramos are very humid, this does not preclude the occurrence of natural fires—Givnish, McDiarmid & Buck (1986) describe a fire started by lightning in an exceedingly rainy tepui in Venezuela. From the arguments presented above, burning should affect the composition of páramo communities through its influence on plant population dynamics. Smith & Young (1987) noted the apparent cyclic succession induced by fire in the páramos of Colombia and Ecuador, and pointed to the lack of data on such phenomena.

With this in mind, a number of experiments were set up to investigate the dynamics of páramo tussock grass communities. The physiognomy of páramo grassland is not suited to a comprehensive strategy of sampling, particularly at the individual plant level, because it consists of both large and small plants and may consist of several layers. In addition, the study period was very short. For both these reasons, a number of different approaches, both descriptive and probabilistic, were employed to examine mechanisms involved in the maintenance of the community and its recovery from burning.

Three approaches were used: the measurement of fire temperatures, general observations of changes in plant communities and monitoring the fate of individual plants. Each of these approaches will be described and the results presented. Finally, the discussion will draw upon the results from all three studies.

Methods

Study Sites

Most of the data were collected in the valley of Daldal, Chimborazo Province, on the Cordillera Oriental about 40km south-east of Riobamba (one of the areas surveyed in Chapter 2). This páramo begins around 3,500m, the lower reaches maintained by regular burning. The grasslands extend thence to more than 4,200m before the Andes begin their descent to the tropical lowlands of the Amazon Basin.

In general. the vegetation is grassy, dominated by *Calamagrostis* sp. [251] tussocks. The lower páramo also contains shrubs (including members of the genera *Lupinus, Brachyotum, Chuquiraga, Baccharis, Pentacalia, Gynoxys* and *Pernettya*), a number of grasses (notably *Paspalum* sp.) and a large plant of the Cyperaceae, *Uncinia phleoides*. These plants extend up to around 3,750m. At around 4,000m the tussock grass is largely displaced by large cushions of *Plantago rigida*.

Throughout the Páramo de Daldal, burning is a major feature of land management by local farmers. Bolívar Coronel, the owner of the land on which the study was carried out, burns areas of páramo at least every three years, but the practice appears to be somewhat erratic: burning is carried out according to the appearance of the vegetation and only if the weather conditions are suitable. Usually, only one match is needed to start a blaze (if the fire base needs to be widened, pieces of tussock are used to carry the flames from one spot to another). The fire is left to extinguish itself.

The experiments to measure fire temperatures were carried out near Laguna Luspa in El Area Nacional de Recreación Cajas on the Cordillera Occidental (near Cuenca), and above Laguna de Hoyas in the Páramo de Guamaní on the Cordillera Oriental (not far from the road between Quito and Baeza). Tussocks of *Calamagrostis* sp. [251] dominate the vegetation in both areas, in much the same way they do in Daldal. In Cajas, agriculture is restricted to certain valleys within the national recreation area, but many areas are subject to acts of vandalism by tourists and fishermen (Ramsay, 1988). The Páramo de Guamaní, a much wetter area than Daldal or Cajas, still appears prone to agricultural burning below 4,000m.

Temperatures during Páramo Fires

Two experimental burns were conducted to determine the fire temperature in the vegetation structure during a fire. The first burn was carried out beside Laguna Luspa in Cajas in September 1985, the second above Laguna de Hoyas in the Páramo de Guamaní in November 1987.

In both of these experiments, THERMOCHROM® crayons by A.W. Faber-Castell were used. Each crayon contains a pigment which changes colour at a set temperature: by using a number of crayons containing different pigments, a range of temperatures were encompassed. A set of 18 such crayons covering a temperature range from 65°C to 670°C was used (Table 4.1).

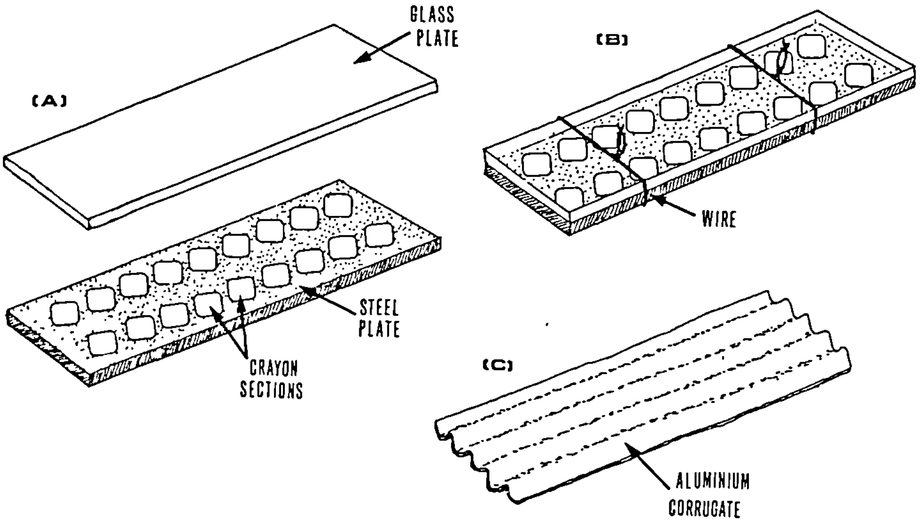


Figure 4.1.

THERMOCHROM® crayon pyrometer construction. For the experiment conducted in the Páramo of Cajas, thin slices of crayon were sandwiched between a steel base-plate and an upper plate of thermal glass (A), secured with wire (B). In the Páramo of Guamaní, crayon slices were held between two corrugated sheets of aluminium (C).

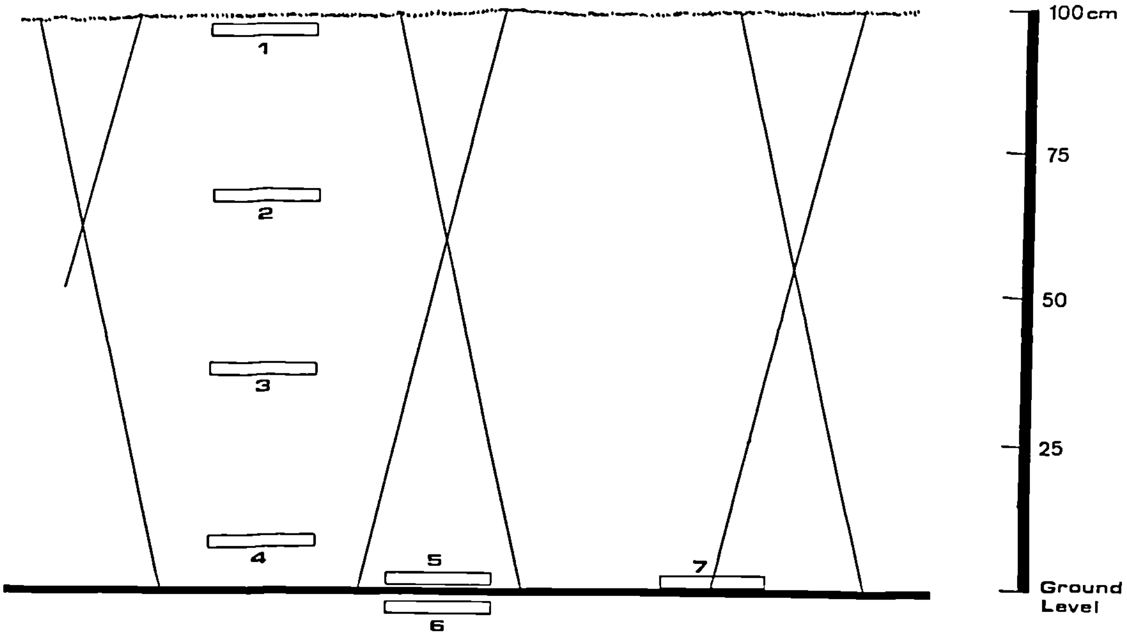


Figure 4.2.

The positioning of the pyrometers in the tussock structure. Pyrometers were placed within tussocks at approximately 1 m (position 1), 650 mm (position 2) and 350 mm (position 3) above ground. Pyrometers were also placed within the dense tussock bases approximately 50 mm above surrounding ground level (position 4), and at the edge of tussock bases (position 7). In the spaces between tussocks, pyrometers were placed on the ground surface (position 5) and 20 mm below ground (position 6). It should be noted that pyrometers at position 6 were not placed directly beneath pyrometers at position 5 – it is shown this way for diagrammatic purposes only.

Colour No.	Original Colour	Changed Colour	Temp. at which Colour Changes
2815/65	Pink	Blue	65°C
2815/75	Pink	Blue-Green	75°C
2815/100	Pink	Blue	100°C
2815/120	Light Green	Blue	120°C
2815/150	Green	Violet	150°C
2815/175	Violet	Blue	175°C
2815/200	Blue	Black	200°C
2815/220	White	Yellow	220°C
2815/280	Green	Black	280°C
2815/300	Green	Brown	300°C
2815/320	Green	White	320°C
2815/350	Yellow	Red-Brown	350°C
2815/375	Pink	Black	375°C
2815/420	White	Brown	420°C
2815/450	Pink	Black	450°C
2815/500	Brown	Black	500°C
2815/600	Blue	White	600°C
2815/670	Green	White	670°C

Table 4.1.
THERMOCHROM® crayon information, calibrated for an exposure time of 30 minutes (data from manufacturer).

These crayons were developed for use in industry to detect the temperatures of pre-heated hot bodies within about two seconds. The pigments they contain are the same as those used in thermocolour paints but are mixed with various waxes and extruded in strand form.

In Cajas, thin slices of the crayons were sandwiched between a stainless steel plate and a thermal glass plate, held in place firmly with wire (Figure 4.1 a, b). This allowed the pigments to be viewed, whilst protecting them from direct flames and smoke. In the Páramo de Guamaní aluminium corrugates (cut from the sheets used to ventilate plant presses) replaced the steel and glass plates (Figure 4.1 c). These pyrometers were positioned in six parts of the vegetation structure (Figure 4.2). The pyrometers in positions 1, 2 and 3 were suspended by wire in the leaves of the grass tussocks, those in position 4 were placed in amongst the dense bases of the tussocks. They correspond to 1000 mm, 650 mm, 350 mm and 50 mm above ground level respectively. Positions 5, 6 and 7 correspond to the intertussock region, 20 mm below ground in the intertussock region and the tussock/intertussock boundary, respectively. In Cajas, three replicates were used in each of positions 2 to 7. The base of one of the tussocks was then lit and the fire's progress recorded. In the Páramo de Guamaní, nine replicates were used in position 1 with three replicates in each of positions 4-6.

Qualitative Observations on the Recovery of Grass Páramo from Fire

The dominant species in the Páramo de Daldal is *Calamagrostis* sp. [251] and is crucial to the functioning of the community. The dense, 1m-tall tussocks that this grass forms make its detailed study difficult. The short time available for the fieldwork ruled out the possibility of all but the most basic of investigations. A sample of tillers at 3,750m provided a figure for the average number of leaves per tiller. The ratio of live to dead leaves is of interest and was examined by random samples of a number of tussocks at 3,750m and 3,950m. A recently burned area provided an excellent opportunity to accurately map tussock bases in a 25m^2 area, with subsequent measurements of basal area of the species involved.

Near to this sampling area, two recently burned tussocks were randomly selected and 40 tillers tagged using small plastic rings. The survivorship of these tillers was monitored. In the same area, general notes were made in June and July 1987 on the recolonization of burned areas and some quantitative data collected on the number of colonists on newly burned tussocks and older, established ones. In addition, the relationship between *Calamagrostis* tussocks and *Paspalum* sp. was noted in this burned area and in adjacent recovered vegetation.

Transition Matrix Experiments

The basic unit of a plant community is the individual plant, and to study dynamics at this level requires a sampling technique with sufficient resolution to differentiate between individuals. It must also be capable of recognizing gaps which might be important in the regeneration process (Grubb, 1977). Empirically, 100 mm^2 was found to be adequate, containing one plant only with reasonable consistency. Therefore, this area was used as the basis for this part of the investigation. Single plant modules (tillers, *etc.*) were treated as individuals for vascular plants, but grouped together for mosses.

To record changes in occupancy in the intertussock areas, 1 m x 10 mm belt transects were used, each containing one hundred 100 mm^2 microquadrats in which the presence of individuals was noted, similar to the approach adopted by Thórhallsdóttir (1990).

For each sampling plot, three times the number of transects ultimately required were mapped and the transects to be used were randomly selected from them.

In order to identify the positioning of the transects with the degree of accuracy required, two wooden pegs were securely fixed in the ground, 50 mm from the beginning and end of the transect (primary and secondary pegs, respectively). A tight string from peg to peg marked the exact line of the transect and the starting point, measured from the primary peg. The 10 mm wide transect lay to the left of the string

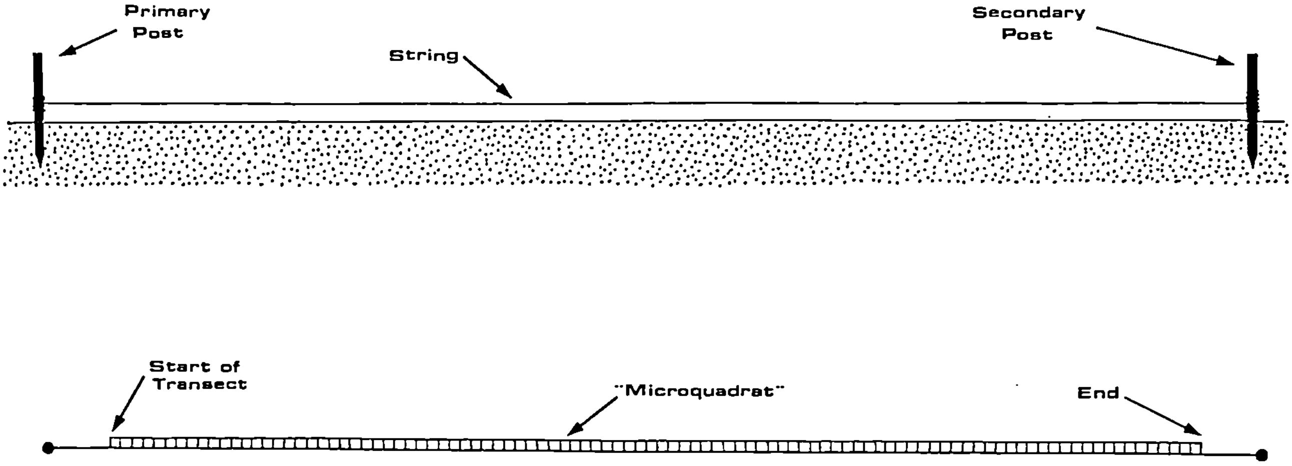


Figure 4.3.
The layout of the transects used for the transition matrix studies.

running from primary to secondary post (Figure 4.3). The pegs were located with the aid of sketch maps of the tussock bases in the immediate vicinity of the sampling plots.

The species occupying each microquadrat were noted. Only rooted individuals were recorded and sampling units in which nothing was rooted were defined as gaps. Both mosses and vascular plant species were registered, though in the case of the bryophytes, their small size called for a different approach: the presence of a bryophyte species in a microquadrat was counted as one individual, regardless of the actual number of individuals there. If one of the larger plant species was rooted across several microquadrats, it was recorded for each of those quadrats (for example, the large tap root of *Hypochaeris sessiliflora* can span 30-40 mm). No special treatment was made for clonal individuals: if rooted in the sampling units they were recorded as individuals. This is an important point since many páramo plants reproduce vegetatively (for example, *Azorella pedunculata, Paspalum* sp and *Geranium multipartitum*). Where more than one species occurred within a unit, the frequency was recorded as a fraction of 1. Thus, two individuals in the same microquadrat each received a score of ½. Using this method, the total frequency for each transect always added up to 100. Frequency measures for each species were obtained by summing their frequencies in each transect.

The pattern of replacement of species within the sampling plots was analysed by constructing a matrix such that the rows represented the species recorded at the start of the study period, the columns the species present at the end. The j^{th} column of the i^{th} row represents the number of microquadrats where species i has been replaced by species j. It is then possible to test the individual cells in the matrix, using Chi-Square (χ^2) analysis, to determine whether the pattern of replacement is random or not.

The analysis is complicated by an assumption inherent in the χ^2 test. Consider the case where a microquadrat is occupied by a certain species both at the start and the end of the experiment. The χ^2 test assumes that the last individual has replaced a member of the same species over the course of the experiment. Since the experiment was conducted within the lifetime of many plants, this is probably not the case: the same individual has probably persisted during the time interval. This would result in an over-estimation of the frequency with which a species replaces one of its own kind, and may disguise the actual changes taking place elsewhere. This situation is undesirable and therefore the principal diagonals of the matrix (representing "no change") were eliminated from the χ^2 test. Of course, this hides any replacement of a species by another individual of the same species and no probabilities are available for such transitions. Another assumption of the χ^2 test is that every change of occupancy is a single transition. Bearing in mind the brevity of the experiment this is a reasonable assumption: the case of an individual replacing another then being itself replaced is unlikely.

Simply stated, the χ^2 test will determine the probability that the pattern of replacement observed is completely random. If for each species pair, the species present at time 1 is called the i^{th} species and the species present at time 2 the j^{th} species, then the null hypothesis states that "species *i* will be replaced by species *j* in that proportion which the total replacements made by species *j* contribute to the overall number of changes" or:

$$E_{ij} = \frac{\sum (n_{ir} - n_{ii}) \times (n_{rj} - n_{jj})}{\sum (n_{rj} - n_{jj})}$$

where '*r*' represents all species other than *i* or *j*, 'n_{ir}' *the total number of times* species *i* is followed by all other species, 'n_{ii}' the total number of quadrats occupied by species *i* at time 1 and time 2, 'n_{rj}' the total number of times species *j* follows all other species, and 'n_{jj}' the total number of quadrats occupied by species *j* at time 1 and time 2 (Thórhallsdóttir, 1990). Put another way, the expected value is:

$$E_{ij} = \frac{\text{Total number of quadrats vacated by } i^{th} \text{ species} \times \text{Total number of quadrats invaded by } j^{th} \text{ species}}{\text{Grand Total of All Changes}}$$

provided the diagonal terms (the species replacing themselves) in the matrix are subtracted before making the calculation. An example calculation is provided in Appendix 2.

Most of the species involved in the data were rare and to avoid bias in the χ^2 values those species with an expected value less than 5 were not subjected to a χ^2 test. The rarer species were treated as a group to overcome this problem. Yates' correction for continuity was applied (Zar, 1984).

Experiments were set up at 3,750 m and 3,950 m the Páramo de Daldal. For each altitude, observations were made between tussocks in three vegetation types:

- Control areas where burning had not taken place for a number of years. Ten transects were recorded at 3,750 m and six at 3,950 m.
- Recently burned areas. Five transects were recorded at 3,750 m and three at 3,950 m.
- Artificially bared ground (prepared by removing the top few centimetres of the ground surface, exposing the bare soil beneath). Five transects were recorded at 3,750 m and three at 3,950 m.

Data were collected at the beginning of July 1987 and again at the end of October of the same year.

Results

Temperatures during Páramo Fires

Table 4.2 presents the maximum temperatures reached within the typical vegetation structure during experimental burns in two different locations. The chromatic thermometer crayons used in the construction of the pyrometers are said to be accurate to 5°C, but since the colour changes are a function of time, and because the casing of the crayon slices may shield them slightly from radiated heat, it is suggested that 10°C is more appropriate in this instance. Fire temperatures were maximum in the upper leaves of the tussocks, with temperatures over 500°C. Temperatures greater than 420°C occurred just 350 mm above the ground surface, but 250 mm lower in the dense tussock bases, the temperature was much lower: often less than 65°C and with a maximum of 100°C. The edges of the tussock bases at ground level, however, were subjected to much higher temperatures similar to those midway up the tussock (375-420°C).

Position	Maximum Temperature (°C)	
	Cajas	Guamaní
1. Top of Tussock (1000 mm above ground)	-	420-450
	-	420-450
	-	420-450
	-	420-450
	-	420-450
	-	450-500
	-	450-500
	-	500-600
	-	500-600
2. Inside Tussocks (750 mm above ground)	350-375	-
	420-450	-
	450-500	-
3. Inside Tussocks (350 mm above ground)	420-450	-
	420-450	-
	420-450	-
4. Tussock Bases (50-100 mm above ground)	<65	<65
	<65	<65
	75-100	100-120
5. Intertussock (ground level)	350-375	75-100
	350-375	65-75
	220-280	100-120
6. Buried (20 mm below ground)	<65	<65
	<65	<65
	<65	<65
7 Intertussock/Tussock Interface (ground level)	375-420	-
	375-420	-
	375-420	-

Table 4.2.
Maximum fire temperatures, obtained from THERMOCHROM® crayon-based pyrometers, in the páramo grasslands of El Area Nacional de Recreación Cajas and the Páramo de Guamaní. The positions of the pyrometers in the tussock grass structure is shown in more detail in Figure 4.2.

Qualitative Observations on the Recovery of Grass Páramo from Fire

Figure 4.4 presents a detailed map of tussock bases in a 5 x 5 m plot at 3,750 m. *Calamagrostis* species tussocks dominate the area with a basal area of approximately 0.2871 m^2 m^{-2} or about 29% of the total. *Uncinia phleoides* (Cyperaceae) is much less important tussock-former with a basal area of around 0.0327 m^2 m^{-2} or around 3% of the total area. In all, the bases of these two tussock species account for roughly 32% of the ground surface in the sample plot. It should be remembered that this is basal area and not the area shaded by the plants' leaves: this often exceeds 75% at this altitude.

From a random sample of tillers taken from a single mature tussock, each tiller has on average 2.86 leaves per tiller (range 2-4; sd 0.7827). This species does not shed its dead leaves but retains them amongst the living ones. At 3,750m, just over half of the standing leaves are dead (54.2%) and decay within the tussock itself. This reduces the photosynthetic potential of the plant, with dead leaves shading out living

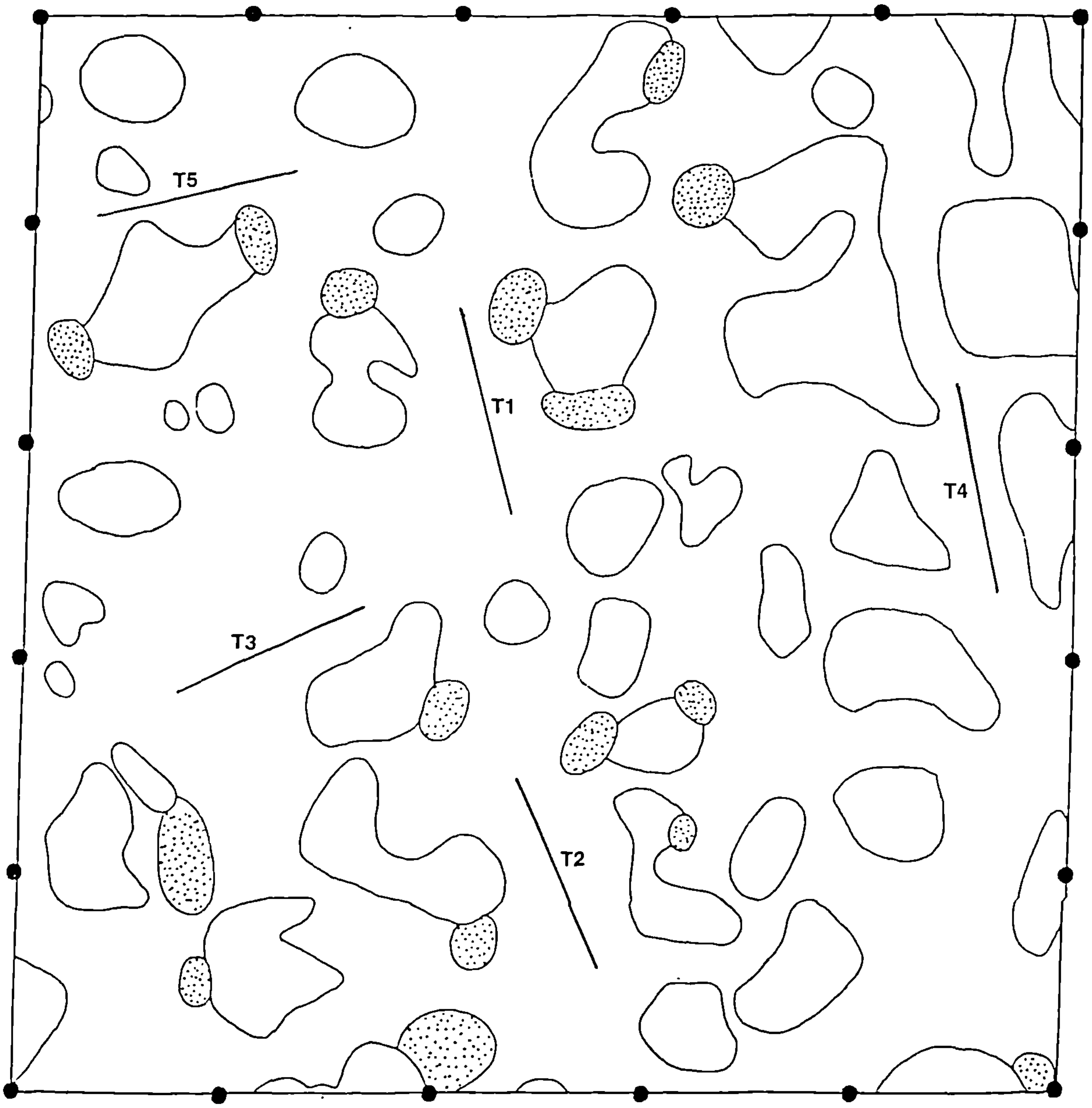


Figure 4.4.
Detailed map of tussock bases in a recently burned 5 m x 5 m plot at 3,750 m in the Páramo de Daldal. The enclosed areas represent the tussock bases, mostly belonging to *Calamagrostis* sp. (clear) with some *Uncinia phleoides* (dotted). The positions of the five transects used to sample the small-scale changes in the community are also shown.

tissue, but may serve as a defence against predation by herbivores by decreasing the overall nutritional value of the leaves (Schmidt & Verweij, 1992).

Continual burning of the tussocks and the destruction-renewal cycle that results can produce cyclical patterns of species dynamics. One example of this is the interaction between *Calamagrostis* tussocks and *Paspalum* sp. Areas of páramo at 3,750m which have not been burned for a number of years do not possess much *Paspalum.* This plant has a growth form which is highly suited to opportunistic vegetative spread after a fire (Figure 4.5). The addition of each new leaf moves the growing point along the ground and invades new territory.

Although *Paspalum* does not survive burning well, some individuals remain after a fire and grow rapidly, utilizing the abundant nutrients released by the fire. Owing to this response to burning, *Paspalum* has been noted as a characteristic plant of burned areas (Cleef, 1979; Ramsay, 1988). The species favours drier ground and so grows onto the tussock bases. Once there, it rarely descends back into the intertussock spaces (Figure 4.6). After a time, *Paspalum* 'stolons' come to cover much of the tussock, suppressing the recovery growth of the *Calamagrostis* tillers. Other species are then able to colonise the tussocks, among them *Rumex acetosella, Disterigma empetrifolium, Geranium multipartitum, Oxalis* sp. and *Lachemilla* sp.

At this point two possibilities exist. Burning may occur again, soon after the first fire. Since *Paspalum* does not survive fires well, this may be to the advantage of the *Calamagrostis* particularly since the temperatures produced by a fire at this stage are not so great. However, the tussock base can be damaged by repeated burning and may start to crumble. If *Calamagrostis* has become so weakened by repeated burning and competition from *Paspalum* and the others, the tussock may die. New tussocks are formed in the intertussock zone by the multiplication of any surviving fragment of the original tussock or by seed. The hummock left behind is gradually broken up as it dries and as the old culm bases decay. *Paspalum* becomes less important as the other species suppress its growth.

The other possibility is that the *Calamagrostis* is sufficiently resilient to resprout successfully over much of the tussock base and force *Paspalum* towards the sides of the tussock, by blocking the light to its leaves. In this way, the cycle is completed.

A number of observations were made on the recovery of *Calamagrostis* tussocks after a burning episode. Immediately after a fire, new leaves begin to sprout from the charred tussock base. Many of these first leaves are damaged towards their tips and soon wither. However, re-growth continues with the appearance of many more leaves, borne from tillers produced after the fire.

Two weeks after a burning episode, the tussock gives the appearance of relatively straightforward recovery: new leaves rapidly replacing those lost to the flames. Tiller ringing at this stage revealed that mortality is extremely high, with 37.5% of ringed tillers dead five weeks later, 40% dead after ten weeks and 72.5% dead some fifteen weeks after ringing (Figure 4.7). In fact, twenty weeks after the fire, the tussocks were very similar in appearance to that only two weeks after the event, such is the effect of this mortality.

Clearly, this long-term exposure of the tussock base to light makes colonisation attempts by other species possible. Table 4.3 presents data collected at 3,750m in the Páramo de Daldal. Burning allows species to colonise the tussock by removing the leaves that block light. *Lupinus* sp. shrubs were commonly observed growing in established tussocks. Following a fire, germination of seeds already present in the tussock

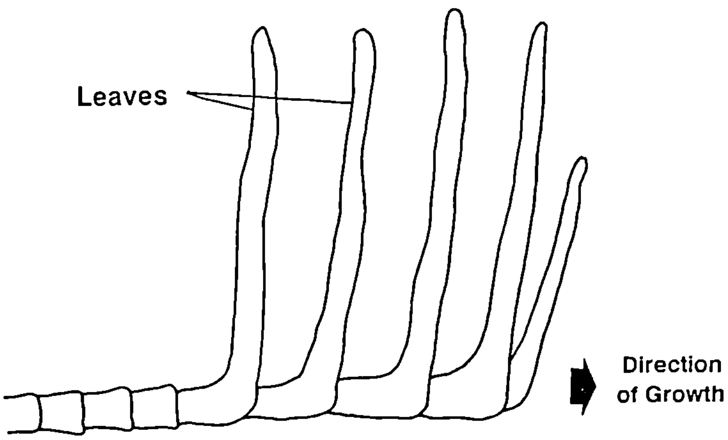


Figure 4.5.
The habit of *Paspalum* sp.

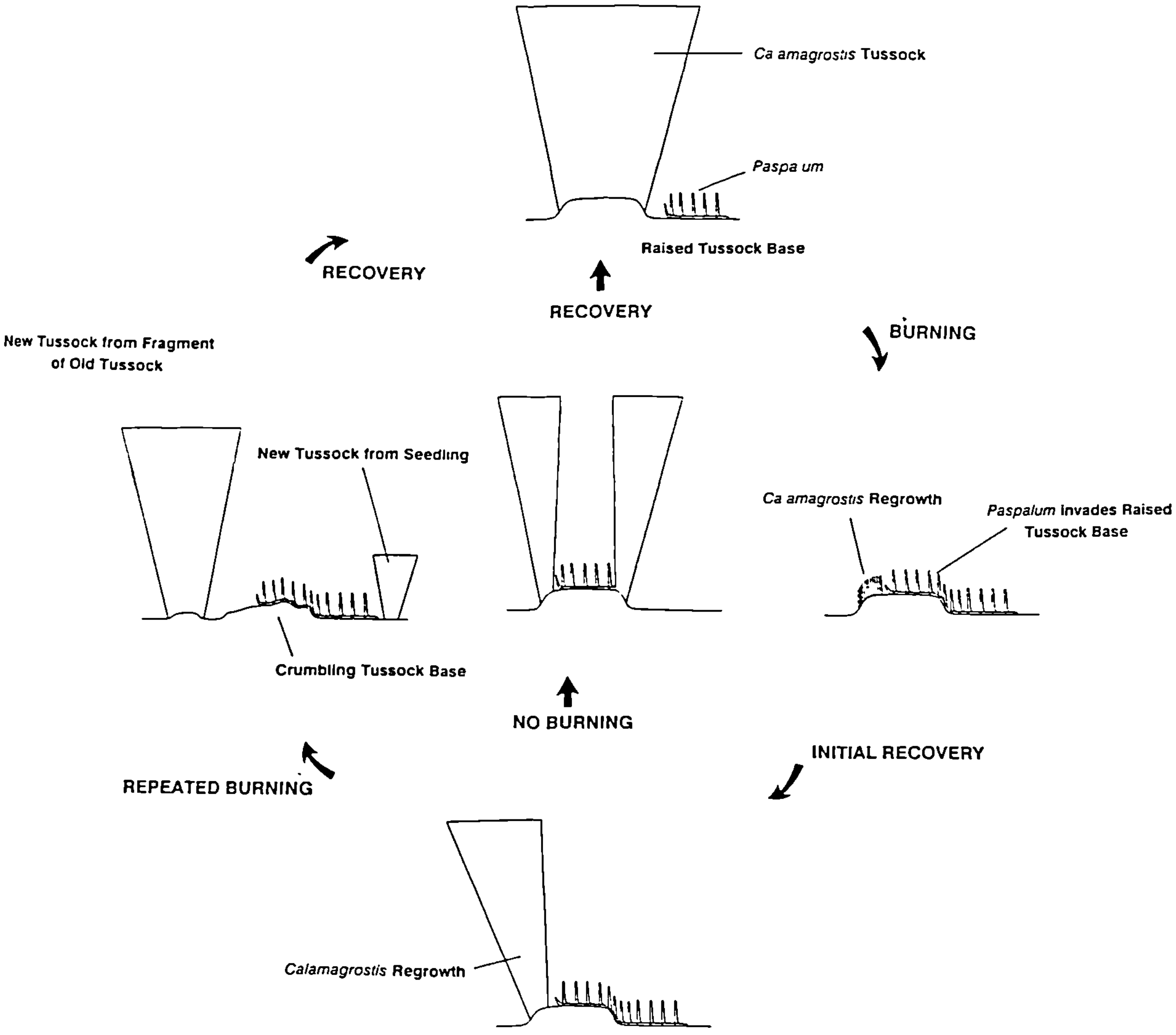


Figure 4.6.
The dynamic relationship between *Calamagrostis* sp. and *Paspalum* sp, mediated by fire at 3,750 m in the Páramo de Daldal.

bases takes place: an average of around 37 seedlings per square metre of tussock was found. *Stellaria leptopetala* shows similar behaviour. Mature individuals of both these species were found exclusively in and around the tussocks and seedlings were not present elsewhere.

	Burned Tussocks			Unburned Tussocks			
Tussock dimensions (cm)	91x56	77x52	60x60	40x40	40x40	87x35	
Tussock area (cm^2)	5096	4004	3600	1600	1600	3045	
Rumex acetosella	47	15	5	B	2		
Lupinus sp-.	28	15	8	2		1	
Stellaria leptopetala	6	3	2	B			
Dryopteris sp. [1066]	1						
Lachemilla rupestris	B	4+B		B		1	
Hydrocotyle bonplandii	B	6+B	2				
Lachemilla orbiculata	B	B	4	B			
Stachys elliptica	B						
Vicia sp. [144]					1		
Geranium sibbaldioides						1	
Pentacalia arbutifolius						1	1
Paspalum sp. [103]						1	
Relbunium croceum						1	

Table 4.3.

Tussock colonisation immediately after a less severe burn in relation to plants occupying mature tussocks. Numbers shown are the number of individual seedlings of each species colonising the tussocks. 'B' indicates species colonising the outer portion around the sides of the tussock base.

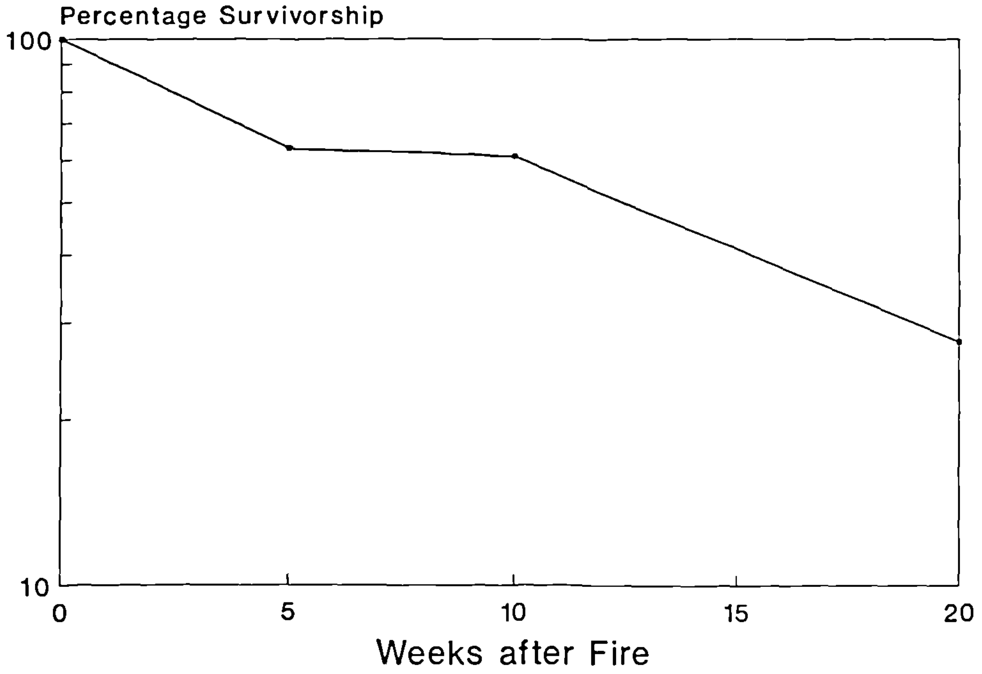


Figure 4.7.

Survivorship of *Calamagrostis* sp. tillers following a páramo fire. The survivorship axis is on a logarithmic scale.

The long period of tussock recovery after a fire gives the seedlings time to reach a size where they can compete effectively for light once the tussock begins to grow again.

The burned tussock is also open to opportunistic colonization. The behaviour of *Rumex acetosella* is a good example of this. Within days of a fire, seeds of this species germinate all over the tussocks. One tussock was seen to have 47 seedlings of *R.acetosella* present. Unlike the other species mentioned, *Rumex* is not found exclusively on tussocks; in fact, it is quite rare in established tussocks of *Calamagrostis* and much commoner between them.

Species such as *Lachemilla rupestris, Lachemilla orbiculata* and *Stachys elliptica* are able to take advantage of the bare ground around the tussock bases which is suddenly opened to sunlight after burning (Table 4.3). They were also present on the tussocks but are eventually killed as the tussock leaves overshadow them.

Some 250 m higher in the páramo, at around 4,000m, tussocks and mats are co-dominant in the community and burning is less frequent. As altitude increases, the tussocks of *Calamagrostis* are gradually displaced by *Plantago rigida* cushions until eventually the tussocks are well spaced out. At 4,000m, a co-dominance exists, with the cover tussocks and mats (covering the intertussock region) more or less equal. It is here that some insight into the processes in operation might be gained. From observations of vegetation showing different stages of development, the following dynamic process is proposed. First of all, large tussocks of *Calamagrostis* are invaded by a mat of *Plantago* rosettes, initially just a 'dent' in the tussock (Figure 4.8). This may be the result of opportunistic growth following a fire, but since such events are rare in this location, it was not possible to verify this by direct observation. Another possibility is that the tussock base develops to the extent that water may become less accessible and the plant's growth is weakened. Having gained a foothold, the mat spreads across the top of the tussock base (which is raised above the surface of the ground by up to 500 mm), splitting the original tussock into smaller ones around the periphery of the mound. By this stage, a *Plantago rigida* cushion has developed. Dissection of ten large cushions of this species revealed that they were all overlying former grass tussock bases.

At this point, other species are able to colonise the cushion covering the centre of the hummock: *Lachemilla orbiculata, Cotula ? mexicana, Oreomyrrhis andicola* and *Lachemilla andina.* These species are common in the intertussock region. Some species, rarely encountered in the low, intertussock depressions are relatively common on the *Plantago* hummocks, namely *Disterigma empetrifolium, Pernettya prostrata* and *Lachemilla hispidula.* These species almost certainly benefit from the better drainage afforded on the mound, but which was previously shaded by the tussock leaves.

With time, the hummock becomes colonised by more species. *Plantago rigida* cover drops from close to 100% to around 40%. In addition to those species already mentioned, *Hypochaeris sessiliflora, Rumex acetosella* and *Festuca* sp. are all later colonists. As more species invade the hummock, it begins to dry up. At first the sloping surfaces become uneven and crumble. Finally, the *P. rigida* rosettes die and only moss species are able to survive on the crown of the hummock. Eventually, this too dies and the mound disintegrates.

While this process is going on, the fragments of the original tussock survive nearby and, given the right conditions, are able to reproduce and gain in size. One or several of these patches of *Calamagrostis* may attain full size and begin building a new mound by repeated tillering on top of dead culm bases. After some time, *P. rigida* may invade once more to begin another cycle.

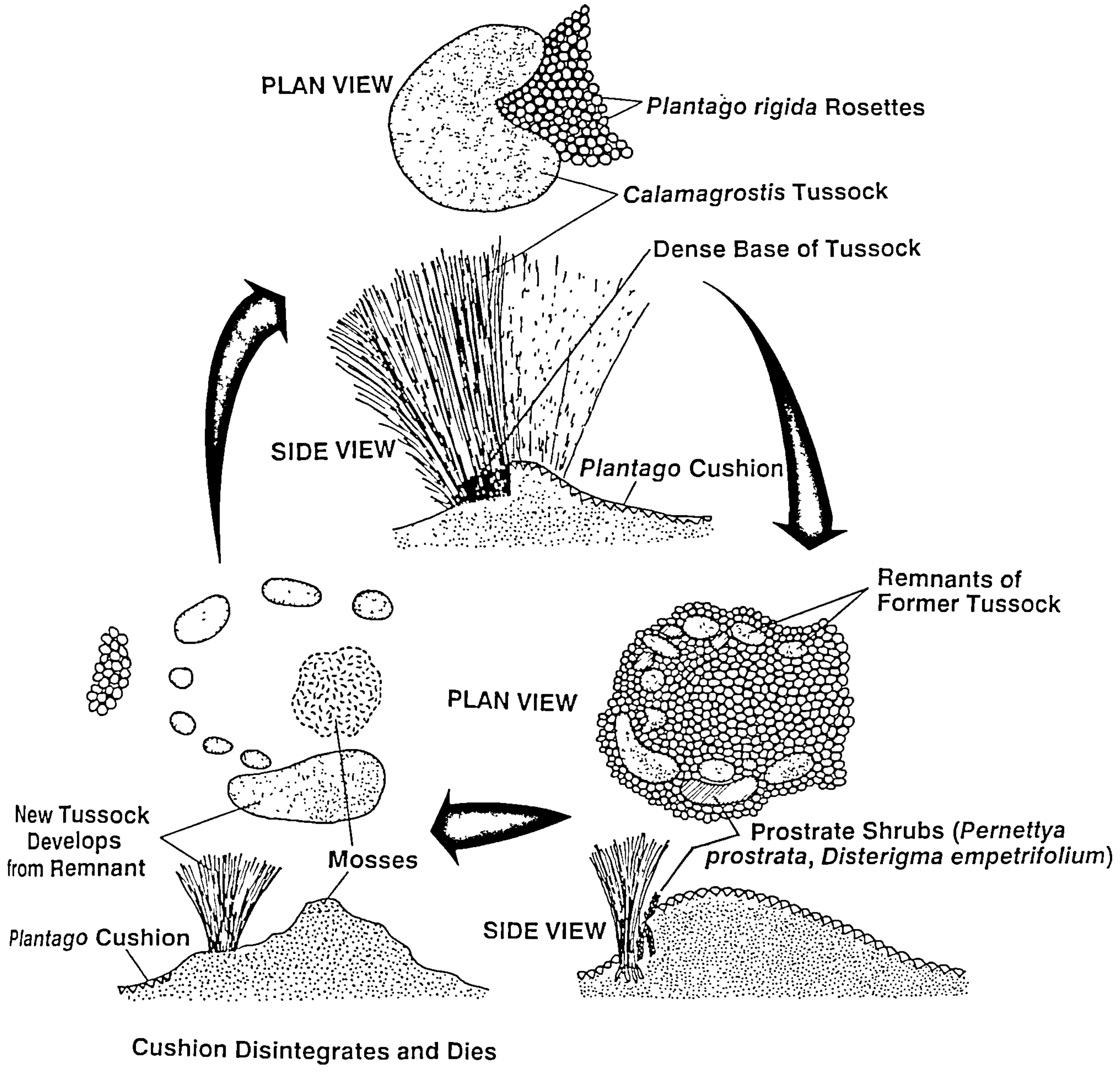


Figure 4.8.
The dynamic relationship between *Calamagrostis* sp. and *Plantago rigida* at 4,000 m in the Páramo de Daldal.

Transition Matrix Experiments

We have already seen that the intertussock vegetation accounted for approximately 68% of the ground cover at 3,750 m. The contributions of the species present in the microquadrat transects were calculated for both sampling times using frequency measures (Figure 4.9). In July, 32 species were recorded in the 1000 microquadrats, rising to 35 species in October.

Much of the intertussock region at 3,750m was bare ground, with 51.0% of microquadrats unoccupied in July, and 40.1% in October. *Azorella pedunculata* was by far the most important plant species beneath the *Calamagrostis* tussocks, accounting for 25.7% and 27.8% of the quadrats in July and October respectively. This species was even more influential in open areas around 3,200-3,500m in this valley, where montane forest had been cleared (see Chapter 5). The other species present were much less frequent, the most abundant being *Paspalum* sp. (4.2 and 6.5% in July and October, respectively).

The dynamic interactions between these species is most interesting. Table 4.4 shows the number of transitions occurring between the main species in the intertussock vegetation. During the study period (115 days), a remarkably high 36.9% of the microquadrats showed a change of occupancy. 61.2% of all unoccupied 100 mm^2 areas remained so throughout. χ^2 analysis showed that most of the transitions were explained by random replacements of one species by another. However, some transitions were found to depart from randomness (Figure 4.10).

42.7% of all changes involved gaps being replaced by *Azorella pedunculata* or *vice versa*. This pattern is characteristic of a short-lived ephemeral species, an opportunist which invades bare ground quickly and vacates it after its short lifetime ends. However, *A. pedunculata* is not an ephemeral. In fact, it is a 'k-selected' species forming mats of tough rosettes borne on thick, woody rhizomes (Figure 4.11). The *A. pedunculata* plant can be viewed as a 'raft' of rosettes on the soil surface, rather like corks on water. As old rosettes die, the raft is rearranged to fill the gaps. Similarly as a new rosette grows, the neighbouring rosettes are "reshuffled" to accommodate it by the turgor pressure of the new growth. Thus, the plant is able to make use of its surface area extremely efficiently. It is not clear whether this process can continue indefinitely: senescence may occur, the mobility of the rosettes lessened as the layer immediately beneath them becomes cluttered with decaying rhizomes.

Five 1 m transects were used to sample burned intertussock areas not far from those samples just described. Figure 4.12 shows the principal species in the intertussock zone, notably *Azorella pedunculata, Lachemilla orbiculata, Hydrocotyle bonplandii* and *Viola humboldtii*. Of the five hundred 100 mm^2 samples, 59.0% were devoid of plants. In total, nineteen species were present in the intertussock community samples one week after a fire (double this sample size revealed 32 species in nearby unburned vegetation at the same time). Moss species were noticeably infrequent at 1.2%, about one-fifth of that observed in the unburned vegetation.

Species at	Species at Time 2												
Time 1	1	3	5	9	14	15	24	29	42	46	R	G	T	T-D
1 Alch orbi	2	-	-	-	-	-	-	-	-	-	-	1	3	1
3 Azor pedu	½	169¾	3	1	10¼	¼	3	-	-	1	2¾	65	256½	86¾
5 Pasp sp.	-	3	31	-	-	-	-	5	-	1	-	6	41½	10½
9 Cala sp.	-	-	-	9	-	-	-	-	-	-	-	-	9	0
14 Relb croc	-	8	5	-	13	-	5	-	-	-	-	8	34½	21½
15 Care tris	-	1¼	-	-	-	11¼	-	-	-	-	-	-	12½	1¼
24 Gnap pens	-	-	-	-	-	-	12½	1	-	-	-	-	13½	1
29 Dist empe	-	-	-	-	-	-	-	5½	-	-	-	-	5½	0
42 Moss 2	-	-	-	-	½	-	-	-	9½	-	3½	3	16½	7
43 Moss 3	-	-	1	-	-	-	-	-	6½	-	3	-	10½	10½
44 Moss 4	1	-	1	-	1	-	-	-	1½	-	8	3	15½	15½
R REST	-	3½	2	-	2¾	-	-	-	3½	1	54¾	3	70½	15¾
G GAPS	4	92½	22	2	17	4	9	2	4	14½	27	316	514	198
T TOTALS	7½	278	65	12	44½	15½	25	9	25	18½	99	401	1000	
T-D	5½	108¼	34	3	31½	4¼	15½	3½	15½	17½	44¼	89		368¾

Table 4.4.

Transition matrix for "unburned" vegetation at 3,750m in the Páramo de Daldal. **Codes:** 1 *Alchemilla orbiculata*; 3 *Azorella pedunculata*; 5 *Paspalum* sp.; 9 *Calamagrostis* sp.; 14 *Relbunium croceum*; 15 *Carex tristicha*; 24 *Gnaphalium* aff. *pensylvanicum;* 29 *Disterigma empetrifolium;* 42 Moss 2; 43 Moss 3; 44 Moss 4; 46 Moss 6. REST: *Hypochaeris sessiliflora, Halenia weddelliana, Rumex acetosella, Trifolium repens, Gentiana sedifolia, Alchemilla andina, Hydrocotyle bonplandii, Geranium multipartitum, Festuca* sp., *Poa* sp., *Equisetum bogotense, Holcus lanatus, Plantago major, Oreomyrrhis andicola, Ranunculus pilosus, Aphanactis jamesonia, Nertera granadensis, Bidens andicola, Geranium reptans, Viola humboldtii,* Moss 1, Moss 7, Moss 8, Moss 11. G Gaps; T Totals; T-D Totals – Diagonals.

125 days later, the same samples in the burned area had 24 species, of which eight were new to the transects. Bare ground had fallen to 45.8%. The most frequent species was *Hydrocotyle bonplandii*, with *Azorella pedunculata* abundant too. *Lachemilla orbiculata, Rumex acetosella* and *Viola humboldtii* were also important elements in the intertussock community at this time.

A high proportion of the samples showed a change of occupancy (47.3%) from the first sampling one week after the fire to the second one, 107 days later (Table 4.5). A number of transitions within the matrix were significantly different from that expected by chance (Figure 4.13).

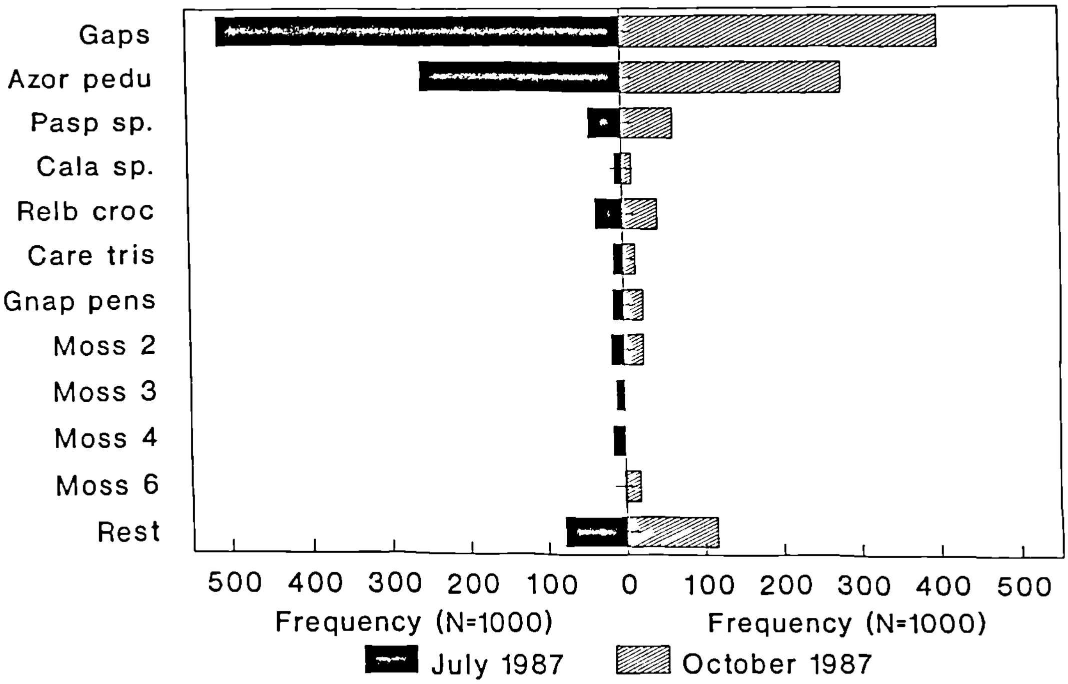


Figure 4.9.
The composition of unburned intertussock vegetation at 3,750 m in the Páramo de Daldal. The frequency of occurrence in one thousand 100 mm^2 microquadrats was recorded in July 1987 and 115 days later in October 1987. Full species names are given in Table 4.4.

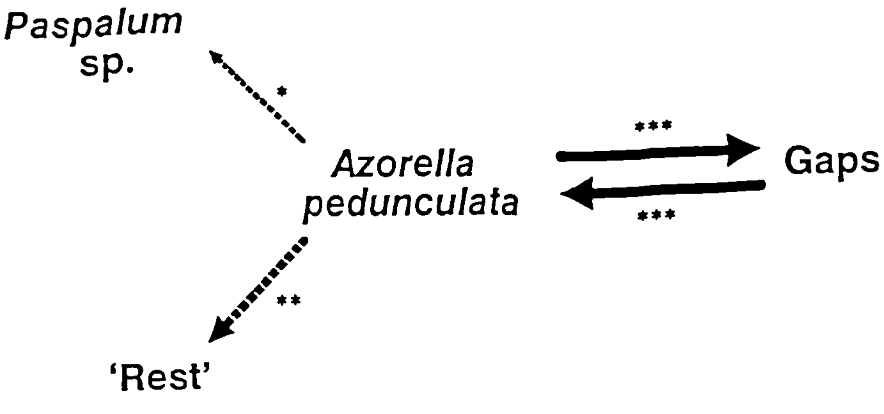


Figure 4.10.
*Constellation diagram showing significant deviations from random species re*placements in recently unburned vegetation at 3,750m in the Páramo de Daldal. The species comprising the 'Rest' are given in Table 4.4. Solid arrows = more than expected. Dashed arrows = less than expected. * $p<0.05$; ** $p<0.01$; *** $p<0.001$.

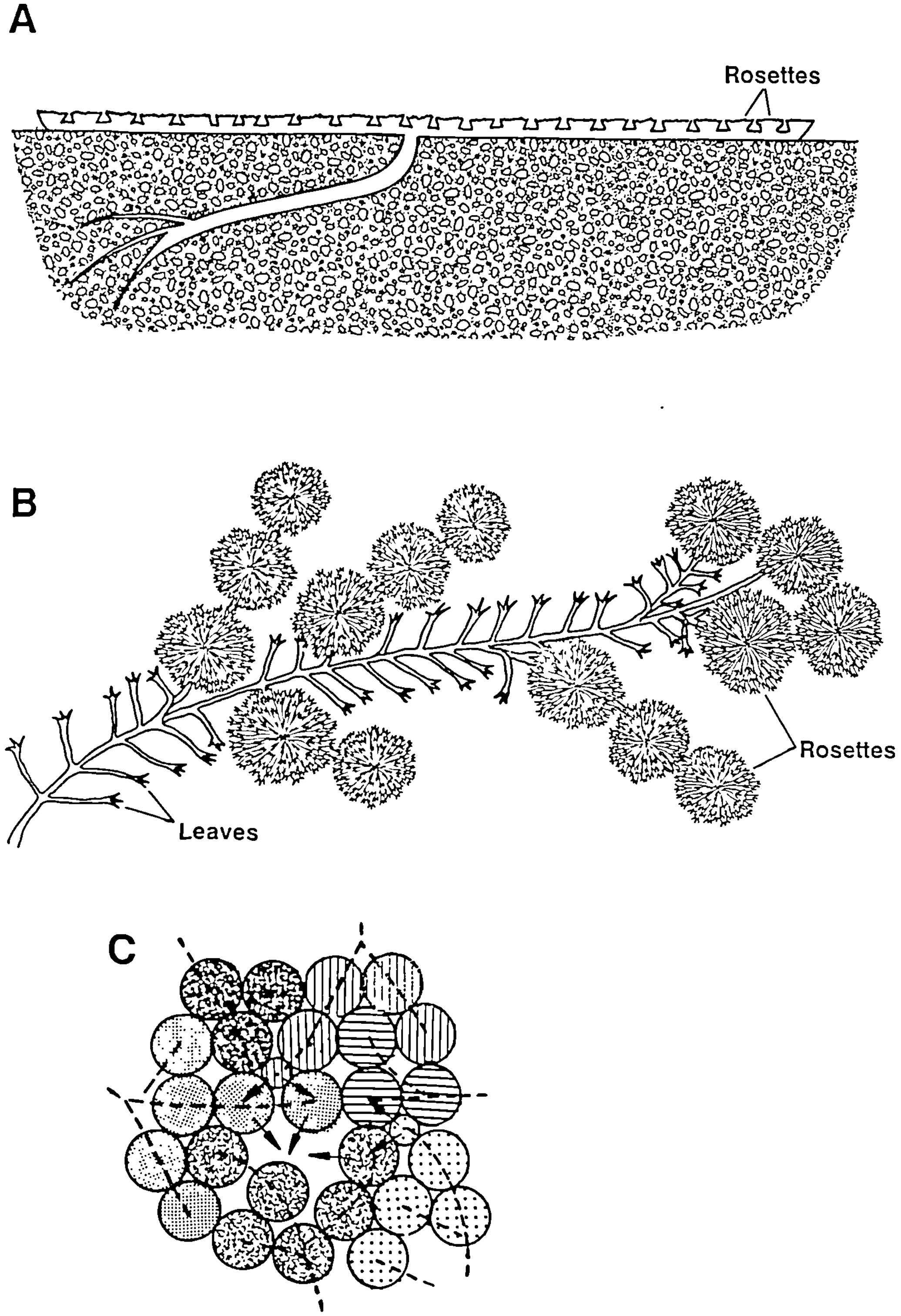


Figure 4.11.
The habit of *Azorella pedunculata*. A. Cross-section. B. Details of a portion of a branch. C. Diagrammatic representation of an area of *Azorella pedunculata* mat. Rosettes belonging to the same parent plant are the underlying branch system are indicated. The arrows show the forces applied by new rosettes and the movement of existing rosettes into spaces left by the death of other rosettes.

Species at Time 1	Species at Time 2								
	1	2	3	12	28	R	G	T	T-D
1 *Lachemilla orbiculata*	7½	-	2	13	1	3½	11	38	30½
2 *Rumex acetosella*	-	4	-	-	-	3½	-	7½	3½
3 *Azorella pedunculata*	2	-	45¼	5	-	7¼	24	83½	38¼
12 *Hydrocotyle bonplandii*	½	-	-	22½	-	1	6	30	7½
28 *Viola humboldtii*	-	-	-	-	4	-	-	4	0
R REST	-	-	2¼	3½	1	13¼	21	41	27¾
G GAPS	8	12	24	51	9	25	167	296	129
T TOTALS	18	16	73½	95	15	53½	229	500	
T-D TOTALS-DIAGONALS	10½	12	28¼	72½	11	40¼	62		236½

Table 4.5.
Transition matrix of replacements at 3,750m in the burned páramo of the Daldal valley. REST: *Trifolium repens, Paspalum* sp., *Bidens andicola, Geranium multipartitum, Relbunium croceum, Carex tristicha, Cotula ? mexicana, Plantago linearis, Gnaphalium* aff. *pensylvanicum, Holcus lanatus, Disterigma empetrifolium, Aphanactis jamesonia, Hypochaeris sessiliflora, Gentiana sedifolia, Geranium reptans, Plantago major, Valeriana microphylla*, Moss 2.

Once again, the reshuffling behaviour of *Azorella pedunculata* was evident from its higher than expected replacements of, and by, bare ground (but with a net loss overall). Bare ground was replaced by *Hydrocotyle bonplandii* and *Rumex acetosella* more often than random. As a group, the rarer species showed a very significant mortality rate ('being replaced by gaps'). This was probably the result of delayed fire damage. These species tended not to replace *Hydrocotyle bonplandii*, which in turn replaced *Azorella pedunculata* less than expected.

For comparison, Table 4.6 shows the species present in five sample transects located on ground that had been artificially cleared of vegetation. After 15 weeks, 10% of the microquadrats had been colonized—about two-fifths of these by *Rumex acetosella*, again demonstrating its opportunistic abilities. *Viola humboldtii* and *Cotula ? mexicana* between them accounted for a further quarter of the occupied quadrats. *Azorella pedunculata* was present in only two of the 500 microquadrats; probably regenerated from underground fragments of previous individuals.

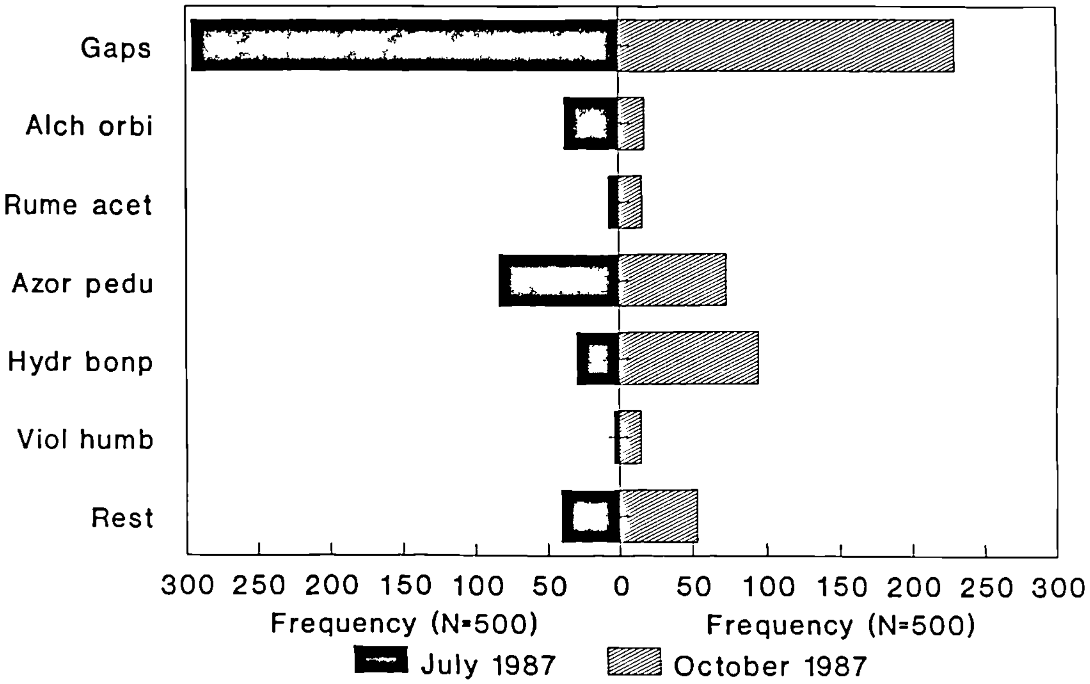


Figure 4.12.
The composition of burned intertussock vegetation at 3,750 m in the Páramo de Daldal. The frequency of occurrence in five hundred 100 mm^2 microquadrats was recorded in July 1987 and 125 days later in October 1987. Full species names are given in Table 4.5.

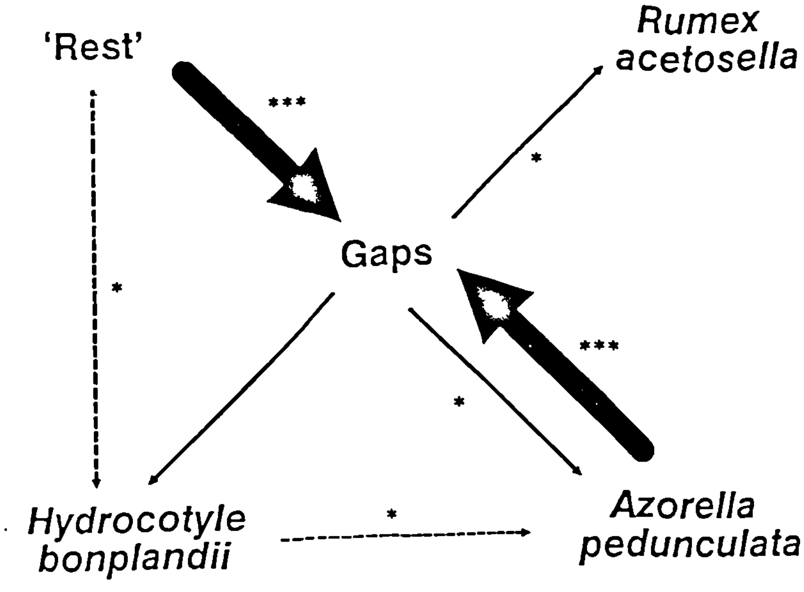


Figure 4.13.
Costellation diagram showing significant departures from random replacements in burned vegetation at 3,750m in the Páramo de Daldal. The species comprising the 'Rest' are given in Table 4.5.Solid arrows = more than expected.Dashed arrows = less than expected. * $p<0.05$; ** $p<0.01$; *** $p<0.001$.

Species	Freq.	%Freq.
Rumex acetosella	19	3.8
Viola humboldtii	6	1.2
Cotula ? mexicana	6	1.2
Hydrocotyle bonplandii	4	0.8
Gnaphalium aff. *pensylvanicum*	3	0.6
Aphanactis jamesonia	3	0.6
Hypochaeris sessiliflora	2	0.4
Moss 2	2	0.4
Azorella pedunculata	2	0.4
Carex tristicha	1	0.2
Stachys elliptica	1	0.2
Stellaria recurvata	1	0.2
Gaps	450	90.0

Table 4.6.
Composition of bared ground transects (500 microquadrats) at 3,750m after 108 days.

Similar experiments were carried out at 3,950 m. Figure 4.14 shows the major plant species found in this vegetation. There were fewer species in this area (27 at both times) than at 3,750m, though the sample area was smaller (0.06 m^2 rather than 0.10 m^2). Bare ground accounted for 34.8% of the microquadrats at the start of the study and 26.5%, 107 days later – much less than that observed 200m lower. *A.pedunculata*, so important at 3,750m, was not so frequent, occupying less than 5% of the microquadrats. Mosses were better represented, with a cover around 25% at both sampling times. *Geranium multipartitum, Lachemilla andina* and *Festuca* sp. were all important members of the intertussock community.

The transition matrix in Table 4.7 shows that 27.7% of the microquadrats were occupied by a different species at the end of the study from the one resident at the start; this is a much slower turnover than the 36.9% observed 200m lower. In fact, omitting the unchanged quadrats, only one replacement value departed significantly from random expectation. As a whole, the category in which all the rarer species were grouped ('Rest') did not invade gaps as frequently as chance alone would predict ($p < 0.001$). It is also worth noting that 64.1% of those quadrats which were unoccupied in July remained in this state throughout the course of the study period.

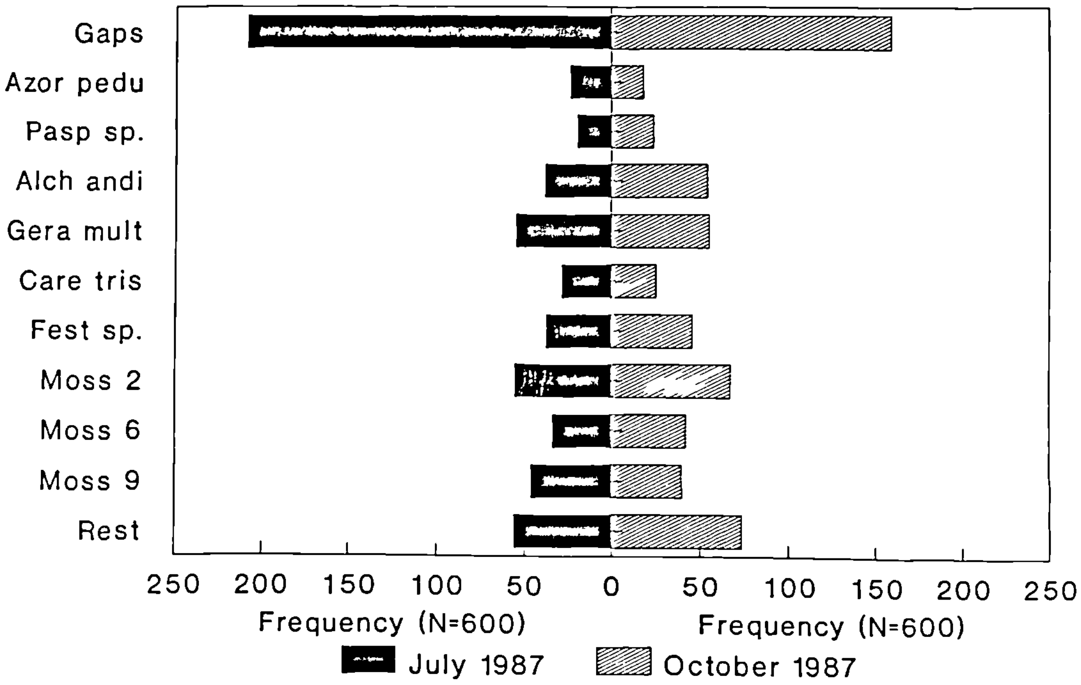


Figure 4.14.
The composition of unburned intertussock vegetation at 3,950 m in the Páramo de Daldal. The frequency of occurrence in six hundred 100 mm^2 microquadrats was recorded in July 1987 and 107 days later in October 1987. Full species names are given in Table 4.7.

Species at	Species at Time 2												
Time 1	3	5	11	13	15	16	42	46	49	R	G	T	T-D
3 *Azorella pedunculata*	15	-	1	-	-	-	1	-	-	1	5	23	8
5 *Paspalum* sp.	-	17½	-	-	-	-	1	-	-	½	-	19	1½
11 *Lachemilla andina*	-	-	33½	-	-	-	½	-	-	-	4	38	4½
13 *Geranium multipartitum*	-	-	-	41½	1	2	4½	1	-	3	2	55	13½
15 *Carex tristicha*	-	½	-	1	18½	1	2½	1½	-	1	2	28	9½
16 *Festuca* sp.	-	-	-	2	-	30½	½	-	-	1	3	37	6½
42 Moss 2	-	-	2	4	1	2	41½	-	-	4	1	55½	14
46 Moss 6	-	-	1	-	1	2½	1	25	-	3	-	33½	8½
49 Moss 9	-	-	2	-	-	-	-	2	36	5	1	46	10
R REST	-	-	2	1	2	-	1	1	1	41	7	56	15
G GAPS	3	6	13	6	2	2	14	12	3	14	134	209	75
T TOTALS	18	24	54½	55½	25½	40	67½	42½	40	73½	159	600	
T-D Totals-Diagonals	3	6½	21	14	7	9½	26	17½	4	32½	25		166

Table 4.7.

Transition matrix for "unburned" vegetation at 3,950m in the Páramo de Daldal. REST: *Lachemilla orbiculata, Calamagrostis sp., Hypochaeris sessiliflora, Rumex acetosella, Relbunium croceum, Geranium reptans, Pernettya prostrata, Azorella aretoides, Gentiana sedifolia, Hydrocotyle bonplandii, Trifolium repens, Oreomyrrhis andicola, Ranunculus pilosus, Gnaphalium* aff. *pensylvanicum, Stellaria recurvata*, Moss 1, Moss 3, Moss 5, Moss 7, Moss 10.

At 3,950m, bryophytes are responsible for most of the vegetation cover one week after a fire (Figure 4.15). The 300 microquadrats contained just eight species and 65.3% of the 100 mm^2 units were unoccupied. Fifteen weeks later, bare ground had dropped to 59.3% and the vegetation comprised 14 species with bryophytes again dominant. The transition matrix (Table 4.8) indicates the changes of occupancy of the microquadrats over the 108 days between these sampling times. In all, 45.2% of the microquadrats showed a change, nearly double that of the unburned vegetation nearby. By χ^2 analysis, the rarer species taken as a group were shown to be significant invaders of gaps (Figure 4.16). The relationship between Moss 6 and gaps was significant in both directions, with the moss both vacating and invading bare ground. This may be the result of delayed burning-related mortality and opportunistic behaviour in colonizing gaps.

Moss 6 was shown to be capable of invading bare ground in the study transects located in the artificially bared areas at 3,950m (Table 4.9). 93.6% of the area remained uncolonized after 15 weeks. *Hypochaeris sessiliflora* regenerated from its thick tap roots.

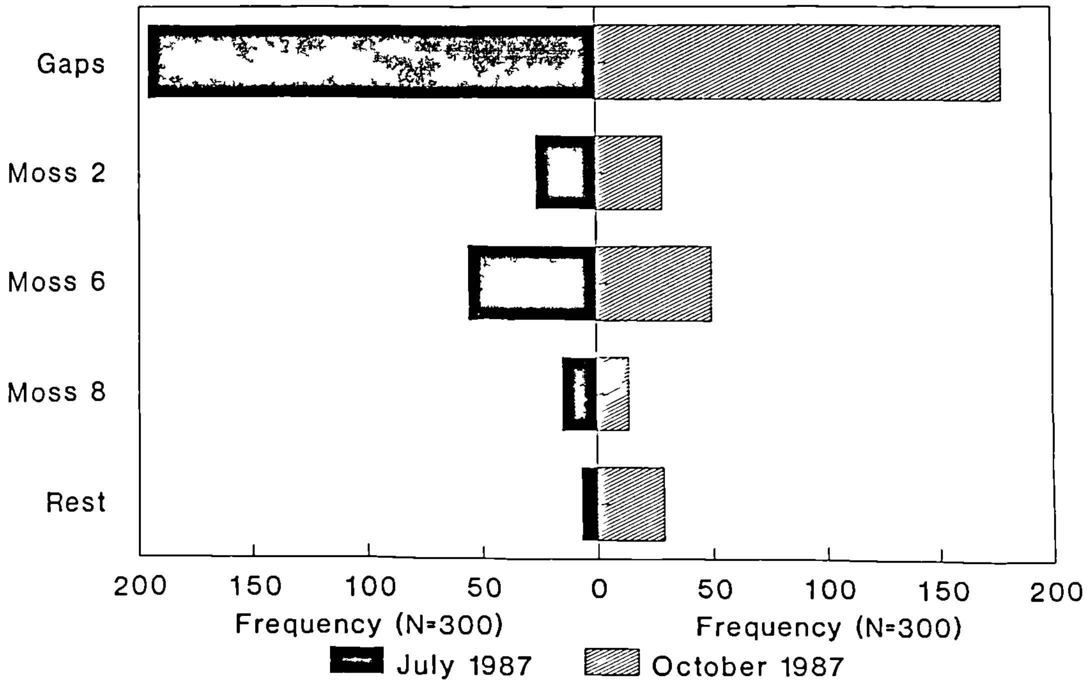


Figure 4.15.
The composition of burned intertussock vegetation at 3,950 m in the Páramo de Daldal. The frequency of occurrence in three hundred 100 mm^2 microquadrats was recorded in July 1987 and 107 days later in October 1987. The species comprising the 'Rest' are given in Table 4.8.

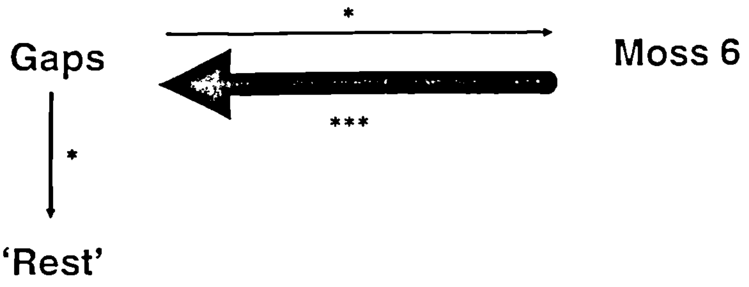


Figure 4.16.
Constellation diagram showing significant departures from random replacements in burned areas at 3,950m in the Páramo de Daldal. Solid arrows = more than expected. Dashed arrows = less than expected. * $p<0.05$; ** $p<0.01$; *** $p<0.001$.

Species at Time 1	Species at Time 2						
	42	46	48	R	G	T	T-D
42 Moss 2	8	8	1	1	8	26	18
46 Moss 6	6	12½	½	5	32	56	43½
48 Moss 8	-	3	7	-	5	15	8
R REST	-	-	1	5	1	7	2
G GAPS	15	26½	4½	18	132	196	64
T TOTALS	29	50	14	29	178	300	
T-D TOTALS-DIAGONALS	21	37½	7	24	46		135½

Table 4.8.

Transition matrix of replacements at 3,950m in the burned páramo of the Daldal valley. REST: *Lachemilla orbiculata, Rumex acetosella, Azorella pedunculata, Hydrocotyle bonplandii, Geranium multipartitum, Cotula ? mexicana, Geranium reptans, Plantago linearis, Azorella crenata, Viola humboldtii, Sibthorpia repens,* Moss 5.

Species	Freq.	%Freq.
Hypochaeris sessiliflora	7	2.3
Moss 2	5	1.7
Moss 6	4	1.3
Hydrocotyle bonplandii	1	0.3
Lachemilla andina	1	0.3
Aphanactis jamesonia	1	0.3
Gaps	281	93.9

Table 4.9.

Composition of bared ground transects (300 microquadrats) at 3,950m after 107 days.

Discussion

The páramo sites used for these studies were subjected to burning practices similar to those reported throughout the páramos (Smith & Young, 1987b; Laegaard, 1992; Verweij & Budde, 1992) and in other tropical alpine grasslands (Smith, 1975; Beck, Scheibe & Schulze, 1986; Velázquez, 1992). Generally, in a single páramo area, there exists a mosaic of vegetation representing different periods of recovery from burning which is clearly visible in the colouration of the vegetation.

The temperature distribution within the vegetation structure during a páramo fire has great implications for plant survival. Firstly, all plant material forming the upper part of the tussock is destroyed during a fire by high temperatures, sometimes approaching 600°C. Clearly, growth forms with unprotected meristems in or above this zone, such as upright shrubs, may be disadvantaged by burning (Hedberg, 1964). A number of species are able to regenerate from their roots. In the Páramo de Daldal, such species included: *Monnina crassifolia, Brachyotum ledifolium, Pentacalia andicola, Hypericum laricifolium, Valeriana microphylla, Chuquiraga jussieui, Vaccinium ?*

floribundum and *Lupinus ramosissimus*. Laegaard (1992) reports similar findings for some of these species. Beck *et al.* (1986) found that shrubs have a high capacity for regeneration in the East African tropical alpine grasslands: even after a severe burn nearly all shrubs regenerated.

The middle part of the tussock also reaches lethal temperatures (350-450°C), and this is of relevance to species living within the tussock. Such species include climbing herbs such as *Lobelia tenera, Draba* sp., *Vicia ? setifolia, Ageratina azangoroensis* and *Oxalis* sp., as well as erect herbs like *Festuca* sp. and *Trisetum spicatum*.

However, for these species and for *Calamagrostis* itself, the dense tussock bases offer protection from the intense heat generated in the canopy above. In both burning experiments, the dense base was subjected to relatively low temperatures, often below 65°C because the dense leaves of the tussock shielded the inner parts from the heat. Therefore, those plants with apical or axillary buds or rootstock capable of suckering within this region may be able to regenerate even though parts of the plant have been lost by fire.

Despite these relatively low temperatures during a fire, the subsequent exposure of new shoots to the harsh páramo environment can slow regeneration of the tussock. This allows opportunistic species, lying within the tussock as seed, to establish on the tussock. Some of these young plants will survive only until the tussock canopy closes (such as *Rumex acetosella*). Others can survive for longer periods of time and become established within the mature páramo community, though this may be only a small proportion of those seedlings which germinated. A good example of a species of this nature is *Lupinus* cf. *pubescens*.

Certain species appear to favour the edge of tussocks, demonstrated by a number of species in Table 4.3. The distribution of *Uncinia pheleoides* in Figure 4.4 shows the pattern well. It is not clear whether these distributions reflect a degree of protection from fire afforded by the tussock base or are the result of favourable sites for seedling establishment. The latter explanation was proposed by Miller & Silander (1991) to explain why *Puya clava-herculis* was frequently found inhabiting the tussock edge in Ecuadorian páramos.

The intertussock spaces and the sides of the tussock bases may reach temperatures on the ground of up to 375°C or 420°C if there is a good deal of dry matter in the tussocks. Temperatures of around 100°C are probably commoner in Daldal, where burning is a regular practice. This is also true of more humid páramos such as the Páramo de Guamaní, which produced temperatures between 65-120°C in the experimental burn.

Though temperatures on the ground may be lethal, temperatures remained low 20 mm under the surface (in all cases less than 65°C, the minimum limit for the pyrometers). Therefore, plants occupying the spaces between tussocks may have their aboveground parts destroyed but the subterranean organs are unaffected by the fire. Many plants can 'recolonise' a burned area simply by regenerating from rhizomes or roots (for example, *Azorella pedunculata* and *Hypochaeris sessiliflora*). Other species, including those just mentioned, shield delicate buds within less sensitive plant parts.

According to Laegaard (1992), the apical buds of acaulescent rosettes and cushion plants are often situated 10-20 mm below the surface. From the results of the experiments described here, this would afford such plants adequate protection from lethal temperatures.

At 3,750 m in the Páramo de Daldal, the species surviving a fire could be seen to benefit from the above factors. The commonest survivors following a fire were those able to resprout from rhizomes or rootstock: *Lachemilla rupestris, Lachemilla orbiculata, Hydrocotyle bonplandii, Rumex acetosella, Halenia weddelliana, Viola humboldtii, Sonchus oleraceus, Plantago major, Uncinia pheleoides* and *Cotula ? mexicana.* It is interesting to note that those species shielding the apical buds with plant parts did not survive the most intense fire, but were present following a less severe burn. Such species included *Azorella pedunculata* and *Hypochaeris sessiliflora.* It was also evident that particularly after a less intense fire, small patches of intertussock vegetation were commonly left alone by the fire. Within these patches, plants which did not appear to survive by means of one of the above strategies were observed. Such fortuitous survival enabled species such as *Paspalum* sp. to capitalise on the abundance of space and nutrients after a fire, as described earlier. Laegaard (1992) confirms these strategies for the majority of the above species.

The transition experiments corroborated these findings. In addition to the species mentioned above, the burned transects at 3,750 m also contained *Trifolium repens, Bidens andicola, Geranium multipartitum, Relbunium croceum, Holcus lanatus, Aphanactis jamesonia* and one species of moss.

Following this initial survival, remaining bare ground was colonised by opportunistic species from seed. In particular, *Rumex acetosella* and *Hydrocotyle bonplandii* were shown to increase their presence more than chance alone would predict. *Hydrocotyle bonplandii* was shown to be resistant to invasions by the rarer species, but was itself less likely to replace *Azorella pedunculata* rosettes.

By contrast, a highly significant mortality of *Azorella pedunculata* rosettes and a number of the rarer species was observed in the transects. This indicates that a number of individuals which survived the fire initially did not persist, perhaps because they sustained critical damage which could not be repaired.

Although colonisation was taking place, this was a slow process: the proportion of gaps in the transects decreased from 59% to 46%. However, nearby unburned vegetation showed a similar proportion of gaps (51% and 40%). The data from the control transects suggest that *Azorella pedunculata* is likely to proliferate at the expense of many of the other species which have colonised the burned area, and that a further reduction in bare ground is unlikely.

Of the twelve species found in the cleared transects at this altitude, all but two rare species were present in the burned plots. This indicates that these colonists do not rely on burning for seed germination, but merely take advantage of disturbance, whatever form it may take. Interestingly, 90% of the bared transects were unoccupied, compared with 40% and 46% in the associated control and burned plots. Removal of the upper 20 mm of soil has much more serious implications for the regeneration of intertussock vegetation than a fire. The importance of regrowth from plant parts just beneath the surface is confirmed.

At 3,950 m, survival following burning was much lower than in the transects just described. About 65% of the intertussock spaces were bare, and only eight species survived, with half of these being bryophytes. The diversity of these transects increased in the following 108 days to fourteen species, largely by the invasion of bare ground (which decreased to 59%). There was a high turnover of species in these plots, however, mostly the result of delayed mortality in Moss 6. This species also colonised bare ground, and replaced a number of other bryophyte species.

Unburned vegetation at 3,950 m was found to contain almost twice as many species (in twice as many sample units). The commonest species from the burned plots were also present in the controls. Bare ground was very low: 35% at the start of the experimental period and 27% at the end. In this crowded situation, it was found that the rarer species did not colonise gaps as frequently as chance would predict, perhaps because competition for resources was high.

When this vegetation was cleared by removing the upper 20 mm of soil, recolonisation was slow (similar to that 200 m lower in the páramo). After 107 days, only 6% of the ground had become occupied, more than half of this by regeneration by *Hypochaeris sessiliflora* from tap roots. Bryophytes were less successful colonists than in the burned plots, but the two principal species in the burned transects were important in bared ground. In experimental studies in the Venezuelan páramo, Pfitsch, Smith & Rodriguez Poveda (unpublished – cited by Smith & Young, 1987b) also found that recolonisation of bared plots at high altitudes was a slow process. These plots were colonised by a gradual accumulation of species from the mature community, without early specialist species. In the Páramo of Daldal at 3,950 m, there appears to be some evidence to support these observations (the establishment of *Hypochaeris sessiliflora*) but other colonists were more opportunist species which characterised the invasion of disturbed ground at lower altitudes (*Hydrocotyle bonplandii* and *Aphanactis jamesonia*). However, the climatic conditions at this altitude were not so severe as those reported in the Venezuelan experiment.

From these studies in the Ecuadorian páramos, a number of generalisations can be made:

- The temperature during a fire is determined mainly by the structure of the vegetation. The highest temperatures are produced in the tussock canopy, the lowest within the tussock base and just beneath the surface.
- Regeneration from below ground plant parts (including those within the tussock bases) is the main form of recovery from fire.
- The severity of the fire (largely a function of the interval since the last burn) determines the degree of survival of intertussock species on the ground surface.

- Initial survival does not guarantee persistence in the community. Both tussock grasses and intertussock species show significant mortality rates in subsequent months.
- Recovery is slower at higher altitudes.
- Burning may induce cyclical patterns of community development, illustrated by the interactions of *Calamagrostis* sp. and *Paspalum* sp. in the Páramo de Daldal.
- Certain species quickly colonise bare ground by seed. These may persist to maturity, but most will be killed by competition from neighbours as the vegetation matures.
- Some species (such as *Lupinus* cf. *pubescens*) appear to rely heavily on burning for establishment within tussocks (where mature individuals are found).

It is clear that páramo vegetation in Ecuador is able to regenerate relatively rapidly after burning. Similar rates of renewal are inferred from studies in Colombian páramos (Pels & Verweij, 1992; Verweij & Budde, 1992). In Chirripó National Park, Costa Rica, recovery was well underway a few months after a huge páramo fire (Boza, 1978). This contrasts with observations by Janzen (1973), again in Costa Rica, where regeneration was very slow, with large patches of bare ground still present three years after the fire.

Transition matrix studies have often been associated with predictions of succession (Horn, 1975; Usher, 1979, 1981; Noble & Slatyer, 1981; Hobbs & Legg, 1983; Lough *et al.*, 1987). However, in the present study this approach was considered inappropriate, mainly because of the short timescale over which the observations were made. The early changes in specific composition during recovery from disturbance are usually faster than the later changes (Shugart & Hett, 1973), and several of the pressures acting upon individuals are not uniform over time (for example, grazing influence is especially common immediately after a fire – Verweij & Kok, 1992). Therefore, the fixed transition probabilities demanded by Markov modelling do not apply to páramo vegetation after a fire (Pels & Verweij, 1992).

Further to this argument, in East African tropical alpine grasslands, the studies of Beck *et al.* (1986) indicated that linear succession after burning did not take place. Rather, burning began a series of complete or incomplete (if burning was repeated too soon) successional cycles. In order to predict the patterns of replacement during such cycles, observations are required over the entire simulation period. It is not clear how long such recovery cycles might be in the Ecuadorian páramo, and complete recovery could involve several decades or more.

Apart from the dynamics directly relating to páramo burning, these studies have brought to light interesting aspects of the small-scale changes associated with unburned vegetation. Notably, the majority of changes of occupancy in the transition studies involved gaps and appeared to be random replacements. Similar findings were made by Thórhallsdóttir (1983, 1990) in a grassland community in North Wales.

Gaps are known to be important in the dynamics of many plant species, and even small ones can influence local conditions (Silvertown, 1981). The frequency of gaps was high bearing in mind the dense appearance of the vegetation (51.0% and 40.1% at 3,750 m, and 34.8% and 26.5% at 3,950 m, in July and October 1987 respectively). Thórhallsdóttir (1983, 1990) reported gap frequencies of 17-60% (mostly around 30%) in North Wales. She also noted that clonal species tended to replace and be replaced by gaps more often than chance would predict. This was found to be true in the páramo, exemplified by the behaviour of *Azorella pedunculata*.

The mobility of mats of *Azorella pedunculata* in many ways resembles the floating rafts of the Water Hyacinth (*Eichhornia* sp. — Watson & Cook, 1982). Clearly this mobile collection of rosettes and underlying rhizomes presents several problems to other plant species. To compete with *A. pedunculata* a plant must be capable of resisting the movement of the mat or must itself be flexible to move with the rosettes. Certainly, *Paspalum* sp. and the rarer species (grouped together) were found to be significantly less likely to replace an *A. pedunculata* rosette than chance would predict.

The fact that the main means of spread for *Calamagrostis* sp. is by vegetative reproduction from large, established tussocks may explain why the mat is unable to exclude the tussock grass. While the *A. pedunculata* mat may be an able competitor for space, it may not be so adept at competing for light. The leaves of the grass shade out the *Azorella* rosettes, allowing new tillers to develop at the tussock edges.

Grubb (1977) noted the lack of information on *Calamagrostis* sp. regeneration in the Andes. Although some seedlings of *Calamagrostis* sp. were encountered in the transition matrix studies, these were relatively uncommon and vegetative spread in kaleidoscopic pattern is the principal means by which tussocks are maintained within the community.

Some 250 m higher in altitude, and the dominance of *Calamagrostis* tussocks over cushion and mat species is lost. The cyclical processes in operation in the boundary zone between grass and cushion páramos was described earlier and is similar to that described by Lough *et al.* (1987) for a New Zealand alpine cushion community.

It is not clear what forces drive this process. However, the existence of an apparently persistent and stably cyclic dynamic relationship implies either an extrinsic environmental cycle (unlikely in the páramo) or a cycle in one of the dominant species (Horn, 1974). Since both species can exist both above and below this altitude (personal observation), it would appear that some environmental factor or factors result in a spatial change in relative competitive abilities of the two dominant species. The lower limit of extensive cushion vegetation elsewhere in the Andes seems to be the result of interspecific competition (Armesto, Arroyo & Villagran, 1980; Alliende & Hoffmann, 1985).

It may be, as suggested by Laegaard (1992), that tussocks become overmature and can no longer supply water and nutrients to satisfy the needs of the plant (water requirements become more difficult to meet at higher altitudes – Meinzer & Goldstein, 1986). The same factor may also explain the reduced vitality of the cushions and their subsequent decay, also observed in the Colombian páramos by Cleef (1981). With the competitive ability of the tussock reduced, the cushion invades. Alternatively, it could be that occasional burning at this altitude exerts a significant stress on the tussocks (fire can spread between the widely-spaced tussocks if it is windy). Some other factors, relating to climatic or edaphic features of the local environment may also be involved.

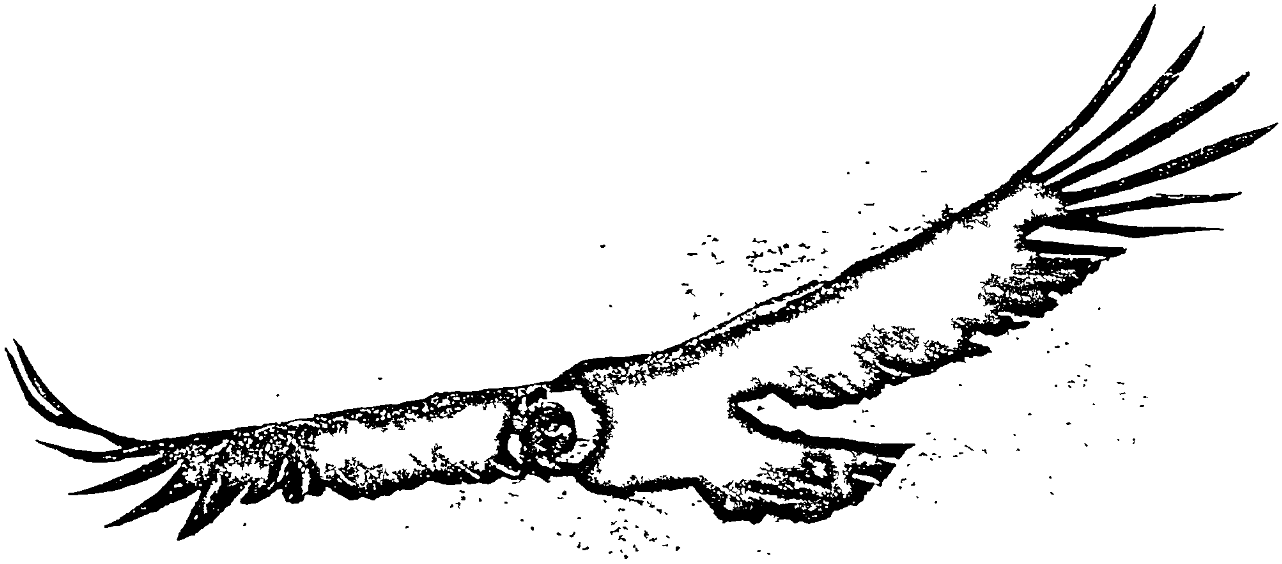
The invasive behaviour of *Plantago rigida*, overgrowing other plants to form cushions is mirrored elsewhere. Nathaniel (1985) describes a similar mechanism in the formation of *Plantago rigida* cushions on the slopes of Volcán Cotopaxi, Ecuador, and *Werneria humilis* also appears to share this behaviour (personal observation). Lough *et al.* (1987) observed an analogous process with different species in New Zealand.

The widespread existence of this transition from grass páramo dominated by *Calamagrostis* sp. tussocks to cushion páramo dominated by *Plantago rigida* implies that the controlling factor or factors are also widespread. The explanation of this fundamental physiognomic change would provide a valuable insight into the mechanisms operating throughout the páramo ecosystem.

Clearly, fundamental research into the small-scale dynamics of páramo vegetation is a rewarding undertaking. Even very brief studies, such as those described here, can facilitate the interpretation of the large-scale community in terms of the agents that maintain them.

Chapter 5

An Assessment of Net Aboveground Primary Productivity in the Andean Grasslands of Central Ecuador



Introduction

The severity of the high altitude tropical environment has often lead to comparisons with arctic and temperate alpine ecosystems (Bliss, 1971; Tieszen & Detling, 1983). Comparisons between temperate alpine and tropical alpine areas have shown that, although temperate alpine regions experience more favourable conditions during the growing season, the tropical montane environment experiences a greater number of degree hours per year (Billings, 1973). From this evidence, Smith & Young (1987b) suggest that tropical alpine communities may be more productive on a yearly basis than their temperate counterparts.

The páramos throughout the Northern Andes are used for extensive grazing of cattle, sheep, horses and mules. In the early 1950s, it was estimated that over half of Ecuador's cattle and around 85% of its sheep were grazed on the páramos (Acosta-Solís, 1960). With the colonisation of Amazonia in recent times, the páramos no longer contribute such high proportions of Ecuador's cattle production, but they are nevertheless a critical element of the rural economy in highland regions. In fact, it seems likely that increasing population pressure, diminishing isolation and the loss of self sufficiency in many rural communities has led to a recent increase in the head of domestic livestock on the páramos of Ecuador. A particularly important feature of livestock is that they represent an investment immune from inflation – a "living bank account on the hoof" (Brush, 1976).

The previous chapter looked at the dynamic processes associated with burning to improve forage quality in the páramo. Grazing and trampling pressures are also important influences on plant community composition (Verweij & Budde, 1992). Unfortunately, such pressures have resulted in the degredation of some páramo ecosystems (Grubb, 1970; Smith, 1981; Acosta-Solís, 1984; Ramsay, 1988; Grubb, Lloyd & Pennington, unpublished) and the neighbouring ceja andina forests (Brandbyge & Holm-Nielsen, 1986; Laegaard, 1992; Verweij & Beukema, 1992).

Up to this date, there have been few published studies of the productivity of natural communities in any tropical alpine region of the world (Smith, 1987). One study carried out by Hnatiuk (1978) reported net aerial productivity rates of 1.28-4.42 t ha^{-1} yr^{-1} in the grasslands of New Guinea. Acosta-Solís (1984) estimated a yield of 4.35 t of dry matter per hectare per year in the Páramo de Chiquicagua, Ecuador, though the methodology described indicates that the value given is in fact an estimate of standing biomass rather than productivity *per se*. A table of data for plots in the páramo of Volcán Antisana, Ecuador, appears in Black (1982). Values range from 2.60-21.40 t and plots were subjected to burning, cutting and fertilizer treatments. However, the reported details of the experimental design (exact method of data collection, sample sizes, whether harvested material was dried before weighing, *etc.*) are not sufficient to allow any interpretation of the values presented.

This chapter reports preliminary studies of grassland productivity over an altitudinal gradient in the Andes of central Ecuador. Apart from providing data on standing crops, comparisons are made between the aboveground net primary productivity of

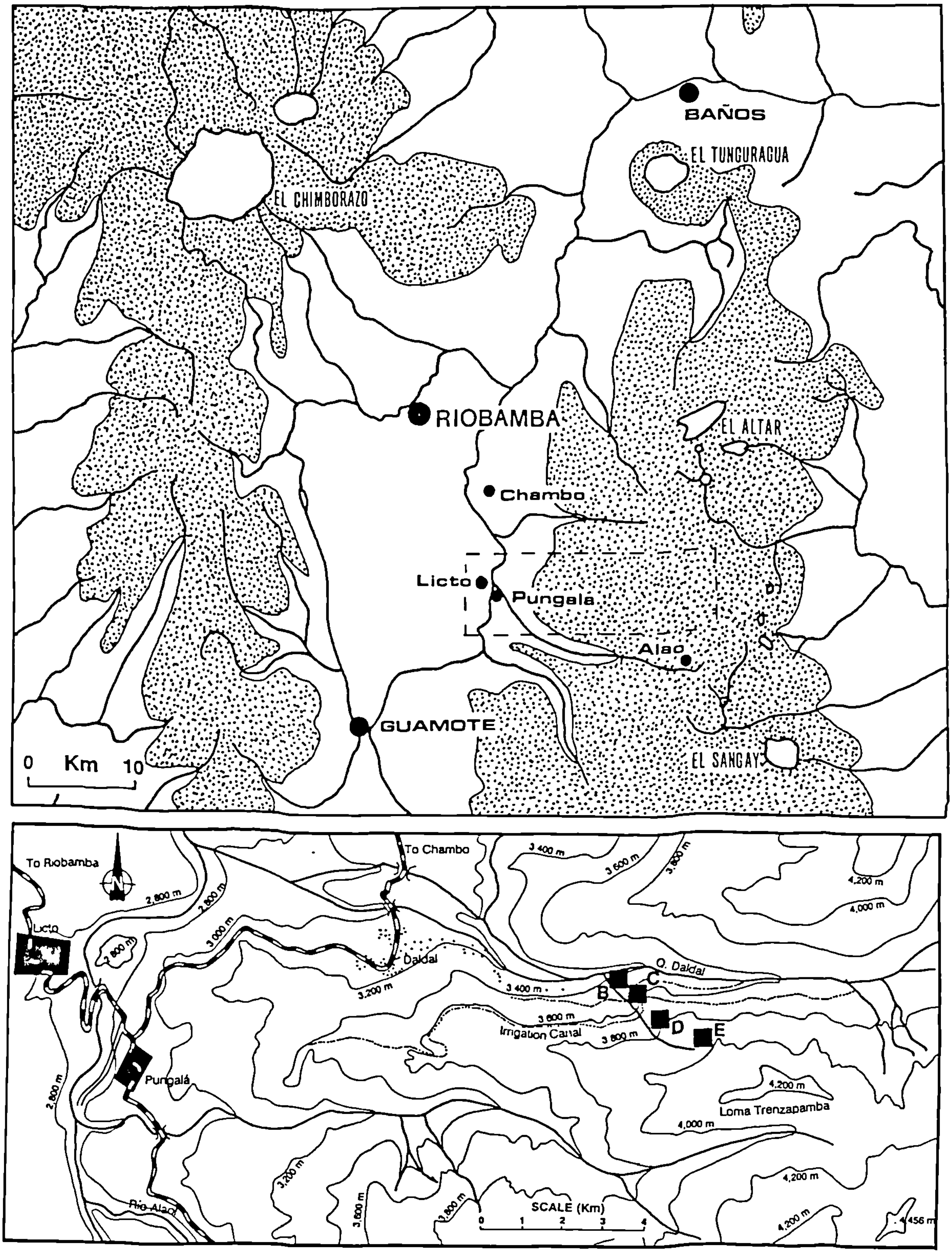


Figure 5.1.
The location of the productivity experiments. A. The village of Alao is situated to the south-east of Riobamba. One exclosure (site A) was located at the Sangay National Park guardpost in Alao. B. The general location of this area is shown in (A) as a box with dashed lines. Four exclosures (sites B-E) are shown in the upper Daldal valley.

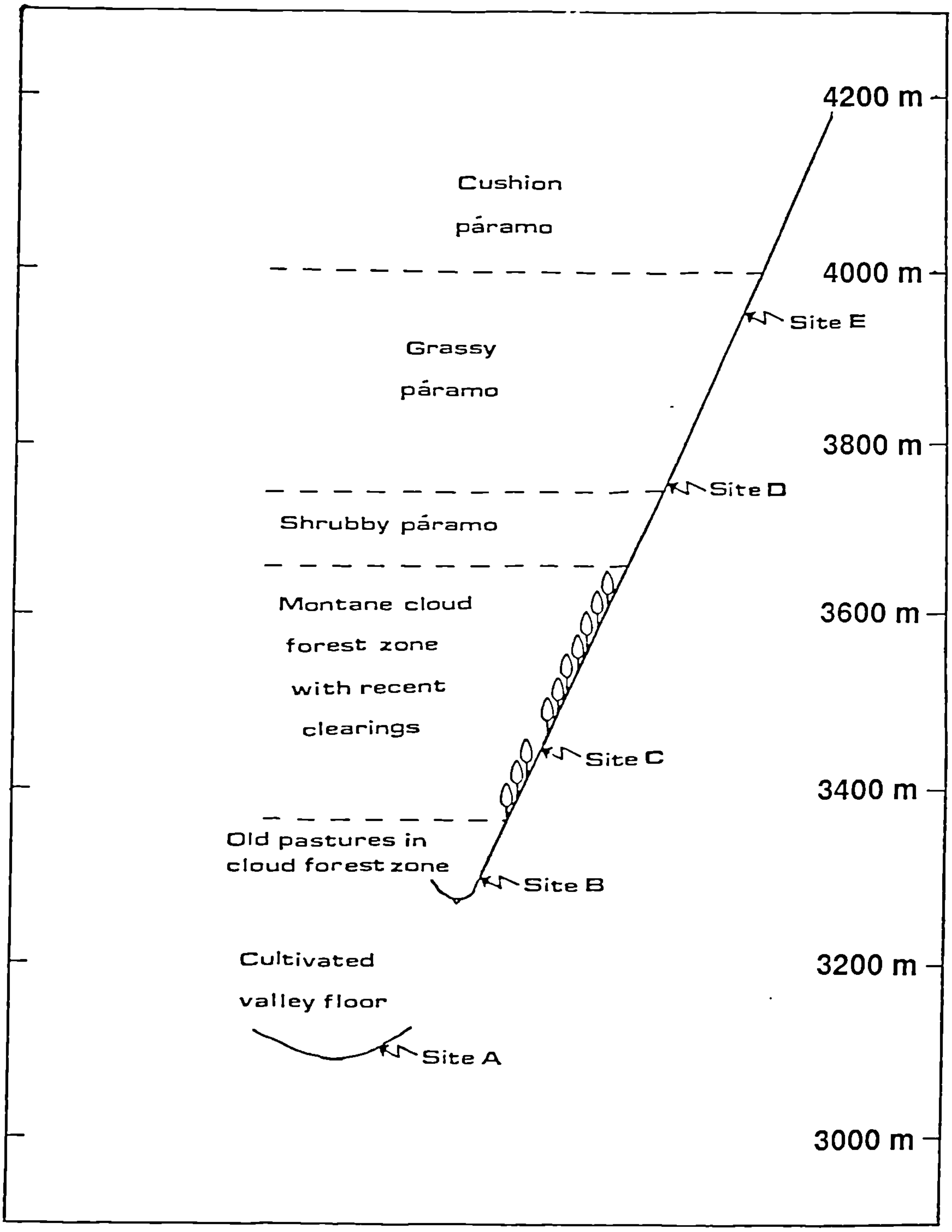


Figure 5.2.
Diagrammatic representation of the five exclosure sites used in the productivity studies in the valleys of Alao (lower valley system with site A) and Daldal (upper valley system with sites B-E). The slopes have been greatly exaggerated.

areas covering an altitudinal range of nearly 1,000m, from improved pastures in the valley bottoms to the upper reaches of agricultural use in the grass páramo at nearly 4,000m. Applications of fertilizer were used to assess the potential improvement of natural grasslands and cutting regimes were applied to simulate grazing and burning.

Methods

Study Sites

The experiments were carried out in the highland valley systems of Alao and Daldal, about 40-50km south-east of Riobamba (Figure 5.1). Five pastures were chosen to cover the altitudinal gradient and the transition from improved grasslands to unimproved ones (Figure 5.2).

The Alao Valley, Site A: 3,100m

The valley of Alao has been used intensively for agriculture for many years. Cereals, potatoes and other crops are grown on the steep slopes of the valley, and animals are

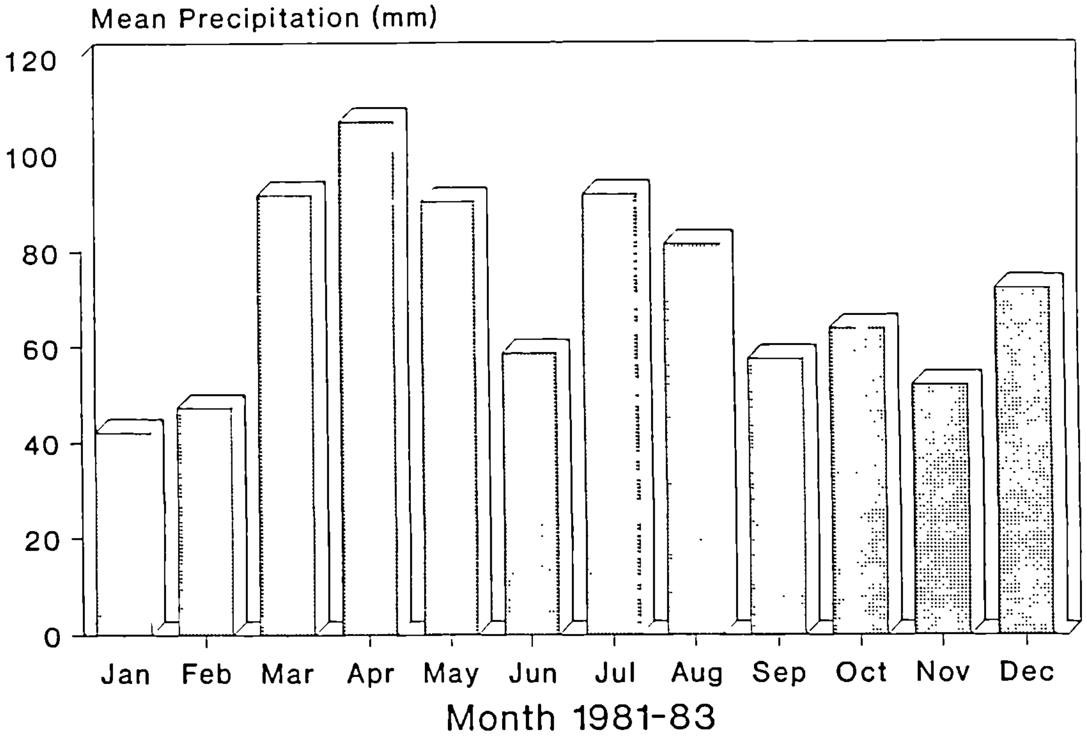


Figure 5.3.
Monthly precipitation for Alao, with means calculated from data for the period 1981-1983 (from the Instituto Nacional de Meteorología e Hidrología, Quito, for station M396 Alao). Temperature records for this period were incomplete.

reared on small pastures and amongst the crops. Alao is also the gateway to Sangay National Park and a guardpost has been built on the flat valley plain to monitor visitors. The experimental site was located within the grounds of this guardpost. The area was flat and sheltered to some extent by trees and buildings. The soil showed good drainage.

The meteorological station at Alao recorded 100 and 147 days of rain in 1981 and 1983, amounting to precipitation totals of 737.7 and 975.3 mm yr^{-1} respectively. Over these years, a maximum of 33.8 mm fell during any 24-hour period. The pattern of rainfall for the years 1981-83 is presented in Figure 5.3. Around 61% of the annual precipitation falls between March and August, with a peak in March to May. No other meteorological data was available.

The vegetation consisted of short-cropped grasses (about 5cm tall), which were intensively grazed from time to time by horses and cattle. There were no signs of cultivation, though nearby, vegetable crops were growing in tilled soil.

		Site			
Species	**A**	**B**	**C**	**D**	**E**
Dactylis glomerata	d	+			
Trifolium repens	+	+	+	+	
Holcus lanatus	+	+	+		
Anthoxanthum odoratum	+		+		
Lolium sp.	+				
Alopecurus sp.	+				
Azorella pedunculata		d	d	+	+
Carex tristicha		+	+	+	+
Lachemilla orbiculata		+	+	+	+
Ranunculus sp.		+	+	+	+
Bidens andicola		+	+	+	
Gentiana sedifolia		+		+	+
Geranium sibbaldioides		+		+	+
Paspalum sp.		+	+		
Hydrocotyle bonplandii		+	+		
Taraxacum officinale		+	+		
Bromus sp.		+			
Agrostis sp.		+			
Stellaria leptopetala		+			
Gnaphalium aff. *pensylvanicum*		+	+		+
Geranium multipartitum			+	+	+
Cerastium sp.			+	+	
Bromus lanatus			+		+
Festuca sp.			+		
Trisetum spicatum			+		
Festuca sp.			+		
Calamagrostis sp.				d	d
Paspalum tuberosum				+	+
Cotula ? mexicana				+	+
Halenia weddelliana				+	+
Senecio pimpinellifolia				+	+
Valeriana microphylla				+	+
Hypochaeris sessiliflora				+	+

Table 5.1 (Part 1).

Species list for the exclosures at the five study sites. Site codes: A, 3, 100m; B, 3,250m; C, 3,450m; D, 3,750m; E, 4,000m. "d" represents the dominant species.

		Site			
Species	**A**	**B**	**C**	**D**	**E**
Rumex acetosella				+	+
Hieracium frigidum				+	+
Lachemilla andina				+	+
Plantago major				+	+
Ranunculus peruvianus				+	+
Relbunium sp.				+	+
Poa sp.				+	+
Agrostis sp.					+
Gramineae					+
Gramineae					+
Sisyrinchium jamesoni					+
Vaccinium sp.					+
Equisetum bogotense					+
Vicia sp.					+
Lycopodium sp.					+
Ericaceae					+
Oreomyrrhis andicola					+
Pernettya prostrata					+
Sibthorpia repens					+
Disterigma empetrifolium					+
Oritrophium peruvianum					+
Cerastium sp.					+
Azorella aretoides					+
Niphogeton dissecta					+
Viola humboltii					+

Table 5.1 (Part 2).
Species list for the exclosures at the five study sites. Site codes: A, 3, 100m; B, 3,250m; C, 3,450m; D, 3,750m; E, 4,000m.

The stand was characterized by grasses such as *Dactylis glomerata, Lolium* sp., *Anthoxanthum odoratum, Holcus lanatus* and *Alopecurus* sp. Other herbaceous elements included *Trifolium repens* (Table 5.1).

The Daldal Valley

The remaining four sites were located in the valley of the Río Daldal (Figure 5.1, b). A small farming community occupied the lower end of the valley, but the huts above 3,400m were used solely for temporary accommodation. The lower part of the valley above the settlement of Daldal was once forested, perhaps within the last century. Some small patches of forest still remained but they were highly modified. Clearance of these patches was taking place and during the course of the study, a significant area was cleared for firewood. Forest clearance was carried out more for local fuel requirements than for agricultural purposes. As a result of these activities, this part of the valley showed a mosaic of forest and clearings of varying ages, some of the older pastures having been colonized by species characteristic of 'improved' grasslands. In this zone, some tributaries of the Río Daldal showed signs of re-routing by man and irrigation ditches had been skilfully constructed along the contours to channel water for agricultural and domestic use. Above 3,650m, the forest was replaced by shrubby grassland (sub-páramo). The upper limit of the forest was gradually being pushed lower by burning from above. In some parts of the valley only a narrow belt of forest existed between 3,400-3,450m, a consequence of burning from above and felling from below. The higher portions of the Daldal valley were covered with páramo grassland, typical of the highest reaches of the northern Andes. From 3,750-4,000m, the páramo was dominated by tussock grasses, but above this level, cushion plants became co-dominant. The vegetation of the Daldal páramo has been discussed in earlier chapters. No meteorological data exists for this area.

The experiments were carried out on the land of Bolívar Coronel, a local farmer, who owned a stretch of pastures and forest from 3,250m to 4,200m.

Site B: 3,250m

The chosen area was sited on the valley floor, beside the Rio Daldal at 3,250m. The vegetation at one time would have been naturally forested, but at the time of study it consisted of short grasses (no more than 3cm high) and other herbs with a substantial cover of a mat-forming species. The field was used to graze 10 cattle throughout the year. There was little evidence for significant grazing by rabbits. At one time, a small rivulet flowed through the pasture to join the R. Daldal, but had since been re-routed. The ground sloped 5° from horizontal with a north-westerly aspect, and no visible signs of previous cultivation. The pasture had been colonized by some species characteristic of improved grassland. The dominant species, however, was *Azorella pedunculata*, which formed a dense mat over the surface of the ground. Small patches and individual plants of other species grew through this mat, notably *Paspalum* sp., *Holcus lanatus, Dactylis glomerata, Trifolium repens* and *Bidens andicola* (Table 5.1).

Site C: 3,450m

Amongst the remnants of secondary *ceja andina* cloud forest in the Daldal valley were cleared patches of land up to half a hectare in area (but usually much less than this). Often, the stumps of the once-dominant trees and shrubs were still very much in evidence, some resprouting to form small bushes. The exclosure was erected in an area free from such bushes, at 3,450m on sloping ground (8° from horizontal) with a westerly aspect. Cattle freely grazed, dividing their time between these forest clearings and the field lower down (site B), this latter site being favoured more often. Rabbit grazing was more important here than at site B.

Like the exclosure at Site B, these plots were dominated by the presence of a mat of *Azorella pedunculata*. Other important floristic elements included *Paspalum* sp., *Holcus lanatus, Trifolium repens* and *Bidens andicola* (Table 5.1).

A small area of land not far from the study plot was used to cultivate potatoes, beans, oca and carrots.

Site D: 3,750m

The fourth exclosure was situated at 3,750m, above the forest patches, in páramo grassland. The slope of the ground was 18° from horizontal with a northerly aspect. The plots were exposed to strong up-slope winds. Tussock grasses of *Calamagrostis* sp. dominated the vegetation with other grasses and herbs performing a secondary role within the dense tussocks or in the intertussock spaces. Small, woody plants of *Valeriana microphylla* and *Lupinus* sp. were frequently found amongst the tussocks, and larger shrubs (*Brachyotum ledifolium*, in particular) were locally common, though absent in the experimental plots (Table 5.1). This type of vegetation is often described as sub-páramo (Cuatrecasas, 1958, 1968). Cattle were allowed to graze freely in this area, the vegetation being regularly burned (once every 2-4 years) to remove dead leaves and to stimulate the production of nutritious, young shoots. Rabbit grazing may have been as important as that of livestock, but there was no data available to support this.

Site E: 4,000m

The highest exclosure was located at 3,900m in grassy páramo or páramo proper (Cuatrecasas, 1958, 1968). The plot sloped 12° from horizontal towards the southwest, and was more sheltered than the exclosure at 3,750m. Tussock grasses of *Calamagrostis* sp. were dominant and the only noteworthy physiognomic difference between this and the páramo 250m lower was the absence of large shrubs and lupins, though *Valeriana microphylla* was still common (Table 5.1). This area was visited by cattle and horses, though less often than the lower vegetation, partly due to old, often ineffective, man-made earthen walls and ditches (to limit herd movements) and partly because of the unfavourable climate.

Above 4,000m, the vegetation became increasingly dominated by cushions of *Plantago rigida*, and, as a consequence, unsuitable for grazing livestock. The unfavourable climate also deterred cattle grazing above this altitude.

Experimental Design

At each of the above sites, 10.5m x 10.5m fenced exclosures were set up (Figure - 5.4). For each exclosure, eight 1.5m tall eucalyptus fence posts were driven into the ground, and joined by wire mesh and barbedwire strand. Sixteen 2 x 2m plots were located within the exclosure, separated by buffer zones of 0.5m between each of the plots and between the plots and the fence. This design excluded cattle but did not prevent small mammals such as rabbits and rodents from entering the areas.

The experiment at each of the five sites consisted of an unreplicated 2^4 factorial plot design, incorporating two fertilizer treatments and two cutting regimes in all combinations. The sixteen treatments were assigned to plots at random within each location.

The treatments were a combination of:

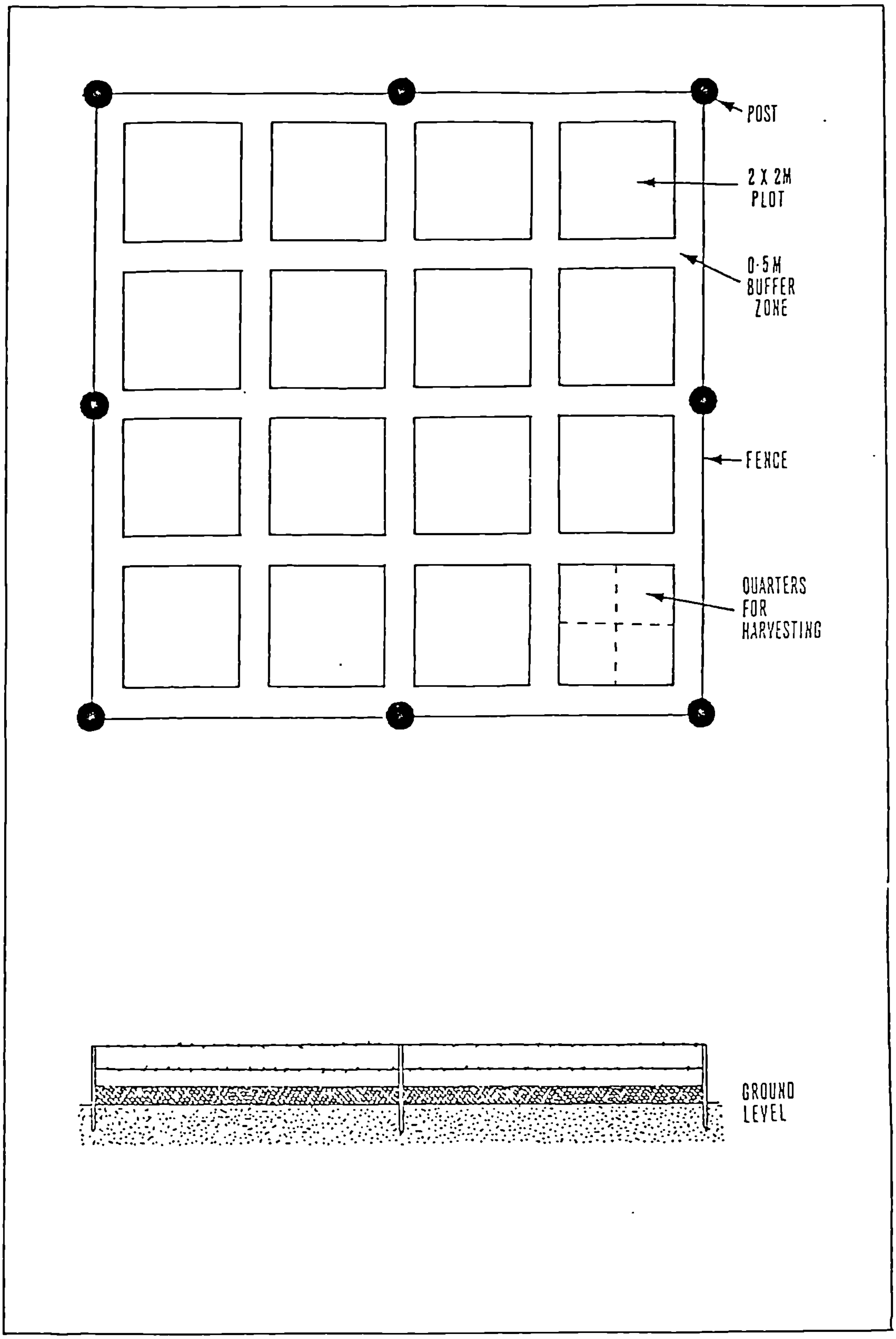


Figure 5.4.
The design of the exclosures used in the productivity studies. Each exclosure consists of sixteen 2 m x 2 m plots, harvested by quarter, and separated by 0.5 m buffer zones. The 1 m high perimeter fences of wire mesh topped with barbed wire strand were supported by eight eucalypt posts.

a. Fertilizer treatments (applied at start of experiment)

- No fertilizer
- 174g per plot of nitrogen (46:0:0) in the form of Urea, corresponding to 200 kg ha^{-1} of nitrogen.
- 87g per plot of phosphorus (0:46:0), corresponding to 100 Kg ha^{-1}, and 133g per plot of potassium (0:0:60), corresponding to 200 Kg ha^{-1}.
- Application of nitrogen, phosphorus and potassium in the above rates (that is, both treatments ii. and iii.).

b. Cutting treatments

- No cuts.
- Early cut at start of experiment only.
- Late cut only after 70 days.
- Cut both at start of experiment and after 70 days.

The experiments were started between the 13-20th July 1987. The initial cutting treatments (ii. and iv.) enabled the weight of the standing crop to be estimated. Harvesting was carried out by plot quarter (that is, a different quarter of each plot was harvested at each time) at approximately 35 day intervals (see Figure 5.5). The plots were cut using small shears. The vegetation was cut back to ground level (or to just above the hummocky bases of the tussocks in the páramo sites, and to the level of the *Azorella pedunculata* mats in sites B and C). In the páramo sites (D and E), much of the harvested material was dead. However, this was not separated from the live material. "Biomass" and "phytomass" are used here to incorporate these dead leaves still attached to the tussocks, but not to include litter. This is only important in previously uncut plots, since the dead leaves take time to accumulate to a significant level.

Assessment of the net primary production of underground plant parts by biomass methods are fraught with difficulties. To begin with, it is a destructive process and cannot be used for repeated measurements of the same area. Also, there is great difficulty in separating recently produced rootstock from older, perhaps even dead, material in the soil. For these reasons, and bearing in mind the limitations on resources, the assessment of belowground productivity was not attempted.

The harvested plant material was then taken to the Sangay National Park guardpost at Alao for initial drying at 65°C in a homemade oven (to prevent rotting), before being transported to the Politecnico Nacional in Quito for final drying at 105°C for 24 hours. Weighing was carried out using an accurate balance to the nearest 1g.

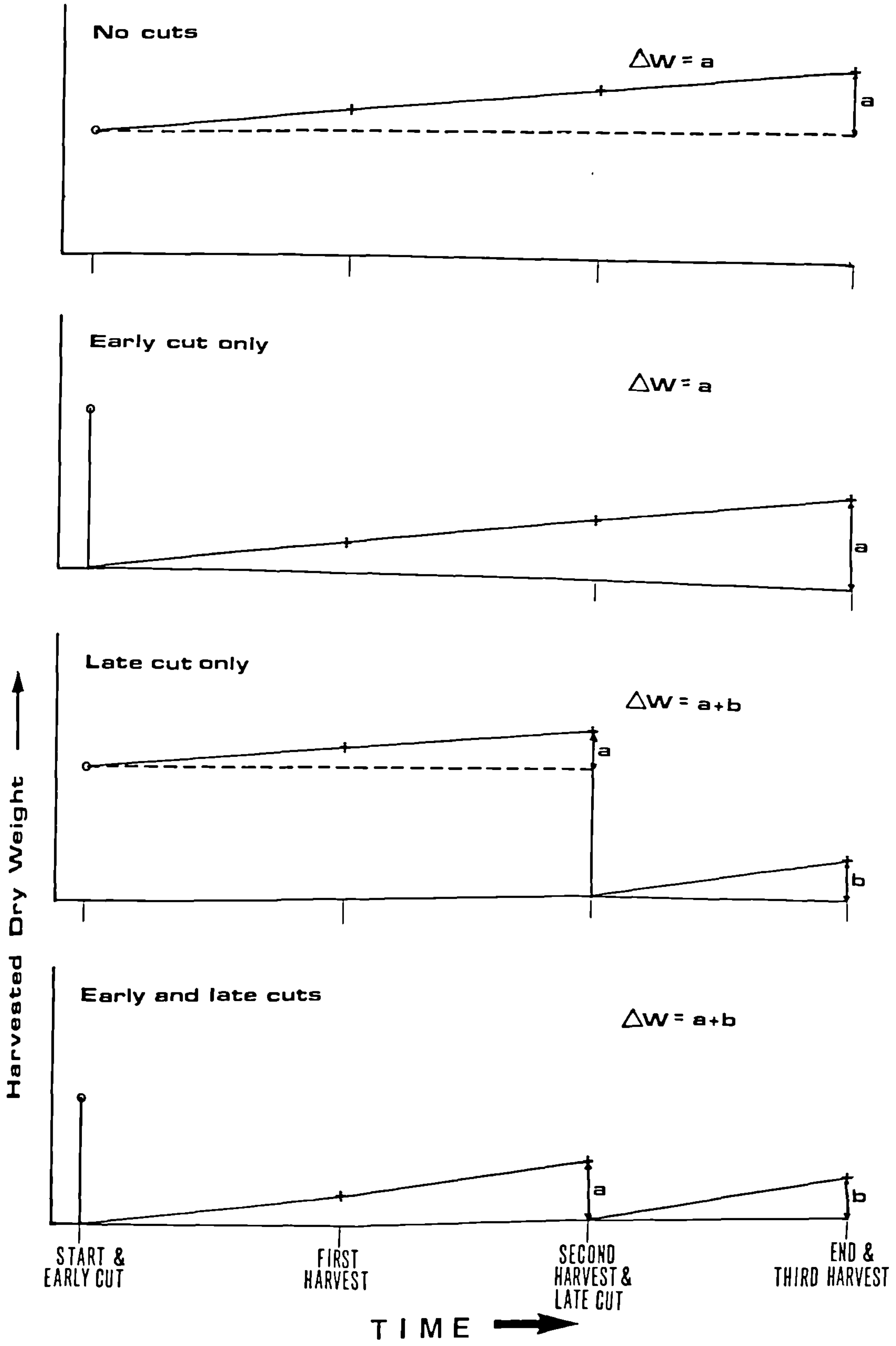


Figure 5.5.

Diagrammatic representation of the cutting and harvesting regimes. At the start of the experiments, half of the plots were cut. The dry weight at the start of the experiment is shown by a small circle. Harvesting was carried out twice during the course of the experiments and once at the end of the study period. The overall change in weight (ΔW) was calculated according to the formulae shown.

Results

Standing Crops

Estimates of the dry weights for the initial aboveground biomass (standing crop) of the five exclosure sites at the start of the experiments are given in Table 5.2. The most striking feature of these data is the very high values for standing crop in the páramo exclosures: at 794 g m^{-2} and 837 g m^{-2}, some 15-27 times larger than the values for the other three sites. The upper four exclosures have roughly the same degree of variability about their means, about half that of the lowest site.

Site	Altitude	Pasture Type	Standing Crop (g m^{-2})	95% Confidence Limits	CV%
A	3,100m	Improved/ Agricultural valley	54	40^a	87.9
B	3,250m	Semi-improved/ Cleared ceja	42	12^a	33.3
C	3,450m	Semi-improved/ Cleared ceja	31	8^a	33.5
D	3 750m	Unimproved Lower páramo grassland	837	161^b	23.0
E	4,000m	Unimproved Upper páramo grassland	794	219^b	33.1

Table 5.2.
Standing above-ground biomass estimates collected 13-20th July 1987 from five exclosure sites at five altitudes in the Andes of Central Ecuador. Based on 8 observations per site of (a) $4m^2$ and (b) $1m^2$.

The increments of dry weight from harvest to harvest were calculated and an analysis of variance (ANOVA) was performed on all of these data. Since there is no replication of treatments, the usual procedure in such cases was followed: using some of the higher level interactions as the error term (in this case, "Harvest × Sites × Fertilizer", "Harvest × Sites × Cuts", "Harvest × Fertilizer × Cuts", "Sites × Fertilizer × Cuts" and "Harvest × Sites × Fertilizer × Cuts"). Despite significant differences between altitude levels and an interaction between the time of harvest and the site position, the exceptionally high coefficient of variation (CV), at 344%, did not allow much confidence to be placed on these results. The data were examined for correlation between variance and sample dry weights: logarithmic transformation of the data did not reduce the variability of any of the data (determined by eye from residual versus fitted value plots) and so, throughout these analyses, it has not been used.

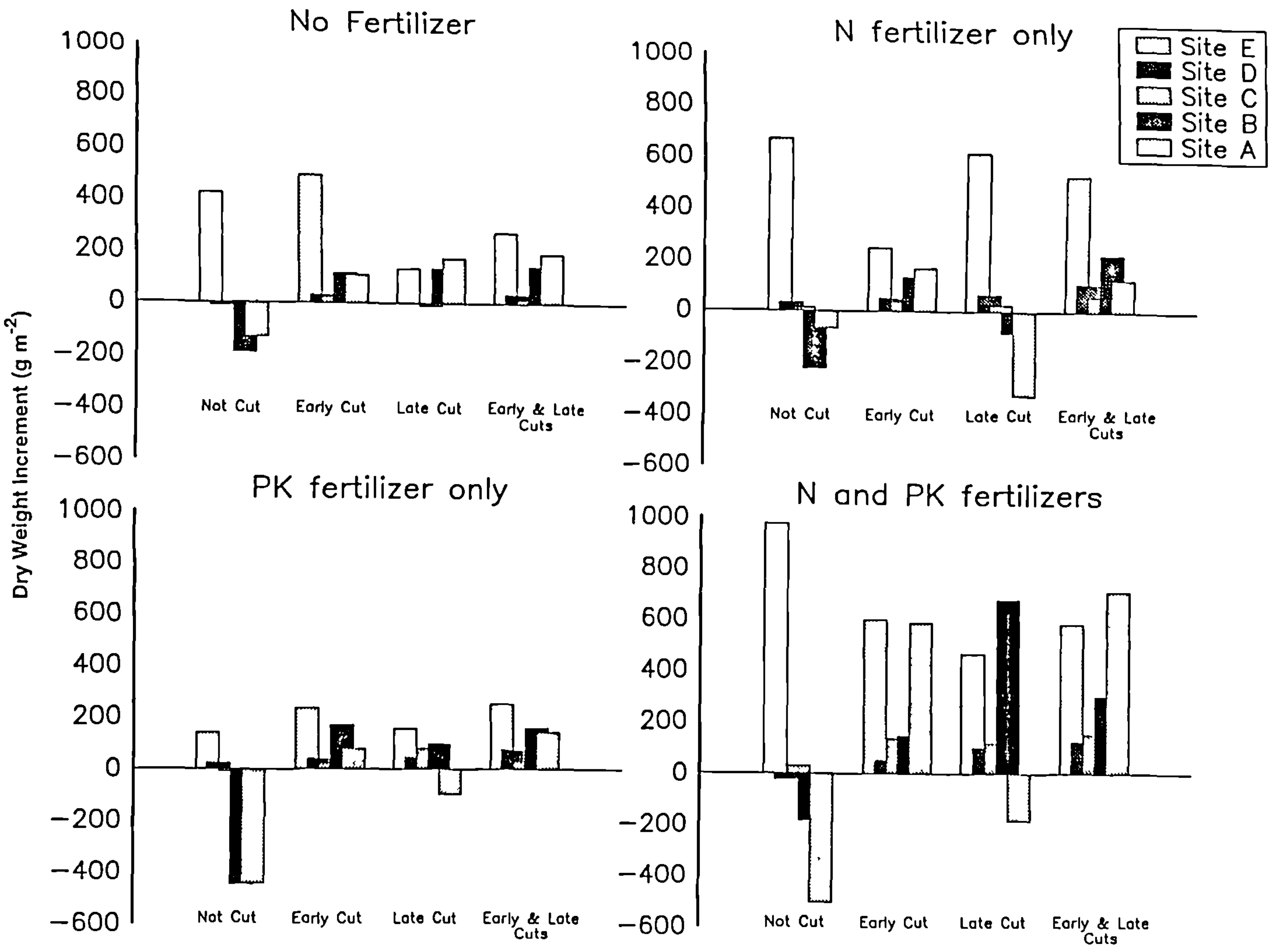


Figure 5.6.
Mean aboveground dry weight increments over the entire experimental period for the four fertilizer and four cutting treatments at each of the five sites.

Owing to the very high variation of the harvest to harvest increment data, an analysis was performed on the overall dry weight changes over the entire experimental period. The method of calculation of these increments is shown diagrammatically in Figure 5.5 and the data is presented in Figure 5.6. Some of the values are negative, showing an overall decrease in weight from the start to the end of the trial period. Only those plots which were uncut at the start of the experiment show this and the páramo sites (D and E) exhibit the greatest tendency to high negative values.

The NPK fertilizer treatment produced higher yields than the other fertilizer treatments. Site A shows the greatest increase, within each fertilizer treatment, and for the majority of cutting treatments. Sites B and C exhibit the smallest changes in aboveground biomass.

The ANOVA results for this data are given in Table 5.3. The coefficient of variation is 101%, still extremely high, but much less than that for the harvest to harvest data.

Source of Variation	*df*	SS	SS%	MS	F	*p*	Significance
Sites	4	1847027	42.86	461757	30.79	0.000	***
Fertilizers	3	401373	9.31	133791	8.92	0.000	***
Cuts	3	242323	5.62	80774	5.3	0.004	**
Sites X Fertilizers	12	398846	9.25	33237	2.22	0.033	*
Sites X Cuts	12	739158	17.15	61596	4.11	0.000	***
Fertilizers X Cuts	9	141235	3.28	15693	1.05	0.424	NS
Error (Sites X Fertilizers X Cuts)	36	539844	12.53	14996			
Total	79	4309805	100.00	54554			

Table 5.3.
Analysis of Variance table for the dry weight increments from the start to the end of the trial period. The highest level interaction term was used as the error, since there was no replication. The level of significance is denoted by the conventional symbols: NS, not significant; *, significant at the 95% level; **, significant at the 99% level; ***, significant at the 99.9% level.

	Site				
	A	B	C	D	E
Mean Dry Weight (g m^{-2})	424.06^a	45.69^b	27.38^b	73.38^b	38.00^b

Table 5.4.
Mean increments of dry weight (g m^{-2}) from the start to the end of the experiment (103-110 days) for each of the sites. Means sharing a letter have not been separated by the Student-Newman-Keuls test.

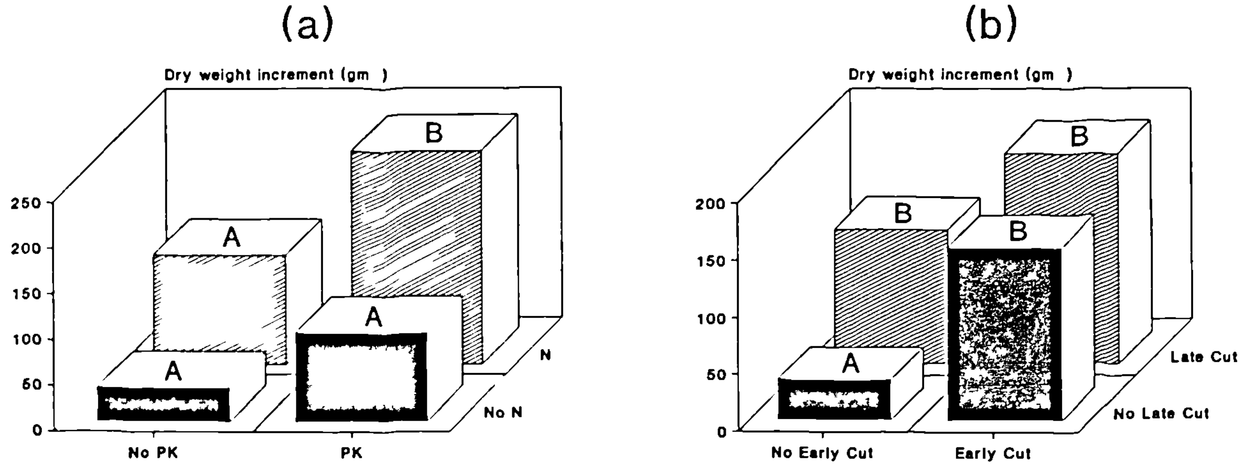


Figure 5.7.
Mean dry weight gains for all five sites. a. Fertilizer treatments, b. Cutting treatments. Means sharing a letter were not separated by a Student-Newman-Keuls test.

	Site				
	A	B	C	D	E
No Fertilizer	330 25^{c}	12.75^{e}	6.75^{e}	50.50^{a}	80.25^{de}
N	515.00^{b}	62.50^{e}	32.75^{e}	12.50^{e}	-25.25^{e}
PK	195.50^{d}	44.75^{e}	31.25^{e}	-5 50^{e}	-80.50^{ef}
NPK	655 50^{a}	62.75^{e}	38 75^{e}	236.00^{d}	170.50^{d}

Table 5.5.
Mean increments of dry weight (g m^{-2}) from the start to the end of the experiment (103-110 days) for each of the site × fertilizer interaction terms. Means sharing a letter have not been separated by the Student-Newman-Keuls test.

The analysis shows a highly significant effect of site position. A Student-Newman-Keuls (SNK) test, a multiple range test for comparing means (Zar, 1984), identifies this difference: the increase in weight at Site A being much higher than that for the other sites (Table 5.4). The fertilizer treatments give a high probability of being different, the NPK treatment being significantly higher than the other fertilizer treatments (Figure 5.7a). Cutting regimes also result in important differences, the no cut treatment being much lower than the other treatments (Figure 5.7b). Significant interactions are shown between sites and fertilizers (site A plots responding more vigorously to the fertilizer applications, and the PK treatment in the highest exclosure showing the poorest response: Table 5.5). Another important interaction was that between sites and cutting treatments. The SNK test revealed seven groups of "sites ×

cuts" means (Table 5.6). The uncut plots at site A produced the greatest increase in biomass (551.75 g m^{-2} on average) and was distinct enough to form a separate group from the rest. The other three cutting regimes at site A constituted the next heaviest group (343.25-408.75 g m^{-2}). The remaining groups showed some overlap, but roughly speaking, the uncut plots from the páramo sites (D and E) formed the bottom group (with a reduction in weight of 261.25 and 126.5 g m^{-2}), the montane forest plots (B and C) formed the next lightest groups (showing increases in weight from 5.25-84.25 g m^{-2}), and the other groups consisted of the remaining plots from the páramo sites (141.5-206.75 g m^{-2}). The only exception was the cut 2 plot from the most elevated site, which, with a reduction in dry weight of 46 g m^{-2}, was placed in the group with the plots from sites B and C.

Although at 101% the coefficient of variation of these data is much less than that for the harvest to harvest increments, it is still too high to allow firm conclusions to be drawn. There are two further approaches available to reduce the variability of the data, both requiring subdivision of the data. The first is to analyse the sites separately, the other to look at the cut plots only.

The complex interactions with site position (Table 5.3) merit analyses of the sites separately. In fact, the interactions, particularly those shown in Tables 5.5 and 5.6, warrant the use of the following groups: site A, sites B + C and sites D + E.

The analysis of variance for the data from Alao (site A) is shown in Table 5.7. The coefficient of variation is 39%. A significant effect of fertilizer is demonstrated by the analysis of variance ($p = 0.015$). The result of the SNK test on the fertilizer means is shown in Figure 5.8a: NPK and possibly N fertilizer treatments are higher than the others. There appears to be little interaction between N and PK fertilizers, the increased growth resulting from the addition of NPK is roughly the sum of that produced by applications of N and PK alone.

No significant differences were found between sites B and C (Table 5.8). Both fertilizer and cutting treatments were found to exhibit pronounced differences. The coefficient of variation for the analysis was 70%. The SNK test of the fertilizer means differentiated the lowest, unfertilized plot from the other fertilizer plots (Figure 5.8b), although the PK treatment was not clearly defined. The NPK plots yielded less than would be expected if the relationship between N and PK was a straightforward additive effect.

	Site				
	A	B	C	D	E
No Cuts	551.75^{a}	5.25^{f}	7.75^{f}	-261.25^{g}	-126.50^{g}
Early Cut	392.50^{b}	42.25^{ef}	34.00^{ef}	141.50^{cde}	146.75^{cde}
Late Cut	343.25^{b}	51.00^{ef}	30.00^{ef}	206.50^{c}	-46.00^{f}
Early & Late Cut	408.75^{b}	84.25^{def}	37.75^{ef}	206.75^{c}	177.75^{cd}

Table 5.6.

Mean increments of dry weight (g m^{-2}) from the start to the end of the experiment (103-110 days) for each of the site × cuts interaction terms. Means sharing a letter have not been separated by the Student-Newman-Keuls test.

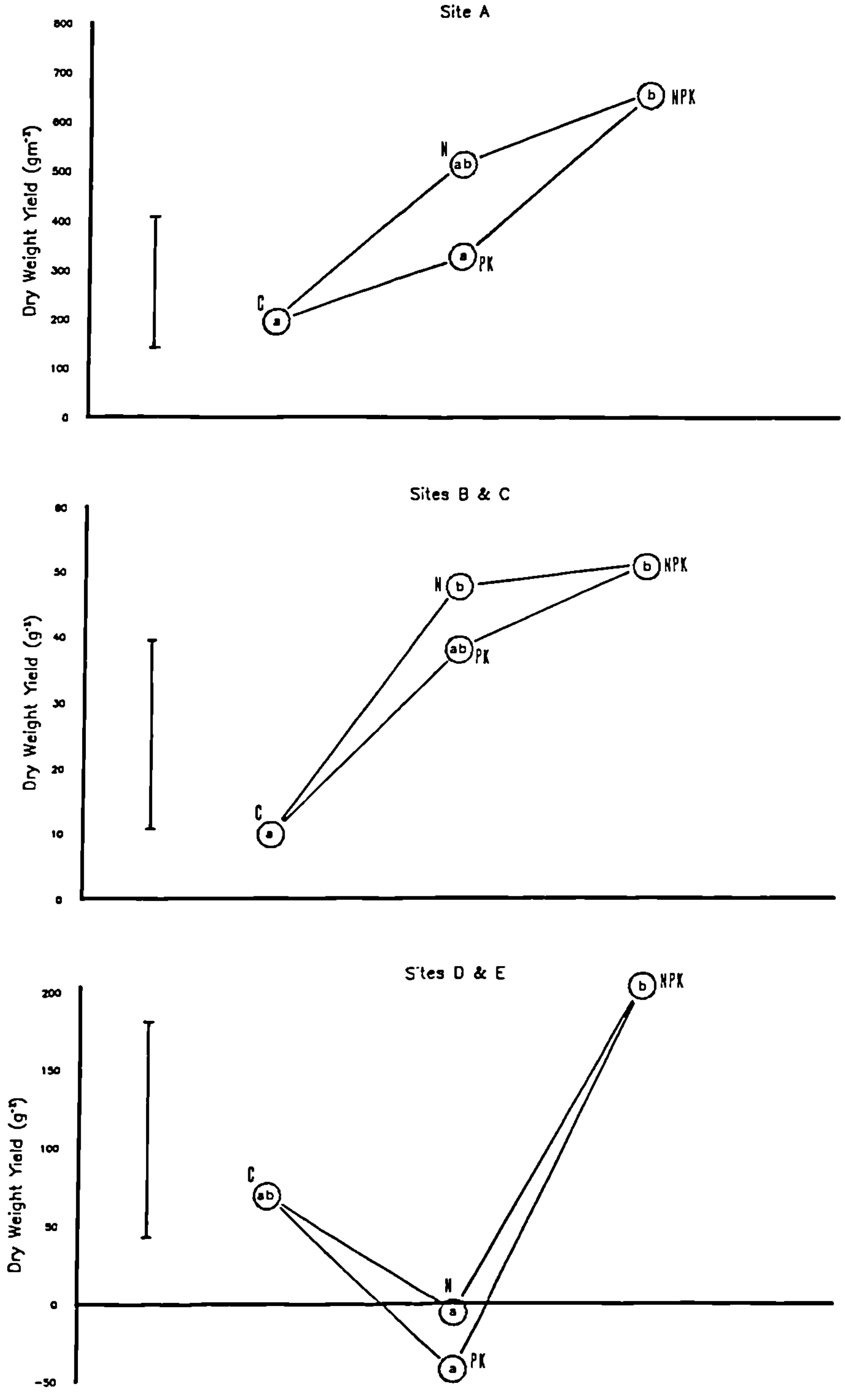


Figure 5.8.
Mean dry weight increments for the four fertilizer treatments.
a. Site A; b. Sites B & C; c. Sites D & E. Means sharing a letter were not separated by a Student-Newman-Keuls test. The bar to the left of each figure represents the Least Significant Difference (LSD). Key to fertilizer treatments: C, Control; N, Nitrogen only; PK, Phosphorus and Potassium only; NPK, Nitrogen, Phosphorus and Potassium.

Source of Variation	*df*	SS	SS%	MS	F	*p*	Significance
Fertilizers	3	491498	19.69	163833	6.04	0.015	*
Cuts	3	96262	11.57	32087	1.18	0.370	NS
Error (Fertilizer X Cuts)	9	244093	29.34	27121			
Total	15	831853	100.00	55457			

Table 5.7.

Analysis of Variance table for the dry weight increments for site A (Alao) from the start to the end of the experiment. The fertilizer × cuts interaction term is used as the error since there is no replication of treatments.

Source of Variation	*df*	SS	SS%	MS	F	*p*	Significance
Sites	1	2682.8	7.32	2682.8	4.15	0.072	NS
Fertilizers	3	8357.1	22.80	2785.7	4.31	0.038	*
Cuts	3	12151.1	33.15	4050.4	6.26	0.014	*
Sites X Fertilizers	3	675.8	1.84	225.3	0.35	0.792	NS
Sites X Cuts	3	2672.3	7.29	890.8	1.38	0.311	NS
Fertilizers X Cuts	9	4287.3	11.70	476.4	0.74	0.672	NS
Error (Sites X Fertilizers X Cuts)	9	5823.5	15.89	647.1			
Total	31	36650.0	100.00	1182.3			

Table 5.8.

Analysis of Variance table for the dry weight increments for sites B and C (Daldal) from the start to the end of the trial period. The highest level interaction term was used as the error, since there was no replication.

Table 5.10 shows no difference between sites D and E, though differences were demonstrated for the fertilizer and cutting treatments. However, the coefficient of variation was 221%—too high to allow confident interpretation of these results. Figure 5.8c illustrates the high variability of these data—both the N and PK treatments resulted in a decrease in yield, while the NPK treatment showed a strong positive effect.

The comparison of cutting treatment means indicated that the uncut plots were, on average, significantly lower than those plots which were cut (Table 5.9).

Another approach to reducing the variability of the data (shown in Table 5.3) is to exclude those plots which were left uncut at the start of the experiment from the analysis. Since half of the original data (the uncut and late cut only plots) depend on the initial estimates of standing crop (which have CV values of values between 23% and 88%), the variability of the data is increased. By removing these data from the analysis, the overall CV of the increments from the start of the experiment to the end was reduced from 101% to 44%. The excluded plots had a CV of 208%. The ANOVA of the early cut plots is given in Table 5.11.

The two cutting treatments (early cut only, early and late cut) were not differentiated and all interactions were insignificant. Once again, the sites contributed a great deal to the overall variance of the data and proved to be highly significant. The SNK test determined three populations from the five means, site A yielding more than the others, with the dry weight increments from sites B and C being significantly lower than the rest (Table 5.12). The fertilizer treatments were significantly different, the plots treated with NPK growing fastest (SNK test: Table 5.13).

In a similar way to the subdivision of the whole dataset previously, it may be possible to eliminate some of the variability of these cut data by looking at some sites independently. It is clear from Table 5.12 that site A, sites B & C, and sites D & E represent meaningful groups to be treated in this way.

The analysis of the Alao (site A) data is presented in Table 5.14, the coefficient of variation being 36%. Despite the percentage sums of squares showing values similar to those of previous analyses, the fewer degrees of freedom in this ANOVA do not allow any significant differences between treatments to be expressed. Figure 5.9a shows the growth increments of the fertilizer treatments, NPK again yielding the highest, with PK depressing the growth rate. The two cutting treatments produced very similar yields of around 400 g m^{-2} over the trial period.

The coefficient of variation for the cut plots of sites B and C was 28%, and the analysis of variance of these data is shown in Table 5.15. The difference between the mean yield of site B (63 g m^{-2}) and site C (36 g m^{-2}) was found to be significant. The plots which were cut twice yielded significantly more dry weight than those which were only cut once, at the start of the experiment (61 g m^{-2} on average as opposed to 38 g m^{-2}). There were no apparent differences between the fertilizer treatments, though the percentage sum of squares was high. The effects of N and PK appear to be independent (Figure 5.9b).

Table 5.16 presents the analysis of variance of the cut plots from the páramo sites (D & E). The coefficient of variation was 34%. Again, there were no significant effects of the treatments, despite the high sums of squares (particularly for the fertilizer treatments). NPK application increased growth dramatically, despite N and PK treatments showing little gain independently (Figure 5.9c).

	Cutting Treatments			
	Uncut	Early Cut	Late Cut	Early & Late Cuts
Mean Dry Weight (g m^{-2})	6.50^{a}	38.13^{b}	40.50^{b}	61.00^{b}

Table 5.9.

Mean increments of dry weight from the start to the end of the experiment (107-108 days) for the cutting treatments at sites B and C (Daldal). Means sharing a letter have not been separated by the Student-Newman-Keuls test.

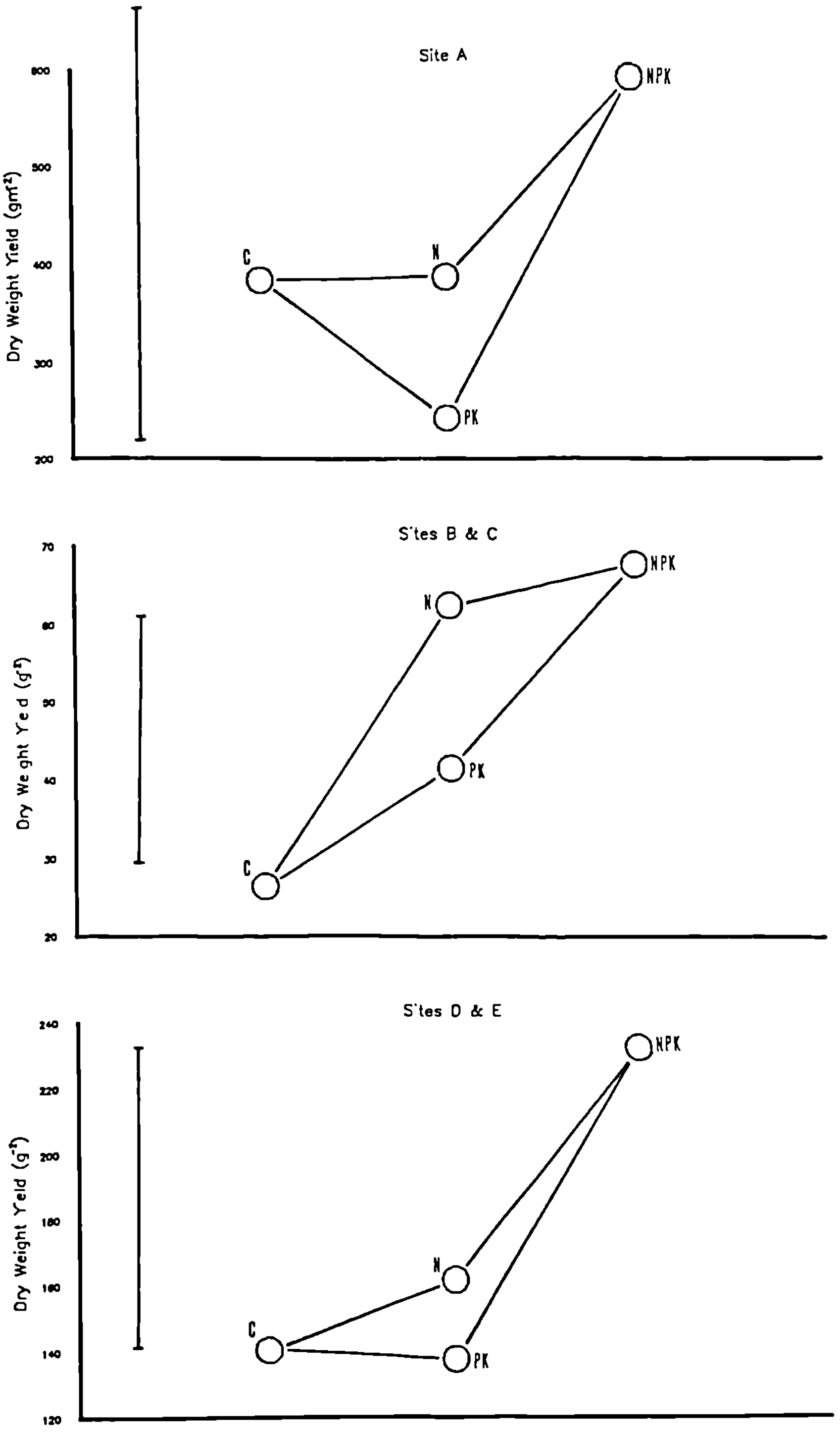


Figure 5.9.

Mean dry weight increments for the four fertilizer treatments in plots which were subjected to an initial cut. Analysis of variance did not indicate any significant difference between the means in all three cases.The bar to the left of each figure represents the Least Significant Difference (LSD). a. Site A; b. Sites B & C; c. Sites D & E. Key to fertilizer treatments: C, Control; N, Nitrogen only; PK, Phosphorus and Potassium only; NPK, Nitrogen, Phosphorus and Potassium.

Source of Variation	*df*	SS	SS%	MS	F	*p*	
Sites	1	10011	0.62	10011	0.66	0.436	NS
Fertilizers	3	284317	17.69	94772	6.28	0.014	*
Cuts	3	714842	44.48	238281	15.79	0.001	***
Sites X Fertilizers	3	15371	0.96	5124	0.34	0.797	NS
Sites X Cuts	3	155554	9.68	51851	3.44	0.066	NS
Fertilizers X Cuts	9	291034	18.11	32337	2.14	0.136	NS
Error (Sites X Fertilizers X Cuts)	9	135841	8.45	15093			
Total	31	1606969	100.00	51838			

Table 5.10.

Analysis of Variance table for the dry weight increments for sites D and E (Daldal) from the start to the end of the trial period. The highest level interaction term was used as the error, since there was no replication.

Source of Variation	*df*	SS	SS%	MS	F	*p*	Significance
Sites	4	660892	72.78	165223	31.10	0.000	***
Fertilizers	3	78117	8.60	26039	4.90	0.019	*
Cuts	1	10017	1.10	10017	1.89	0.195	NS
Sites X Fertilizers	12	77102	8.49	6425	1.21	0.374	NS
Sites X Cuts	4	4570	0.50	1126	0.21	0.927	NS
Fertilizers X Cuts	3	13709	1.51	4570	0.86	0.488	NS
Error (Sites X Fertilizers X Cuts)	12	63757	7.02	5313			
Total	39	908099	100.00	23285			

Table 5.11.

Analysis of Variance table for the dry weight increments from the start to the end of the trial period. Only plots with an early cut treatment are included.The highest level interaction term was used as the error, since there was no replication.

	Sites				
	A	B	C	D	E
Mean dry weight increment (g m-2)	400.63^{a}	63.25^{b}	35.88^{b}	174.12^{c}	162.25^{c}

Table 5.12.

Mean increments of dry weight (g m^{-2}) from the start to the end of the experiment (103-110 days), excluding initially uncut plots, for each of the sites (A, 3,100m; B, 3,250m; C, 3,450m; D, 3,750m; E, 4,000m). Means sharing a letter have not been separated by the Student-Newman-Keuls test.

	No fertilizer	N	PK	NPK
Mean dry weight increment (g m-2)	143.5^{a}	167.0^{a}	120.2^{a}	238.2^{b}

Table 5.13.

Mean increments of dry weight (g m^{-2}) from the start to the end of the experiment (103-110 days), excluding initially uncut plots, for each of the fertilizer treatments. Means sharing a letter have not been separated by the Student-Newman-Keuls test.

Source of Variation	*df*	SS	SS%	MS	F	*p*	Significance
Fertilizers	3	122718	65.76	40906.1	1.94	0.300	NS
Cuts	1	528	0.28	528.1	0.03	0.884	NS
Error (Fertilizers X Cuts)	3	63367	33.96	21122.5			
Total	7	186614	100.00	26659.1			

Table 5.14.

Analysis of Variance table for the dry weight increments for site A (Alao) from the start to the end of the experiment. Only plots with an early cut treatment are included. The fertilizer × cuts interaction term is used as the error since there is no replication of treatments.

Source of Variation	*df*	SS	SS%	MS	F	*p*	Significance
Sites	1	2997.6	23.36	2997.6	15.69	0.029	*
Fertilizers	3	4380.2	34.13	1460.1	7.64	0.064	NS
Cuts	1	2093.1	16 31	2093.1	10.95	0.045	*
Sites X Fertilizers	3	354.7	2.76	118.2	0.62	0.649	NS
Sites X Cuts	1	1463.1	11.40	1463.1	7.66	0.070	NS
Fertilizers X Cuts	3	972.2	7.58	324.1	1.70	0.337	NS
Error	3	573.2	4.47	191.1			
Total	15	2833.9	100.00	855.6			

Table 5.15.

Analysis of Variance table for the dry weight increments for sites B and C (Daldal) from the start to the end of the trial period. Only plots with an early cut treatment are included. The highest level interaction term was used as the error, since there was no replication.

Source of Variation	*df*	SS	SS%	MS	F	*p*	Significance
Sites	1	564.1	1.10	564.1	0.17	0.708	NS
Fertilizers	3	23611.2	46.01	7870.4	2.36	0.249	NS
Cuts	1	9264.1	18.05	9264.1	2.78	0.194	NS
Sites X Fertilizers	3	4154.7	8.10	1384.9	0.42	0.755	NS
Sites 5 Cuts	1	1173.1	2.29	1173.1	0.35	0.595	NS
Fertilizers X Cuts	3	2557.7	4.98	852.6	0.26	0.854	NS
Error	3	9995.7	19.48	3331.9			
Total	15	51320.4	100.00	3421.4			

Table 5.16.
Analysis of Variance table for the dry weight increments for sites D and E (Daldal) from the start to the end of the trial period. Only plots with an early cut treatment are included. The highest level interaction term was used as the error, since there was no replication.

			Net Annual Aboveground Production (g $m^{-2} yr^{-1}$)					
	Altitude	**Length of expt. (days)**	**Overall**	**Fertilized**	**Unfertilized**	**Initially cut**	**Initially uncut**	**Unfertilized Cut**
		n =	**16**	**12**	**4**	**8**	**8**	**2**
Site A	3 100m	103	1,503	1,614	1,170	1,420	1,586	1,359
Site B	3 250m	108	154	192	43	214	95	110
Site C	3 450m	107	93	117	23	122	64	70
Site D	3 750m	110	243	269	168	578	91	430
Site E	4,000m	108	128	73	295	548	292	512

Table 5.17.
Estimated net annual above-ground productivity for the five exclosure sites. At each altitude sixteen productivity estimates were made (including all fertilizer and cutting treatments) and the mean of these values is shown in the "Overall" column. The mean values for fertilized and unfertilized sites are presented, along with those plots which were initially cut and those which were not. The most reliable estimate of natural productivity is given by the final column: those plots which were unfertilized and cut at the start of the experiment.

Table 5.17 shows the increments in dry weight over the experimental period extrapolated to a yearly base. Overall, the lowest site (Alao) was much more productive than the rest. The productivity estimates of the sites in the Daldal valley were an order of magnitude lower.

The addition of fertilizer stimulated production in the lower four plots, particularly at Alao and in the montane forest sites. The highest páramo site showed depressed growth on addition of fertilizer (73 compared to 295 g $m^{-2} yr^{-1}$).

An initial cut at the start of the experiment produced higher yields in the montane forest and páramo plots. This represented roughly a doubling of productivity in three of these sites, and a five-fold increase in the lowest páramo plots. The dry matter production in Alao was not increased by this early cut.

Owing to the extreme variability of the data in plots which were not cut at the start of the experiment, the best estimates of natural productivity rates are given by those plots which were initially cut and not fertilized. The lowest plots in Alao produced an estimated 1,359 g m^{-2} yr^{-1} (13.59 t ha^{-1} yr^{-1}). The two montane forest zone plots at 110 and 70 g m^{-2} yr^{-1} produced ten to twenty time less than the Alao plots. The páramo plots yielded substantially more dry weight (430 and 512 g m^{-2} yr^{-1}).

Discussion

Patchiness within the vegetation was responsible for the high variability of the harvest data. Such heterogeneity is unavoidable in natural vegetation, and is caused by a number of factors. One of these is the distribution of the dominant species and occurs, for example, in the páramo sites (with the patchiness inherent in the tussock grass physiognomy) and in the montane forest sites (with a very high mat cover, restricting growth). The pattern of distribution of other species may contribute to the dry weight variability. For example, in the Alao site, *Dactylis glomerata* forms coarse, spreading culms at maturity, which are heavier but do not possess such a plastic response to the environment as younger *D. glomerata* — the distribution of such mature patches is reflected in the dry weight values. Another possible cause of patchiness at Alao is grazing. The usual practice of tethering animals to a stake would produce patches of different grazing intensity and recovery ages.

Such variability in the vegetation could have been reduced by replication of treatments or by increasing the plot size to a level which was influenced less by pattern. However, neither of these approaches was possible for logistical reasons.

Half of the data are estimated increments (based on the standing crop values, Table 5.1) while the other 50% are exact increments, the plots having been cut back to a known level, namely zero, during the early cut. These latter data are much more dependable than the uncut plots, reflected in the lower CV values (44% as opposed to 208%). Throughout, the CV values are very high, but it should be noted that these data are rates of growth, and rates are susceptible to high variability.

Logistics determined the timespan of the experiment: only slightly more than 100 days. Clearly this is by no means ideal and seasonal trends within vegetation processes may well confound the picture presented here. It may explain, for example, the fact that four of the five control plots decreased in standing crop weights over the experimental period. In addition, plant nutrient deficiency may act by limiting the amount of photosynthetically active organs. Such a mechanism would lead to a lag between fertilizer application and the vegetation's response (Tamm, 1975); thus, a complete response to fertilizer application would require a much longer study of perhaps several years. Both the small plot size and the short duration of the experiment complicated the analyses by over-emphasizing interaction effects, mostly attributable to the high variability of the data (evidenced by the high coefficients of variation).

The harvest approach to plant productivity is a well-established one, but recent studies of productivity have used CO_2 exchange to estimate the rates of energy flow in and out of producers. Such research has shown that traditional harvest approaches seriously underestimate dry matter production. This underestimation is a result of events taking place between shoot harvests and changes of plant material from one category to another. In particular, the role of decomposers has been neglected – Clark & Paul (1970) reported a living biomass of decomposers and consumers in excess of 50% that of the primary producers. Herbivory is also important and while the activities of large herbivores have been intensively studied, the biomass consumed by small herbivores (rabbits, rodents, grasshoppers, etc.) has been largely ignored. Coupland (1972 – cited by Coupland, 1975) has shown that invertebrates may ingest and drop as much as 80% that consumed by cattle.

A major difference between the páramo sites and the lower grassland pastures was demonstrated by their higher standing crop biomass estimates at 837 and 794 g m^{-2} for the plots at 3,750 m and 3,950 m respectively. There was an order of magnitude of difference between these sites and those lower down. In fact, the values are extremely high compared with grasslands throughout the world (Rodin *et al.*, 1975).

However, these estimates are consistent with reports from other páramo and tropical alpine vegetation. Acosta-Solís (1984) recorded a value of 435 g m^{-2} for the Páramo de Chiquicagua in Ecuador. Further north in Colombia, Tol & Cleef (1992) measured the aboveground standing biomass of mainly dwarf bamboos and bryophytes in a Colombian bamboo páramo at 2,282.5 g m^{-2} (63% dead material), much higher than that in Daldal. In a study of Venezuelan páramo (physiognomically very different from the one in this study), Smith & Klinger (1985) recorded values ranging from 130 to 601 g m^{-2}. In a wider context, Hnatiuk (1978) reported aboveground phytomass estimates of 436-628 g m^{-2} in tropical alpine tussock grassland in New Guinea.

The explanation for such high standing crops is straightforward: the tussock grasses which dominate the páramo vegetation retain their dead leaves, which decay whilst still attached to the tussock. A very large proportion of the aboveground standing crop biomass is therefore dead material. It would also be expected that decomposition would take place at a slower rate at higher altitudes because of the colder temperatures. It is suggested that there is adaptive significance attached to the retention of dead leaves – they may insulate the delicate, developing tillers from climatic extremes and from lethal temperatures during grass fires (as discussed in earlier chapters). It is also proposed that this habit may prevent colonization by other species and reduce the overall nutritional value of the tussock, reducing levels of predation by herbivores. Schmidt & Verweij (1992) showed that dead matter in *Calamagrostis effusa* tussocks is of much lower digestibility and that tussock grasses are preferred least by cows (making up just 30% of the diet) despite its availability. Tol & Cleef (1992) suggested that by tying up nutrients in dead material still attached to the living plant, they are not available to other plants and this gives the tussock a competitive advantage.

The lower three sites did not share this tendency to retain dead leaves and their values for aboveground standing crop biomass were much lower as a result. The values were very low, perhaps reflecting grazing pressure at the lowest site and, at the montane forest sites, the additional effect of the dominance of the *Azorella* mats.

From the initial analysis of the harvested material (Table 5.2), the five sites separate into three groups. The lowest site (Alao) was very significantly different from the others, with a much higher production of dry matter. The two montane forest sites made up the second group, with the two páramo sites comprising the third category. However, it is the analysis of the initially cut plots that shows this distinction most clearly (Table 5.13).

Before the start of the experiment, the primary limitation on growth at Alao was grazing. Removal of herbivory (at least by cattle), allowed a massive increase in phytomass to take place. At the other sites, however, grazing was not so limiting on plant growth and, as a result, exclosing the plots did not have such a large effect. The estimated annual productivity of the Alao site, at 1359 g $m^{-2}yr^{-1}$, is very large, comparable to boreal mountain forest and semi-arid savanna (Rodin *et al.*, 1975). However, because the experiment was carried out during the wettest part of the year for Alao, coupled with the removal of grazing, the burst of growth recorded is perhaps not sustainable, leading to an over-estimation of annual production.

That productivity is linked to water availability is well-documented (Tieszen & Detling, 1983). Weischet (1969), Lauer (1976) and Sarmiento (1986) report that the zone of maximum precipitation in the Andes occurs at middle altitudes, corresponding to the position of montane forest vegetation. Therefore, it would be expected that the sites in this zone (B and C) would be the most productive of those studied. In fact, they are the least productive. The steep slopes of the Andes at these elevations may result in high rainwater run-off, and indeed it is common practice for the pastures at site C to be periodically waterlogged with water diverted from a nearby watercourse to promote growth (this suggests water-limitation is a factor in the productivity of this site). The lowest Daldal site (B) is more or less flat and the rate of growth was always higher than site C, 200m above (Table 5.16), though it was only found to be significantly different from the steeper slope on one occasion (Table - 5.14). Water limitation may, therefore, be a constraint on plant growth in these pastures, which may lead to an interaction between the treatments and site position.

The main restriction on growth in these sites is the mat-forming habit of *Azorella*. The mat suppresses the vigour of the species growing within it, allowing only a few shoots through – and these are quickly cropped by herbivores. The annual productivity for these sites, at 110 g m^{-2} and 70 g m^{-2} is roughly equivalent to estimates for desert vegetation (Rodin *et al.*, 1975) and semi-desert (Lieth, 1975). However, it must be pointed out that this study does not take into account the productivity of the *Azorella* mat itself, which may increase the overall annual production very significantly indeed. It was impossible to harvest this species without disrupting the very nature of the vegetation structure, leaving bare earth, and without destroying the other species in the process.

Azorella pedunculata dominance is strongly associated with heavy grazing pressure. Grubb, Lloyd & Pennington (unpublished) reported a similar mat covering at 4,050m on the intensively grazed pastures of Volcán Antisana, Ecuador – although they suggest that some of the mats were probably quite large before the practices of burning and grazing were introduced. This latter point is debatable, since *Azorella pedunculata* is only found in large mats where grazing intensity is high; elsewhere it is found in very small patches and contributes little to the vegetation structure. It would seem likely that light competition, with *Calamagrostis* and other grasses, is a major factor in determining its distribution—where grazing and trampling alters the competitive balance, *Azorella* is able to dominate.

However, it is clear that once an extensive *Azorella* mat has formed, it becomes very difficult for other species to compete. Grubb *et al.* (unpublished) describe the suppression of shoots of other species as the *Azorella* mat comes to surround them. One of the reasons for this could be the mobile nature of the *Azorella* mats, consisting of rafts of rosettes, borne on rhizomes, which are constantly changing position to accommodate the growth of new rosettes. Any shoots of other species must straddle this mat (roots below and leaves above) and therefore must be resistant to the lateral movement of *Azorella*. Such plants would include species with short-lived, easily replaced shoots (for example, grasses) and plants which can physically resist the movement (such as woody plants).

It is difficult to assess the potential for recovery of these mat-dominated pastures, but without the continual cropping of shoots as they appear through the mat (i.e., in the absence of grazing), other species may establish and become locally more dominant. This may eventually lead to the elimination of the mat through competition for resources. It is most likely, however, that in the Daldal montane forest site, these colonists would be woody species and the pastures would revert to forest once more.

If, after the clearance of forest, production is to be maintained at a reasonable rate, grazing pressure must not reach the threshold for the formation of *Azorella* mats. This is an area of research which demands more attention.

The upper two sites, in the páramo zone, were also influenced strongly by biotic factors. Grazing is not so heavy here and conditions are often harsh. The accumulation of dead leaves by the tussock grasses is of major importance, both in terms of "adaptation" to the environment and with regard to the potential for dry matter production. As dead leaves build up within the tussock, the plant loses vigour and becomes less palatable to herbivores. For this reason, burning has become a well-established management technique used by peasant farmers to stimulate available production for livestock. The two páramo sites examined in this study were nearing a condition when burning is applied (though its application is somewhat erratic) and were perhaps at, or near to, a steady state—a condition of equilibrium where decomposition of dead material and respiration proceed at the same rate as production, leading to an absence, in terms of weight, of tussock growth (a common state in vegetation, described by Horn, 1974).

This balance may explain why many of the uncut plots in the páramo did not show weight gains over the course of the experiment (Figure 5.7). In fact, all of these uncut plots showed a loss in weight, indicating, perhaps, that some inhibition of growth was taking place. This phenomenon is also reflected in the annual net productivity estimates for the initially uncut plots in the páramo (Table 5.16), which are much lower than the estimates for the initially cut plots. It would seem, therefore, that the local agricultural practice of burning the grassland to increase production is well-founded, though it is likely that fire would inflict greater damage on the tussocks than mere clipping. The fact that grazing animals tend to concentrate their foraging in recently burned areas further complicates matters.

Physiological water limitation may be a major factor in inhibiting growth in the páramo. Low soil temperatures, particularly during the clear early mornings when photosynthesis and transpiration are occurring at rapid rates, may contribute to overall water stress in the higher altitude sites by reducing water uptake. This has been demonstrated for *Dendrosenecio* (Smith & Young, 1987a) and *Lobelia keniensis* (Young & Van Orden Robe, 1986) for East Africa, and for *Espeletia schultzii* in the Venezuelan páramo (Smith, 1972). Water shortage would inhibit leaf elongation (Wardlaw, 1969) and translocation of photosynthate may be directed to belowground structures as a result. This growth of the root systems would not be apparent in this study.

It is worth noting at this point that, in accordance with the data currently available, tropical alpine grasslands have the highest ratio of aboveground to belowground phytomass of all vegetation (Smith & Klinger, 1985). Root phytomass ranged from 66.7-386.4 g m^{-2} in a Venezuelan páramo (Smith & Klinger, 1985) and 1,084-1,598 g m^{-2} in a Colombian páramo (Rossenaar & Hofstede, 1992). It has been proposed (Smith & Klinger, 1985) that this high ratio is the result of a stressful environment (vegetation is of short stature and therefore extensive root systems are not required for support) with a year-round growing season (less need for storage in roots).

The net annual productivity estimates for these páramo sites (168 g m^{-2} and 295 g m^{-2} for sites D and E respectively) is quite low, similar to that for tundra ecosystems and about one-quarter that of mountain steppe (Lieth, 1975; Rodin *et al.*, 1975). They are in accordance with estimates of North American mountain grasslands (Sims & Singh, 1978) and values recorded by Hnatiuk (1978) in the tropical alpine grasslands of New Guinea (128-442 g m^{-2}). Annual net above ground productivity was estimated for *Espeletia timotensis* at 700 g m^{-2} (Monasterio, 1986) and for *Espeletia grandiflora* at 1,500 g m^{-2} (Sturm & Abouchaar, 1981) in physiognomically different páramos in Venezuela and Colombia, respectively. At higher altitudes, desert páramo productivity was much lower at 140 g m^{-2} yr^{-1} (Lamotte, Garay & Monasterio, 1989).

This rate of growth would be required for at least 3-5 years to accumulate the standing material shown in Table 5.1, which fits in very well with the observed practice of burning the tussocks every 2-4 years to renew the plants' vigour. This rate of growth and renewal is much higher than that estimated by Mann (1966) for Peruvian puna vegetation: the gross annual primary productivity of dry and humid punas being, respectively, 0.3 g m^{-2} and 8 g m^{-2} dry weight (with standing crop weights of 200 g m^{-2} and 700 g m^{-2}).

It is likely that the environment could support a higher rate of carbon assimilation, but this would be exploited with some risk to the plant. In a global survey of mineral nitrogen content in high altitude plant tissues, tropical alpine plants had the lowest content of those latitudes studied (Körner, 1989). A tentative hypothesis for this situation was proposed: that tropical alpine plants keep their growth rates under control (Körner, 1989).

In temperate regions, there is a period of climatic cooling in the autumn, allowing a step-wise 'hardening' of plant tissues to take place before winter sets in. In the tropical mountains, however, with "summer every day, winter every night", the plants must retain the hardy state throughout the year to prevent night-time damage by cold temperatures and desiccation. The induction of frost hardiness may lead to a decrease in photosynthetic capacity and, in any case, only 60% of the optimal CO_2 uptake is achieved by chilling tolerant plants at temperatures between +5 and +10°C, and is completely blocked when ice forms in the assimilatory organs (Larcher & Bauer, 1981). Kaufmann (1977) discussed feedback inhibition via carbohydrate accumulation and stomatal closure induced by water stress in the leaves caused by low temperatures (especially in the soil). Prolonged exposure to low temperatures can further depress the photosynthetic capacity of plants (Larcher & Bauer, 1981). For example, the altitudinal limit of successful potato cultivation is set by the intensity of episodic night frosts (Li & Palta, 1978). There are also structural responses to low temperatures (such as growth form) which may be at the expense of optimum photosynthetic performance.

The analysis of variance for the data from the start to the end of the experimental period for all the sites shows a very significant effect of fertilizers (Table 5.2). The NPK treatment gave significantly better results than the other treatments (Figure - 5.8, a). There was a site-specific effect of fertilizer application, but this was not a straightforward relationship (Table 5.4). It may be linked to soil moisture phenomena. Drier areas are less likely to be limited by nutrients — certainly the páramo sites would be subjected to a relatively high degree of water stress and as a result, the addition of nutrients would not be expected to boost production by any great amount. Furthermore, (Körner, 1989) noted that the nitrogen content of high alpine vegetation globally is naturally much higher than in other areas. Whether plants can respond to further additions of nutrients by increased growth is still uncertain.

Another factor which may lead to a fertilizer-site interaction is the slope of the plots. Generally, Andean slopes are very steep and rainfall quite high. In some of the plots, this may have led to the lateral translocation of nutrients across the buffer zones. The waterlogging practices carried out at site C may have contributed to this phenomenon. It is worth mentioning that the very low value of the PK treatment (Figure 5.8,a) is the result of some heavy weight losses in the páramo sites in the uncut plots (Figure 5.7). Analysis of the initially cut plots only resolves this anomaly, for although the PK treatment is still the lowest, it is much closer to the other treatments in its group (Table 5.12).

The main analysis gives a high significance to the cutting treatments, the uncut plots proving to be much less productive than the cut ones (Table 5.2). Since limited burning is used to increase production in the páramo, it is not surprising that cutting has a similar effect. In fact, clipping would be expected to damage the plants less than burning (which not only removes material but may inflict lethal temperatures on parts untouched by flames). It should also be considered that a certain intensity of grazing may actually stimulate production. The early and late cut treatment increased the yield over the value obtained by either the early or late cut treatments on their own (Figure 5.8b). This was true not only in the páramo, but also in the montane forest sites (Table 5.8). It would appear that the frequency of the cutting in this treatment did not adversely affect production. Further research to determine the optimum cutting/burning/grazing regimes in these environments is required.

Longer-term studies are required to provide more accurate estimates of annual production in the Andes, preferably with replication to reduce the variability of the harvest data. In particular, emphasis should be placed on the overgrazed clearings of montane forest.

Luteyn (1992) highlights the increasing demand for agricultural land in the Andean highlands and the threat this may pose for the fragile páramo ecosystem. This study indicates that better management (to avoid the low productivity associated with overgrazing), the production of the lower pastures in the highlands could be raised to a level that eliminates the need to exploit new areas of land (many farmers exploiting montane forest and/or páramo have pastures at lower altitudes). This area of research must be explored in some detail in the future.

Chapter 6

A Greenhouse Study of Competition Between Three Andean Grasses at Two Regimes of Water Availability

Introduction

Earlier chapters have looked at the zonation of páramo communities and their development with time at both small-scale and large-scale levels. The interactions between species are clearly of major significance in the evolution of a plant community, and are of vital importance to the understanding of community dynamics. Interactions between immediately adjacent plants may largely determine plant performance (Weiner, 1982; Silander & Pacala, 1985). In the ecocline of the Andean altitudinal gradient, each individual species will show a distribution "according to its own genetic, physiological and life-cycle characteristics and its way of relating to both physical environment and interactions with other species" (Whittaker, 1973). In this latter respect, a plant's distribution on the gradient will have been modified by niche differentiation and restriction.

Dramatic, sharp discontinuities in vegetation are usually associated with strong environmental discontinuities or disturbance, most often in the páramo by fire. In general, individual plant species, and the communities of which they are a part, intergrade continuously along the altitudinal gradient, rather than forming distinct zones.

The altitudinal ecocline is far from simple, however. An increase in altitude is associated with several factors, including a reduction in air temperature (the lapse rate for the Andes is around 0.6°C per 100m of altitude), an increase in wind speed and increased cloud cover (Sarmiento, 1986, 1987). These effects are in turn modified by factors such as topography, regional climatic patterns, grazing and disturbance by man. These major processes are then involved in smaller patterns, within the soil for example. To study the whole host of variables relating to altitude would be impractical; so too would be the study of such factors at the community level. A reductionist stance must be applied, dealing with only a few species and varying an artificial environment in clear, measurable ways. By this process, the effects of the measured environmental variables on the growth and interactions of the species can be observed. In spite of the approximate nature of such observations, they can be used to assess the effects that are likely to be important in the field (Williams, 1962).

One of the most important factors governing plant distributions in the páramos was found to be water availability (Ramsay, 1988). It has been postulated by several authors that with increasing altitude physiological drought becomes important (Walter & Medina, 1969; Pérez, 1987; Smith & Young, 1987b). It would be expected, therefore, that plants from higher altitudes might respond better to drought conditions than those from lower elevations, since they are regularly exposed to early-morning droughts in their natural habitat.

To investigate the hypothesis that drought tolerance increases with altitude, three grass species from the Ecuadorian páramo were collected for greenhouse experiments. One of these species was obtained from a high altitude of 4,150m, another from a lower altitude of 3,750m, and the remaining one from an intermediate elevation of 4,000m. Simple diallel tests of competitive interactions between these species were carried out, growing each species with each of the others and with itself.

Materials and Methods

Plant Material

All of the plants used in this study were collected on the 12th November 1987 from the Páramo de Guamaní (Papallacta), between Quito and Baeza (Figure 6.1). This páramo is quite wet, located on the Cordillera Occidental and represents a relatively undisturbed páramo, though burning and grazing do occur in some places, including the areas where grass material was collected.

At 4,150m the vegetation was dominated by *Plantago rigida,* interspersed with low tussocks of *Calamagrostis* sp. A [724] (Plate 6.1). Other components of the vegetation included *Culcitium ovatum, Oritrophium peruvianum, Oritrophium hieracioides, Werneria nubigena, Senecio repens, Senecio chionageton, Lycopodium* sp. [373], *Pernettya prostrata, Disterigma empetrifolium, Gentianella cernua, Gentiana sedifolia, Halenia weddelliana, Hypericum lancioides, Agrostis nigritella, Poa sp.* [723], *Carex lemanniana, Bartsia laticrenata, Castilleja* sp. [222], *Geranium sibbaldioides, Valeriana bonplandiana, Satureja nubigena, Oreomyrrhis andicola, Eryngium humile* and *Aphanactis jamesonia. Thamnolia vermicularis,* a small white tubular lichen was conspicuous, lying on the ground surface. Tillers of *Calamagrostis* A were collected.

Lower down, at 4,000m, the area was covered with tussocks of *Calamagrostis* sp. B (voucher specimen of cultivated plant deposited at the Royal Botanic Gardens, Kew), with *Poa* sp. (voucher specimen of cultivated plant deposited at the Royal Botanic Gardens, Kew) growing within them and in the intertussock spaces (Plate 6.2). The vegetation was burned at intervals, probably once every four years or so, though it was estimated that approximately 2-3 years had elapsed since the last burning of the vegetation at the collection site. Other prominent species in the plant community were *Puya clava-herculis, Oritrophium hieracioides, Senecio repens, Senecio chionageton, Senecio pimpinellifolia, Bidens andicola, Hypochaeris sonchoides, Gnaphalium* aff. *pensylvanicum, Diplostephium glutinosum, Pernettya prostrata, Disterigma empetrifolium, Gentianella nummalarifolia, Hypericum lancioides, Agrostis* sp. [822], *Poa sp.* [944], *Carex tristicha, Bartsia laticrenata, Geranium sibbaldioides, Sisyrinchium jamesoni, Lachemilla andina, Lachemilla orbiculata, Ranunculus* sp. [339], *Azorella pedunculata, Azorella aretoides, Oreomyrrhis andicola, Eryngium humile* and *Aphanactis jamesonia.* Tussock material of *Calamagrostis* B was collected.

The lowest collection site (3,750m) was dominated by tussocks mainly of *Calamagrostis* C (voucher specimen of cultivated plant deposited at the Royal Botanic Gardens, Kew) but also of *Festuca* sp. [742] (Plate 6.3). Important elements of the flora at this elevation included *Oritrophium hieracioides, Bidens andicola, Gnaphalium gnaphaloides, Gnaphalium dysodes, Culcitium adscendens, Gnaphalium* aff. *pensylvanicum, Sonchus ? oleraceus, Vicia andicola, Relbunium hypocarpium, Satureja nubigena, Stachys eliptica, Rumex acetosella, Hydrocotyle bonplandiana, Agrostis* sp. [822], *Poa sp.* [356], *Uncinia pheleoides, Bartsia laticrenata, Geranium reptans, Geranium multipartitum, Sisyrinchium jamesoni, Lachemilla orbiculata, Ranunculus* sp. [339], *Azorel-*

dunculata, Oreomyrrhis andicola, Eryngium humile and *Aphanactis jamesonia*. Tussock material of *Calamagrostis* C was collected.

Sample tillers were collected by excising sections of tussocks of the species concerned. The plant material was immediately placed in polythene bags, the roots covered with damp newspaper, and the leaves emerging out of the top of the bags. The plants were then transported in this state to the greenhouses at the University of Wales, Bangor: a journey which took nearly two weeks. During this time, many of the outer tillers of the tussocks died, but the protected inner ones survived.

The plant material was then divided into individual tillers (though some tussocks were retained to provide stock material for further experiments). The tillers were then placed in deep boxes of soil and allowed to grow: half in a warm house (18-23°C) and the other half in a cold house (5-15°C). Unfortunately, tiller mortality was extremely high. In the warm house, *Calamagrostis* C showed the best survival, with 18.8% of the tillers still alive after six months. Half as many tillers of *Calamagrostis* A survived and *Calamagrostis* B had a survival rate of 7.8% (with 100% of the survivors flowering). In the cold house, lower survival rates were observed of 7.8, 4.7 and 1.5% for *Calamagrostis* spp. A, B and C respectively. None of the cold house plants flowered. The great majority of tiller deaths occurred during the first week after separation from the mother plant. The tillers that survived showed some growth, occasionally prolific. Some tillers from each species had formed small tussocks of over 100 tillers after six months.

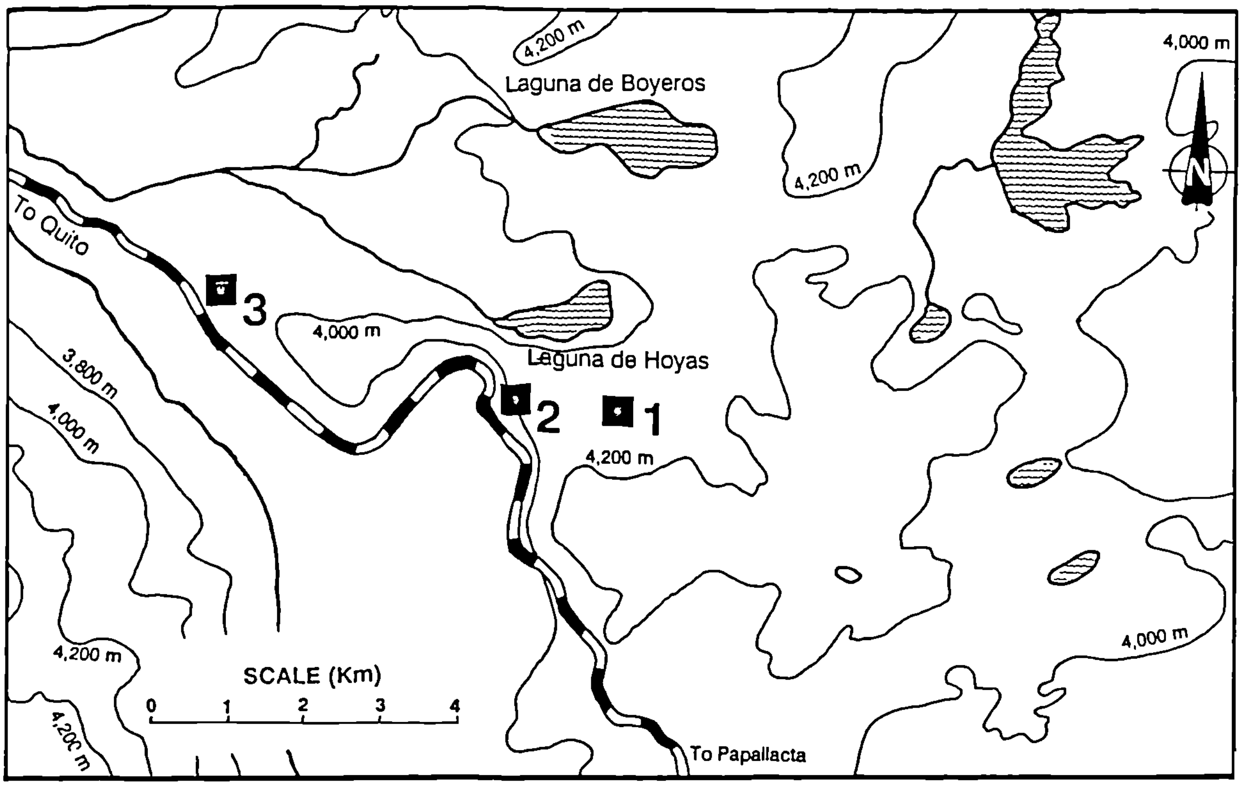


Figure 6.1.
Map of the Páramo de Guamaní, Ecuador, showing the collection localities of the three grass species used in the greenhouse study (■). Based on the Instituto Geográfico Militar (Quito) map for Oyacachi. The scale is 1:1,000.

Experimental Design

The experiment was constructed along the lines of the classic diallel design (see Williams, 1962; Norrington-Davies, 1967). In such an experimental design, plants of two species are grown together in the same pot such that each species is grown with each of the others and with itself once in each replication.

On 28th June 1988, individual tillers of similar size and condition were arranged in pots containing two tillers, one target species and one neighbour species, such that each replication consisted of six pots:

		Neighbour Species *Calamagrostis*		
		A	**B**	**C**
Target Species	*Calamagrostis* A	•	•	•
	Calamagrostis B	•	•	
	Calamagrostis C	•		

Square pots (15cm x 15cm) were used, filled with John Innes' "Humax" compost. Twenty replications were planted, amounting to a total of 120 pots and 240 tillers. Reserve tillers were also planted at the same time.

The pots were well-watered in warm conditions (18-23°C) to allow for the establishment of the tillers. An unusually long establishment period of six months was decided upon (following the slow growth rates and high mortality of the species over previous months). During this time, any dead tillers were replaced with living ones of the same age from the reserve stock. However, mortality was again very high and the number of replicates was reduced.

Following this establishment period the pots were randomly assigned bench positions in the warm house. One set of five replicates was placed on capillary matting, allowing water uptake as necessary for growth: the other treatment, again of five replicates, consisted of watering with a fine rose from above twice weekly, creating periods of water shortage. These regimes were maintained for six months.

Harvesting was carried out on 3rd July 1989, some 270 days after planting. The plant material was washed clean of soil and divided into above and below ground sections. Each of these portions were oven dried at 105°C for 24 hours and weighed.

Analysis of Results

The differences between the competitive abilities of the three grass species and the effects of the two moisture regimes were assessed by way of an analysis of variance and multiple range tests for comparing means (Student-Newman-Keuls tests; Zar, 1984).

Three indices of competitive abilities were also calculated. Relational effects (Harper, 1977), the competitive advantage of species a over species b, were calculated according to the formula:

$$R_{ab} = \frac{1}{2}\left(Y_{ab} - \frac{1}{2}Y_{aa}\right) + \frac{1}{2}\left(\frac{1}{2}Y_{bb} - Y_{ba}\right)$$

where Y_{aa} is the yield of the pure species a, Y_{bb} the yield of the pure species b, Y_{ab} the yield of species a when grown with species b, and Y_{ba} the yield of species b when grown with species a.

Summational effects (Harper, 1977), a measure of how the yield of a mixture compares with that predicted from the pure stands, were calculated following the formula:

$$S_{ab} = \frac{1}{2}\left(\frac{1}{2}Y_{aa} + \frac{1}{2}Y_{bb}\right) - \frac{1}{2}\left(Y_{ab} + Y_{ba}\right)$$

using the same notation as above.

An alternative measure of how the mixture yield performs relative to the pure stands, the Relative Yield Total (RYT—de Wit, 1960), was calculated according to the formula:

$$RYT = \frac{Y_{ab}}{Y_{aa}} + \frac{Y_{ba}}{Y_{bb}}$$

again using the same notation as previously.

Results

The mortality of tillers during the establishment phase of the experiment is of some interest (Figure 6.2). It can be seen that over twice as many tillers of *Calamagrostis* B survived as *Calamagrostis* A, with *Calamagrostis* C higher still. In examining how each species survives when grown with each of the other species it is evident that the survival of tillers of *Calamagrostis* spp. B and C is largely unaffected by the species with which they are grown. *Calamagrostis* A, however, shows much greater mortality when grown with *Calamagrostis* B.

A summary of the dry weight yields of the experiment is displayed in Figure 6.3.

The analysis of variance for the harvested aboveground plant material is presented in Table 6.1. The coefficient of variation (CV) is high for a greenhouse experiment at 69.25%. No important differences were found between the two watering treatments.

The target species performances were found to be considerably disparate ($p < 0.001$), while the neighbour species effects were considered insignificant. The interaction terms proved of little consequence.

Source	*df*	SS	MS	F	*p*	Significance
Water Availability	1	0.97	0.969	0.06	0.811	NS
Targets	2	1181.55	590.776	35.30	0.000	*
Neighbours	2	46.72	23.360	1.40	0.254	NS
Water Availability X Targets	2	76.77	38.386	2.29	0.108	NS
Water Availability X Neighbours	2	53.84	26.918	1.61	0.207	NS
Targets X Neighbours	4	61.01	15.253	0.91	0.462	NS
Water Availability X Targets X Neighbours	4	83.06	20.766	1.24	0.301	NS
Error	72	1205.12	16.738			
Total	89	2709.04	30.439			
	CV = 69.25%					

Table 6.1
Three-way analysis of variance performed on aboveground (shoot) dry weight yields of three species of *Calamagrostis* growing at high and low water availability. The yields of each species are referred to as 'targets' and the yields of plants grown with each species as 'neighbours'.

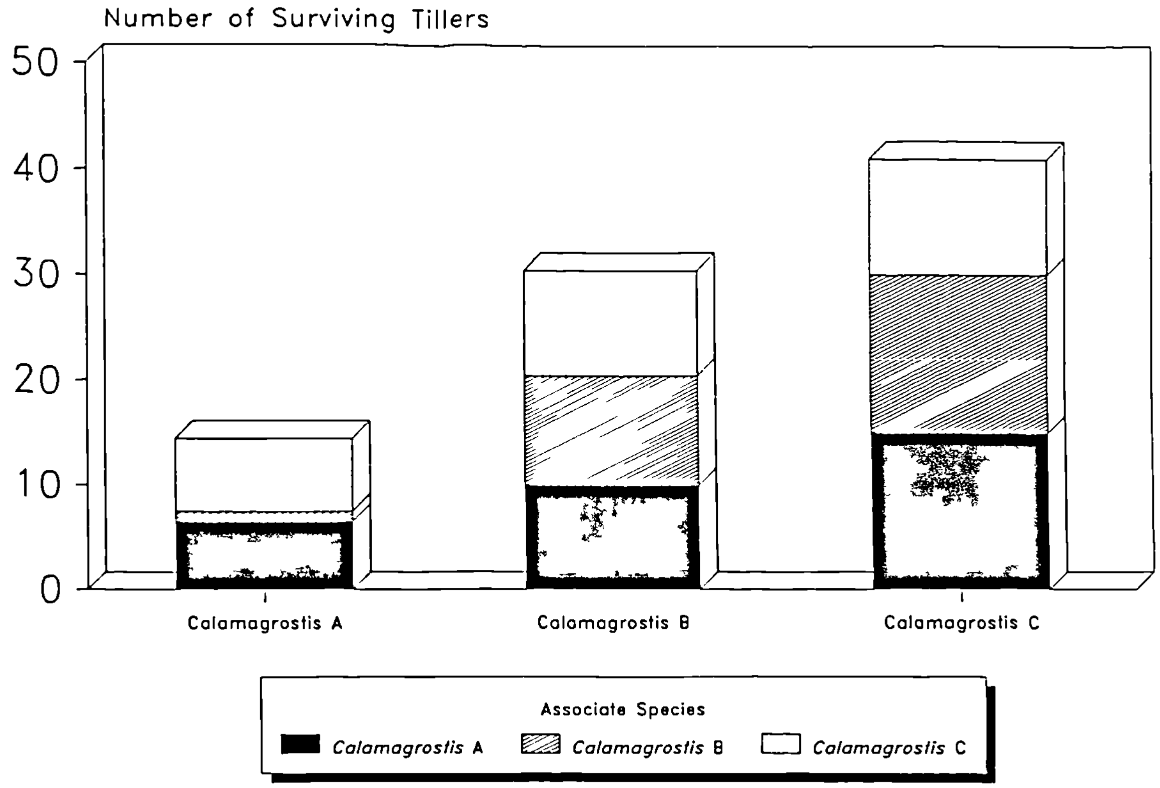


Figure 6.2.
Number of surviving tillers after the establishment phase of six months. The total survivorship for each species is subdivided into the number remaining when grown with itself and each of the other two species. The values for pure stands represent mean half-pot yields. The maximum possible survivorship for each species is thus sixty tillers (twenty with each neighbour species).

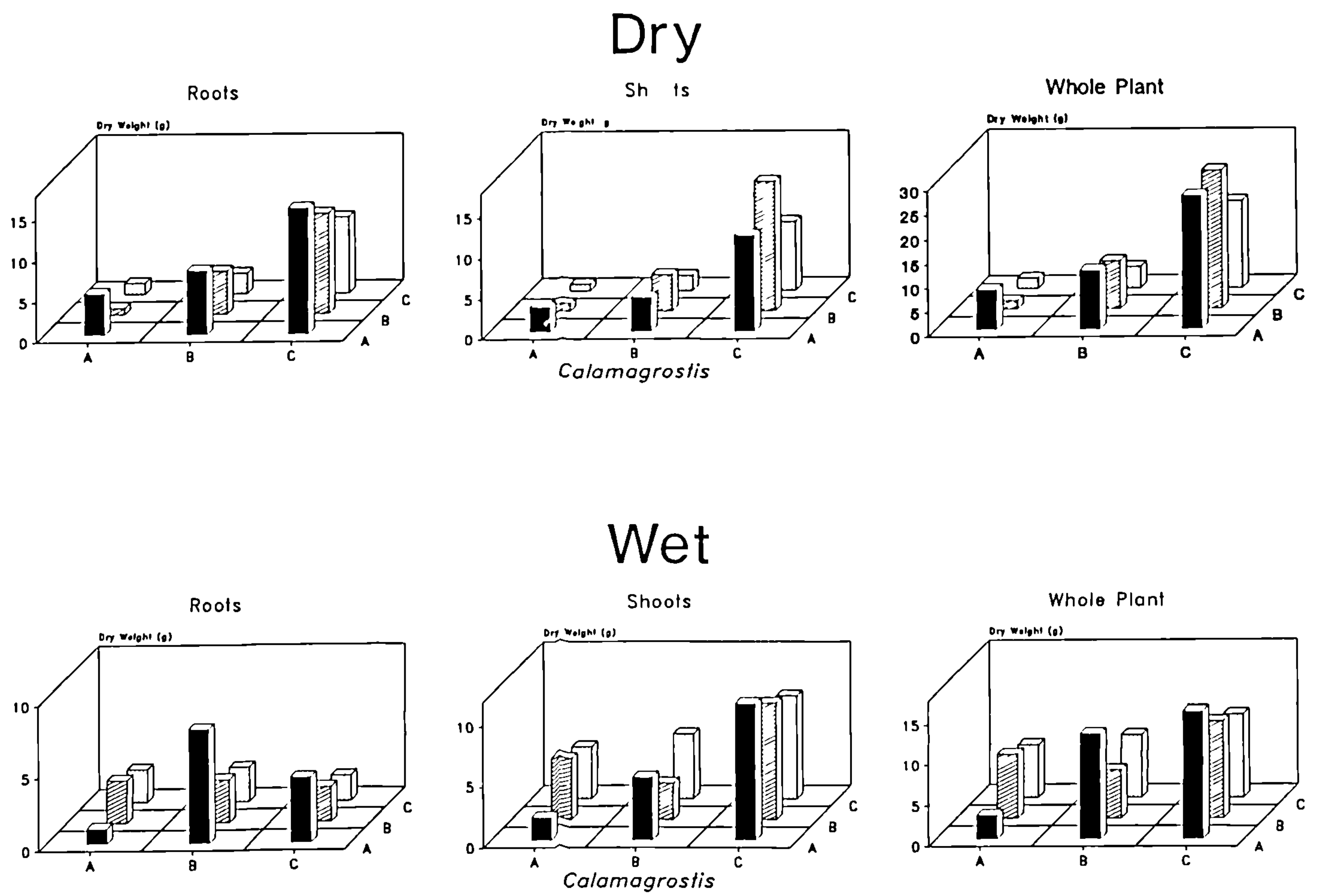


Figure 6.3.

Graphical representation of diallel mean half-pot yields in terms of dry weight. The plant material was divided into below-ground (root) and aboveground (shoot) fractions which were combined for the whole plant values. The yields for the drier watering regime are presented above those for the plants on capillary matting (wet). Five replicates—ten in the case of the pure stands—were used to calculate the mean values. The yield of each target species when grown with each of the other species (the neighbour species is shown on the right-hand horizontal axis) is given. Thus, the yield of *Calamagrostis* B roots when grown with *Calamagrostis* A in the wet regime was 7.9 g.

Table 6.2 presents the analysis of variance for the belowground harvested plant material. A highly significant difference between the watering regimes was exposed ($p < 0.001$), despite a coefficient of variation of almost 90%. Meaningful differences between target species yields and between neighbour effects were also discovered ($p < 0.001$ and $p = 0.005$, respectively). An effect of watering treatment on target species yields was shown to be highly significant ($p < 0.001$).

Source	*df*	SS	MS	F	*p*	Significance
Water Availability	1	296.84	296.84	15.23	0.000	QQQ
Targets	2	439.47	219.73	11.28	0.000	QQQ
Neighbours	2	218.95	109.48	5.62	0.005	QQ
Water Availability X Targets	2	401.62	200.81	10.30	0.000	QQQ
Water Availability X Neighbours	2	30.11	15.06	0.77	0.466	NS
Targets X Neighbours	4	48.39	12.10	0.62	0.649	NS
Water Availability X Targets X Neighbours	4	50.08	12.52	0.64	0.634	NS
Error	72	1403.05	19.49			
Total	89	2888.51	32.46			

CV = 89.67%

Table 6.2

Three-way analysis of variance performed on belowground (root) dry weight yields of three species of *Calamagrostis* growing at high and low water availability. The yields of each species are referred to as 'targets' and the yields of plants grown with each species as 'neighbours'.

The combined root and shoot analysis is presented in Table 6.3. A significant difference was found between watering regimes ($p = 0.031$). Target species yields ($p < 0.001$) and the effects of neighbour species on the yields ($p = 0.031$) were considered noteworthy. Finally, a watering-dependent effect on target species growth was demonstrated as important ($p = 0.001$).

Source	*df*	SS	MS	F	*p*	Significance
Water Availability	1	263.9	263.89	4.85	0.031	Q
Targets	2	2977.1	1488.54	27.34	0.000	QQQ
Neighbours	2	396.3	198.15	3.64	0.031	Q
Water Availability X Targets	2	822.3	411.14	7.55	0.001	QQQ
Water Availability X Neighbours	2	134.2	67.11	1.23	0.298	NS
Targets X Neighbours	4	164.2	41.04	0.75	0.559	NS
Water Availability X Targets X Neighbours	4	226.6	56.65	1.04	0.392	NS
Error	72	3919.9	54.44			
Total	89	8904.4	100.05			

CV = 68.12%

Table 6.3

Three-way analysis of variance performed on whole plant dry weight yields of three species of *Calamagrostis* growing at high and low water availability. The yields of each species are referred to as 'targets' and the yields of plants grown with each species as 'neighbours'.

A series of figures summarize the results of the Student-Newman-Keuls (SNK) tests. Figure 6.4 presents the mean yields for shoots, roots and whole plants for the two watering treatments. Differences in watering regimes were found to be unimportant in aboveground yields. Roots were found to yield significantly more in drier conditions, which was sufficient to influence the importance of the effect of watering on the whole plants.

Calamagrostis A and B were inseparable in terms of mean aboveground dry weight yields, though *Calamagrostis* C was significantly higher than the others (Figure 6.5). The belowground yields of each species were substantially different from the others: *Calamagrostis* C yielding more than *Calamagrostis* B which in turn produced a greater dry weight than *Calamagrostis* A. A similar situation was seen for the whole plant yields.

Figure 6.6 shows the mean yields of the three species when grown with each neighbour species, that is, how well the other species grew when mixed with a particular species. Thus, the mean dry weight yield for shoots of *Calamagrostis* spp. A, B and C when grown with *Calamagrostis* A was 6.3g. No significant difference was found between neighbour species means for the aboveground plant portions. Belowground, a greater mean yield was obtained for plants grown with *Calamagrostis* A than for those grown with the other two species. For whole plant yields, *Calamagrostis* A

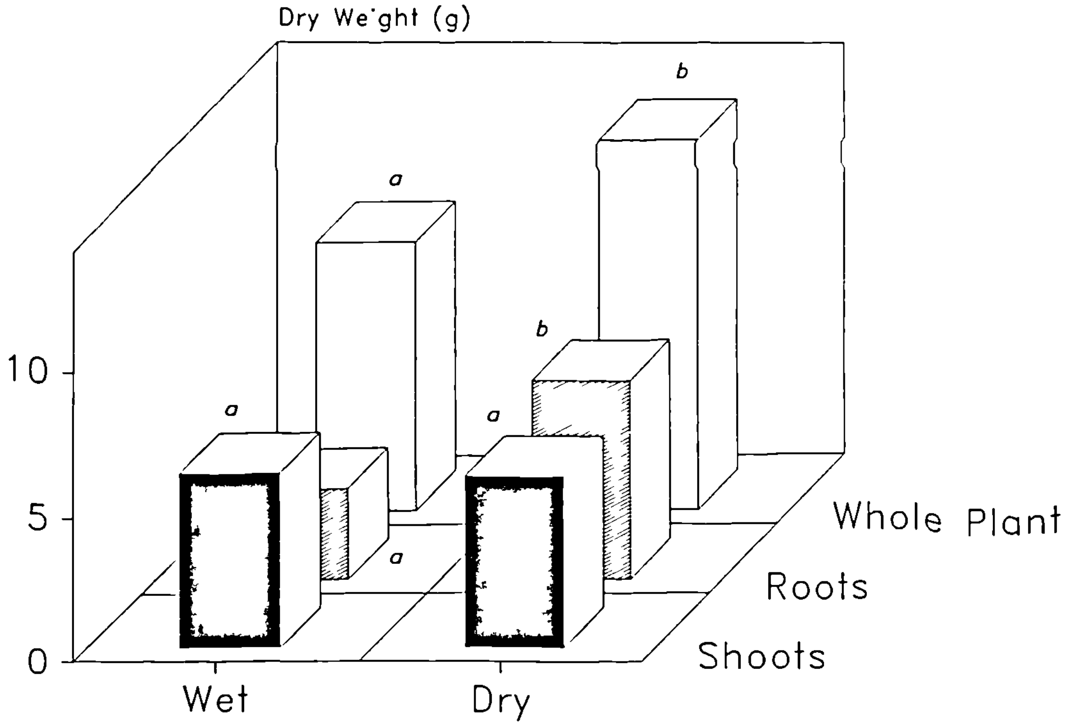


Figure 6.4.
Mean yields of roots, shoots and entire plant (roots and shoots combined) for the two water availability treatments in terms of dry weight. Separate comparisons between the two watering regimes were made for each of the roots, shoots and entire plant datasets. Means sharing a letter were not separated by a Student-Newman-Keuls test (n = 45).

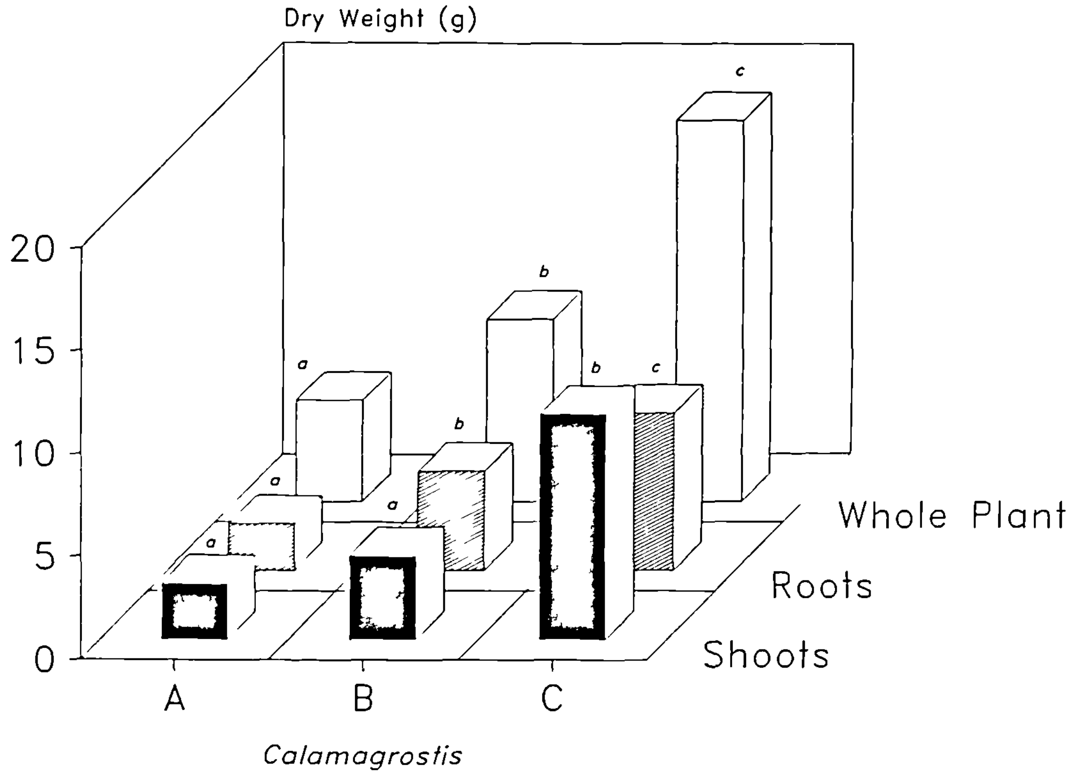


Figure 6.5.
Mean dry weight yields of roots, shoots and entire plant (roots and shoots combined) for each target species regardless of the water availability regime and neighbour species. Separate comparisons between the three species were made for each of the roots, shoots and entire plant datasets. Means sharing a letter were not separated by a Student-Newman-Keuls test (n = 30).

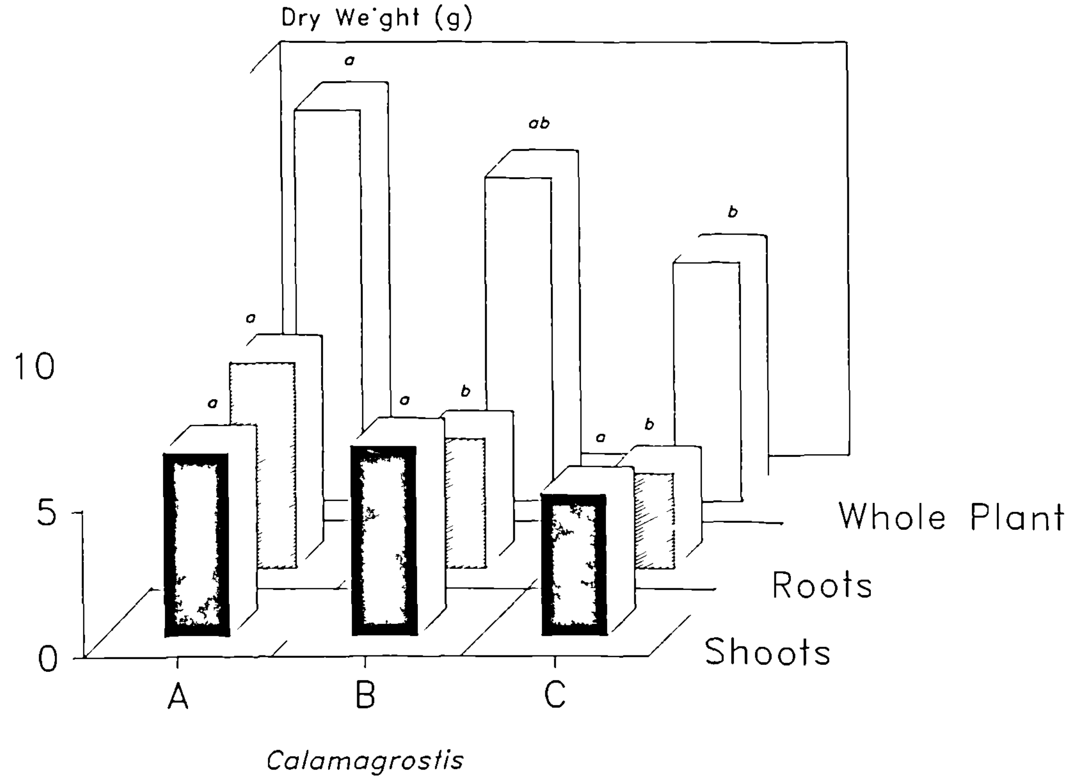


Figure 6.6.
Mean dry weight yields of plants (regardless of species or watering regime) when grown with each of the neighbour species. Separate comparisons between the three species were made for each of the roots, shoots and entire plant datasets. Means sharing a letter were not separated by a Student-Newman-Keuls test (n = 30).

allowed plants growing with it to perform better than they did when grown with *Calamagrostis* C. The mean yield for plants mixed with *Calamagrostis* B was intermediate between the other two species and could not be separated from either of them by a SNK test.

No interaction effects were seen to be significant in aboveground yields. Figure 6.7 presents the mean target species yields for the two watering treatments for roots and the entire plant. For the roots, no difference was found between these target species × watering regime interaction means, with the exception of the *Calamagrostis* C yield in the drier regime, which was significantly higher than the rest. For entire plant production, once again the *Calamagrostis* C yield in the dry conditions was significantly higher than the others. This species also performed well in the wetter watering treatment. *Calamagrostis* A in the drier conditions yielded the lowest dry weight, with the remainder of the means intermediate.

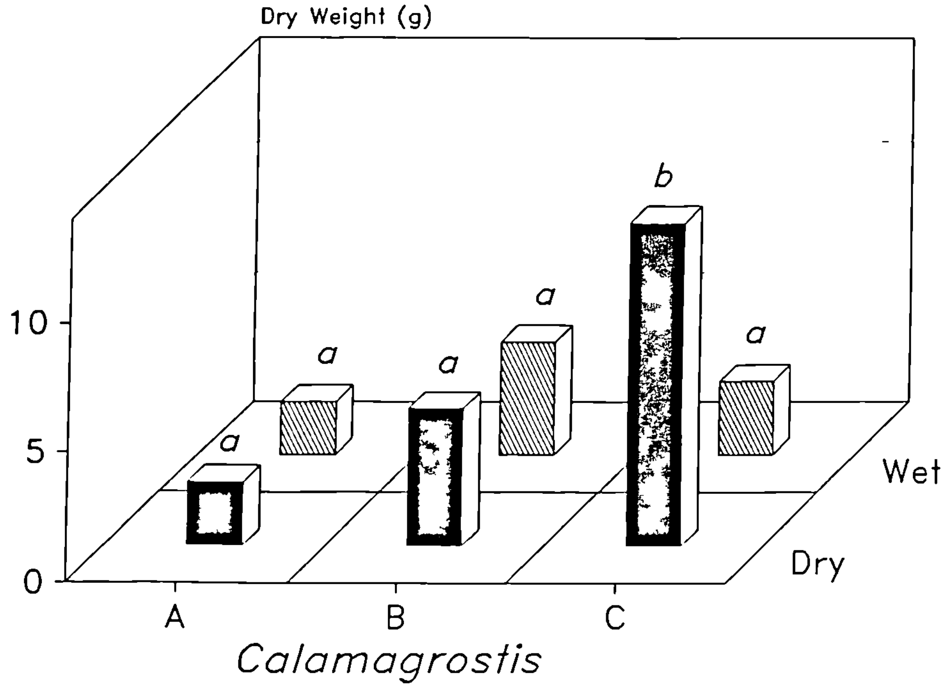
The competitive balances between the species (relational effects) are shown in Table 6.4. The most striking feature of these results is that the competitive differences between the species is much smaller than, sometimes even reversed, in the wetter conditions compared with the drier regime. *Calamagrostis* A is the weakest competitor performing significantly worse than the other two species. The relationship between *Calamagrostis* B and C is interesting. In the dry regime, *Calamagrostis* C yields much more than *Calamagrostis* B. However, in the wet regime, these species yield almost the same overall (with *Calamagrostis* B yielding more aboveground and *Calamagrostis* C more belowground).

The yield of a mixture, when taken as a whole, may differ from that predicted from the yields of the pure stands alone. These elements of interaction, the summational effects of Harper (1977), are given in Table 6.5. Mixtures containing *Calamagrostis* C consistently yield more than predicted from the performance of the pure stands, in both wet and dry conditions. In the wet, the mixture of *Calamagrostis* A and B produced a greater yield than expected, whereas in the drier regime the yield of the same mixture was depressed.

A different approach to comparing the yields in mixture with those of the pure stands is presented in Table 6.6. The Relative Yield Total (RYT) equals one when the yield of the mixture reflects the corresponding yields of the species grown in isolation. A value greater than one indicates that mutual stimulation of yield occurs, while a value less than one indicates suppression. In general, the performance of mixtures in the wetter regime was enhanced compared with the pure stands. In the dry treatment, mixtures containing *Calamagrostis* A were depressed. The mixture of *Calamagrostis* B and C followed expectation from the pure stands for the whole plant (with the shoots yielding more and the roots less than predicted).

Figure 6.8 illustrates this situation for whole plants in the dry treatment. The joint yield diagram for *Calamagrostis* B with C is almost a straight line linking the pure stand yields, which indicates that the mixture yield can be predicted from the yields of both species in isolation. The two other mixtures (A with B and A with C) lie below this hypothetical straight line: the mixture yields are less than predicted. The replacement series diagrams (on the right-hand side of Figure 6.8) illustrate the de-

(a) Roots



(b) Whole Plant

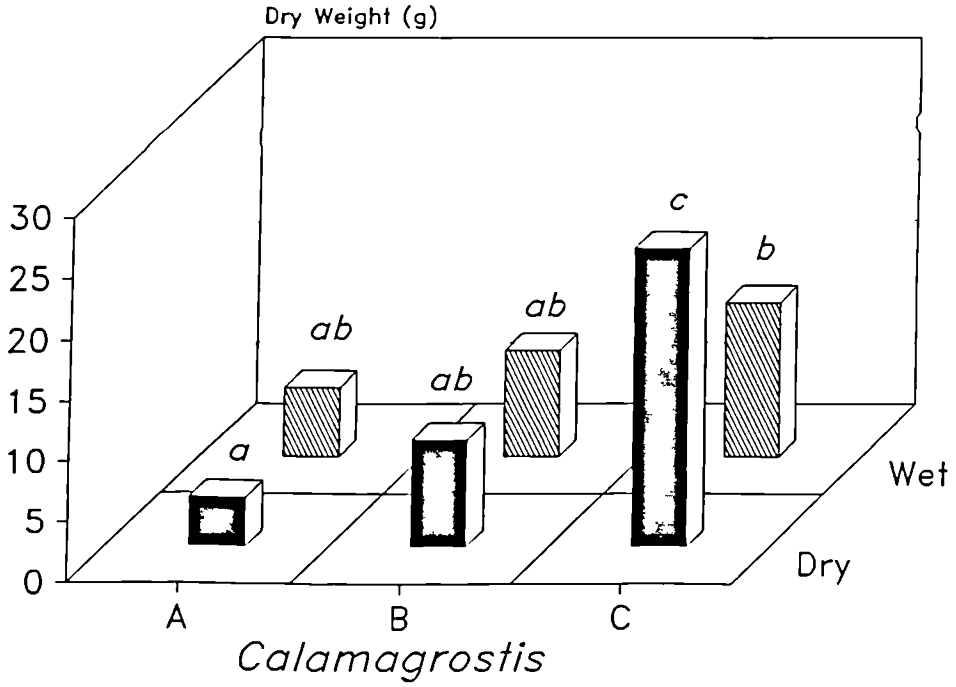


Figure 6.7.
Mean dry weight yields of species regardless of neighbour for the two moisture regimes for (a) roots and (b) whole plant. Yields sharing a letter were not separated by a Student-Newman-Keuls test ($n = 15$).

tail of these findings. Compared with the pure stands (intraspecific effects), one species influences the other more than predicted while itself being affected less.

In the wet regime (Figure 6.9), all mixtures show enhanced performance compared with the pure stands, shown by the convex line in the joint yield diagrams. The replacement series diagrams also share the same form: both species show a convex line, indicating that they both perform better than expected from the pure stand yields.

	Dry			Wet		
Mixture	Shoots	Roots	Whole	Shoots	Roots	Whole
A versus B	-0 93	-4.50	-4.44	0.48	-1.52	-1.05
A versus C	-2.89	-5.01	-7.90	-0.19	-0.75	-0.94
B versus C	-5.12	-2.93	-8.05	0.66	-0.61	0.05

Table 6.4.
The competitive relationships between the three *Calamagrostis* species (Relational effects of Harper, 1977). If the value is positive then the first species holds a competitive advantage over the second species; if negative then *vice versa*. Values are in terms of dry weight (g) per species.

	Dry			Wet		
Mixture	Shoots	Roots	Whole	Shoots	Roots	Whole
A with B	1 22	-0.09	2.13	-2.65	-3.40	-6.05
A with C	-0 59	-1.19	-1.78	-2.58	-1.97	-4.55
B with C	-2 41	-0.10	-2.51	-1.75	-0.03	-1.78

Table 6.5.
The relationships between the yields of mixtures and pure stands of the three *Calamagrostis* species (Summational effects of Harper, 1977). Values are in terms of dry weight (g) per species. If the yield of the mixture exceeds that predicted from the yield of the pure stands then the value is negative; if below this predicted value then the figure will be positive.

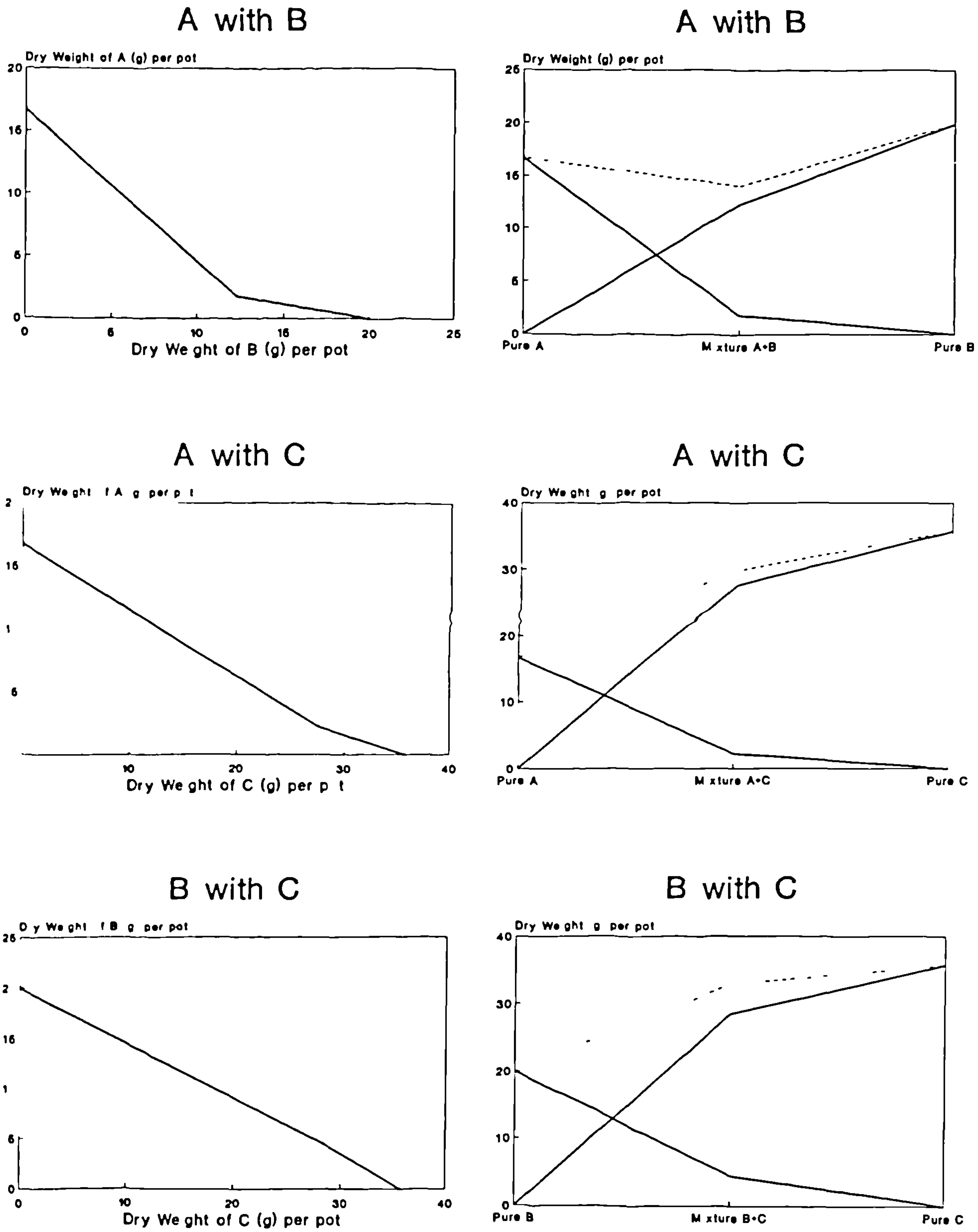


Figure 6.8.

Joint yield diagrams (left) and replacement series diagrams (right) for the three *Calamagrostis* mixtures grown in the dry regime. In the replacement series diagrams, the two solid lines represent the yield of each *Calamagrostis* species and the dashed line the joint yield.

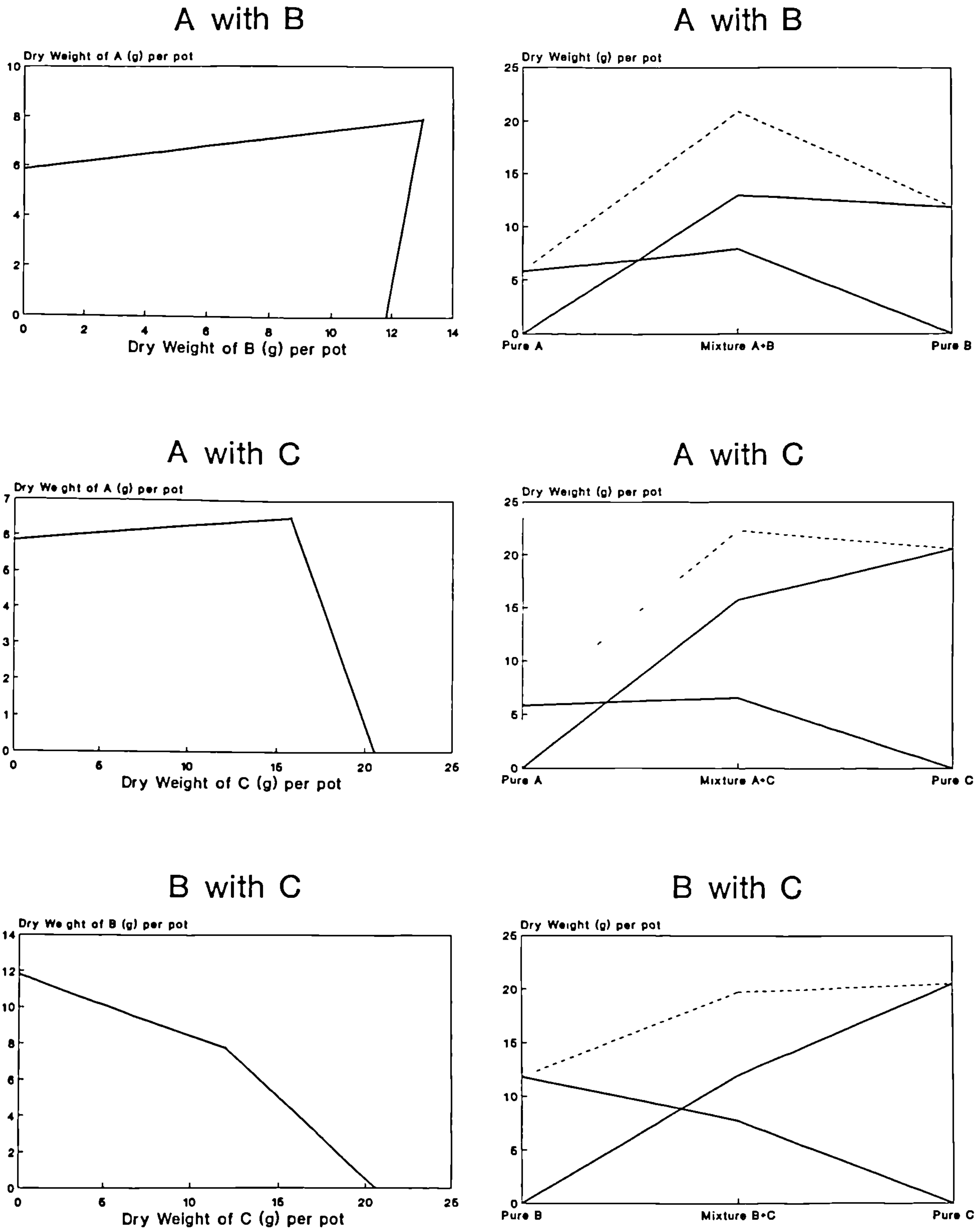


Figure 6.9.
Joint yield diagrams (left) and replacement series diagrams (right) for the three *Calamagrostis* mixtures grown in the wet regime. In the replacement series diagrams, the two solid lines represent the yield of each *Calamagrostis* species and the dashed line the joint yield.

Mixture	Dry			Wet		
	Shoots	Roots	Whole	Shoots	Roots	Whole
A with B	0.63	1.00	0.72	2.20	2.75	2.46
A with C	0.84	0.96	0.90	1.80	2.36	1.89
B with C	1.15	0.90	1.02	1.47	1.08	1.24

Table 6.6.
The relationships between the yields of mixtures and pure stands of the three *Calamagrostis* species (Relative Yield Totals, RYTs, of de Wit & van den Burgh, 1965). The values have no units. If the RYT > 1, then a yield advantage is obtained in mixture; if RYT = 1, no advantage is obtained; and if RYT < 1 a disadvantage is indicated.

Discussion

The Cultivation of the *Calamagrostis* Species

Before dealing with the experimental results *per se*, it would be helpful to look at some of the problems encountered when trying to grow these species in the greenhouse.

It is standard procedure to begin an experiment of this nature with tillers taken from mother plants. In this case, with large mother plants, it was easy to select suitable tillers of the same status. However, these tillers demonstrated remarkably high mortality after separation and planting. The overall mortality was close to 52% (with 76%, 48% and 32% for *Calamagrostis* A, B and C respectively). It seems unlikely that tillers would have been able to exert competitive effects on neighbours at this stage. The discrepancy between the species is probably a result of the performance of the plants themselves rather than the effects of neighbour tillers, despite the high mortality of *Calamagrostis* A when grown with *Calamagrostis* B.

The cause of such mortality is unknown. The cultivation of tropical alpine plants is notoriously difficult. At the Royal Botanic Gardens, Kew, in an attempt to simulate the tropical alpine environment, artificial 12-hour daylength and marked diurnal temperature regimes (21°C during the day and 5°C at night) have been introduced to the greenhouses by Tony Hall at the Alpine Department at the Royal Botanic Gardens, Kew (personal communication). Even under this regime, some plants show very different growth (for example, *Plantago rigida* adopts a very different habit from the cushion growth form seen in the páramo). Such environmental control was not possible in this experiment and may have resulted in the death of a high proportion of tillers. However, the survival of new individual tillers of recently burned *Calamagrostis* tussocks in the field (Páramo de Daldal) was also low, at 85% and 60% for two tussocks studied (Chapter 4). Perhaps low tiller longevity is a natural feature of these plants. Clearly more research is needed to establish the expectations of tiller mortality in these grass species.

Whatever the causes, high tiller mortality makes it difficult to design satisfactory experiments. Further complications to experimental design followed the establishment phase. A number of tillers were found to remain 'dormant' after planting, that is to say, they stayed alive without producing any new growth. The experimental protocol of replacing dead tillers did not allow for the substitution of dormant ones; besides, it would not have been possible to determine the potential of tillers for dormancy during the establishment period.

The presence of tillers more or less unchanged since planting at the start of the experiment contributed greatly to the variability of the data. In all, fifteen tillers were classed as dormant out of the ninety that comprised the dataset: if these are removed then the coefficient of variation is reduced from around 68% to below 28% for the whole plant data. This would probably reduce further if it were possible to compensate for the extra yields obtained by the neighbours of dormant tillers.

The growth of these plants taken as a whole was much slower than that of local Welsh upland grasses grown in similar conditions (Ramsay, unpublished data). The stature of *Calamagrostis* A was always small, even in stock tussocks not involved in the experiment. It would appear that some internal constraint on growth is present, in addition to those limitations imposed on the plants by the greenhouse conditions discussed earlier.

Finally, it is worth noting that a difference between species was observed in root formation. Plants from the highest elevation (*Calamagrostis* A) developed much finer roots than the other species, with the roots of *Calamagrostis* B appearing finer than *Calamagrostis* C. This purely passing observation is supported by the work of Körner & Renhardt (1987) who found that plants from higher altitudes developed about 4.5 times more fine root length per unit leaf area than low altitude plants. In the *Calamagrostis* species used in this study, there appears to be a genetic basis for these differences.

Diallel Yields

The results of the diallel experiment do not support the hypothesis of better performance in drought conditions by species from high altitude compared with low altitude ones. In fact, the results are the reverse of those expected: the species from the highest altitude was the only one to yield less in the drier regime than in the wetter regime. Furthermore, the relative competitive abilities of the plants used in these experiments were more pronounced in the drier conditions.

Overall, *Calamagrostis* C performed best, followed by *Calamagrostis* B with the species from the highest altitude, *Calamagrostis* A, doing worst of all. This pattern was reciprocated, in that the species which yielded most depressed the yield of its neighbours most, and so on. These relative competitive abilities of the species were sometimes influenced by the watering regime. For example, *Calamagrostis* C yielded much more than *Calamagrostis* B in the drier regime, whereas in the wetter treatment they showed almost equal competitive ability. However, in general it appears that *Calamagrostis* grasses from higher altitudes are less able competitors than those from lower altitudes, irrespective of the watering regime. This supports the expectation of Grime (1979) that competition is less important at higher altitudes (where stress is high) and that species from lower altitudes should be fast-growing, capturing resources as quickly as possible. The upper distributional limit of several páramo plants and communities have been attributed to stress tolerance factors (particularly frost), whereas the lower limit has most frequently been ascribed to competitive effects (*inter alia* Armesto, Arroyo & Villagran, 1980; Fariñas & Monasterio, 1980; Alliende & Hoffmann, 1985; Pérez, 1987; Miller & Silander, 1991).

In productivity terms, greater yields were obtained from plants subjected to the drier treatment, mainly due to better root development (aboveground production was little influenced by the watering regime), an effect that was particularly pronounced in *Calamagrostis* C. It seems unlikely that capillary matting would result in root suppression in these species: more likely is that root growth was stimulated in the dry regime.

The relationships between the yields of mixtures and those of their component species in pure stands was also investigated. The RYT has been widely used to investigate the extent to which species in a mixture compete for common limiting resources (Snaydon, 1991). The term 'resource complementarity' was coined by Snaydon & Satorre (1989) to describe such an index. The lower the RYT, the greater is the competition for limited resources. The summational effects, with minor differences, followed the same pattern as the RYTs described below.

In the drier treatment, RYTs were approximately equal to one, or less than one. This implies that the species are making demands on the same limiting resources of the environment (Harper, 1977), and in some cases this results in a reduced yield compared with the pure stand yields.

In the wetter conditions, mixtures exceeded the performance of pure stands, with RYTs greater than 1 and convex lines in the species replacement diagrams. Mixtures containing *Calamagrostis* A resulted in very high RYT values: close to 2 or even higher. This result is very rare in plant mixtures (Snaydon, 1991) and indicates complete or nearly complete resource complementarity (that is, the species avoid competition, making different demands on the environment). The most plausible explanation for these very high RYT values with *Calamagrostis* A in the wet regime is that, owing to the inherently slow growth of this species, competition for resources between the species in the mixture did not occur at all, or was delayed until towards the end of the experimental period.

The lack of phenotypic plasticity in *Calamagrostis* A clearly had an important bearing on the overall result of the experiment, decreasing the potential yield response of this species. This may be advantageous in the High Andes by restraining opportunistic growth (and utilization of precious resources) in response to transient climatic conditions: Grime's (1979) stress tolerant strategy. In the greenhouse, however, it makes experiments of this nature difficult to interpret.

One of the principal drawbacks of replacement experiments, such as that described here, is that the results obtained only apply to the particular conditions under which the experiment was carried out (Jolliffe, Minjas & Ruenckles, 1984; Connolly, 1986). Firstly, the experiments were carried out at fixed densities, a situation which does not reflect the field situation (Inouye & Schaffer, 1981). Secondly, the climatic conditions did not echo those prevalent in the Andes. The limiting factors on growth in such changed conditions may have been different and the competitive balance between the grass species may have been altered in favour of the lower altitude species. For example, the warm temperatures throughout the 24-hour period may have allowed the lower elevation species to capitalize on the potentially higher metabolic activity at the expense of *Calamagrostis* A.

A second possibility is that the drought treatment was not severe enough to exert sufficient influence on the outcome of competition between species. In fact, the grasses did significantly better in the drier regime, yielding over one-third more than in the wetter conditions, largely the result of lower root growth in the wet. *Calamagrostis* A is an exception in this, though, performing better in the wet – this is the result of greater tiller dormancy in the drier conditions. In the design of the experiment the severity of the drier treatment was deliberately restricted because of the high mortality rate experienced with these grasses. More stringent deprival of water would perhaps have produced a different effect.

Therefore, before dismissing the original hypothesis outright, it is worth considering these arguments. Nonetheless, attention should be given to the rejection of the hypothesis in hand, and to alternatives to explain the distribution of plant species over the altitudinal gradient in the Ecuadorian páramos. Temperature certainly shows a marked trend across the elevation gradient with a lapse rate of 0.6°C per 100m. The number of frost days also increases sharply over the altitudinal range of the páramo (Sarmiento, 1986). This factor might influence plant distributions through plant competition, or via flower and seed development and germination requirements. Frost could be particularly important with regard to the latter.

Future research in this direction should combine precise environmental measurements in the field with distributional data for the plant species. Greenhouse studies should aim to simulate the páramo environment as closely as possible, since the complex relationship between environmental factors is perhaps more important than any one factor taken alone. Field experiments to determine the outcome of competition between species, *in situ* in the Andes, may reveal more useful information than the artificial greenhouse environment.

Chapter 7

Overall Discussion

The páramo environment is unique to tropical alpine regions. It presents particular difficulties for the flora, described in earlier chapters. The harshness of these conditions confers a special fragility on the plant communities of the páramos. The evolutionary history of the Andes (principally the uplift of the Andes, periodic volcanic activity and the periods of cooler weather during glaciations alternating with warmer interglacials) has further contributed to this precarious existence.

Geographically, the isolated nature of páramo regions has resulted in distinct floras. During the warmer interglacial episodes, páramo vegetation contracted as the vegetation zones were pushed higher up the mountains. High rates of speciation and extinction are thought to have occurred during these periods of isolation, and accounts for the high level of endemism in páramo taxa. At cooler times, the páramos covered a larger area in the Andes, as the vegetation zones were lower down the mountains. At such times, new taxa, evolved in isolation, were free to migrate through the extensive páramo belt. The vegetation of the páramo has undergone a series of about 15-20 contraction-expansion cycles with accompanying speciation and radiation episodes, each cycle lasting approximately 100,000 years (Van der Hammen & Cleef, 1987).

In a sea of warm tropical vegetation and subject to the above climatic and catastrophic changes, the páramos can be thought of as typically insular and short-lived (Smith & Cleef, 1988). They rely on long-distance dispersal rather than local adaptation from the lowland tropical flora as the primary source of recruitment to the plant communities. Cleef (1979) and Van der Hammen & Cleef (1986) found that about half of the páramo flora of the Colombian Cordillera Oriental were of temperate origin, the remainder of tropical (mostly neotropical) origin. In Ecuador, temperate taxa dominate the zonal páramos, making up about two-thirds of the flora (Chapter 2). In all studies so far, páramo endemics account for just under 10% of the total flora (9% in this work).

As a consequence of the above factors, the vascular plants of the páramo represent the richest mountain flora in the world (Smith & Cleef, 1988). Luteyn, Cleef & Rangel (1992) estimate that it consists of 112 families, 479 genera and between 3,000 and 4,000 species. However, these estimates include all types of páramo vegetation: azonal bogs, woodlands and thickets as well as the zonal vegetation types from shrubby sub-páramo to high altitude desert super-páramo.

In Chapter 2, the zonal páramo vegetation of Ecuador was sampled by means of 192 quadrats, amounting to a total area of 0.48 ha. In these samples, 348 vascular plant taxa were recorded (9-12% of the total páramo flora of the Andes). These belonged to 117 genera and 46 families (24% and 41% of the total Andean páramo estimates, respectively). In view of the objective to sample only the typical zonal vegetation and that the study areas represent only a small fraction of the whole páramo province from Central America to Perú, these numbers are unexpectedly high.

Basing his work on a limited sample of species, Balslev (1988) estimated that 60% of the highland flora of Ecuador were found outside Ecuador, and 72% were trans-Andean (that is, present on both the eastern and western ranges of the Andes). In the present study, 143 trans-Andean species were found (or 41% of all species recorded). Approximately 33%, or 114 species, were restricted to samples from the Eastern Cordillera sites (Páramo de Guamaní, Volcán Tungurahua, El Altar west, El Altar east, Páramo de Daldal, Páramo de Zapote Naida, Páramo de Cumbe and Páramo de Oña). The remaining 91 species (26%) were recorded only in quadrats from study sites on the Western Cordillera (Volcán Chiles, Volcán Cotacachi, Volcán Chimborazo and Páramo de Cajas).

Table 7.1 shows the number of species found in each study site. Less than one-third of the 348 species found in all of the sites was present at any one study area. The three samples from the Páramo de Oña contained just 24 species, while 21 samples from the Páramo de Cajas were comprised of 117 species. These figures represent 0.6-0.8% and 2.9-3.9% of the total páramo flora, respectively.

Páramo Region	No of Samples	Total Area (ha)	No of Species	% of Total Páramo Species
Volcán Chiles	21	0.05	94	2.4-3.1
Volcán Cotacachi	21	0.05	89	2.2-3.0
Páramo de Guamaní	21	0.05	97	2.4-3.2
Volcán Tungurahua	15	0.04	52	1.3-1.7
El Altar (west)	15	0.04	92	2.3-3.1
El Altar (east)	18	0.05	71	1.8-2.4
Páramo de Daldal	18	0.05	91	2.3-3.0
Volcán Chimborazo	21	0.05	37	0.9-1.2
Páramo de Zapote Naida	9	0.02	47	1.2-1.6
Páramo de Cajas	21	0.05	117	2.9-3.9
Páramo de Cumbe	9	0.02	71	1.8-2.4
Páramo de Oña	3	0.01	24	0.6-0.8
Total	192	0.48	348	8.7-11.6

Table 7.1
Distribution of vascular plant species in the twelve study sites in Ecuador. The percentage of páramo species is based on an overall estimate of 3000-4000 species (Luteyn, Cleef & Rangel, 1992).

Almost half of the species were recorded in just one study area and three-quarters were present in fewer than four sites (Table 7.2). Only four species were present in ten or more sites: *Pernettya* sp. [185], *Hypochaeris sessiliflora*, *Calamagrostis* sp. [251] and *Eryngium humile.*

These differences in species composition between the study areas were reflected in the plant communities. The principal patterns were *Espeletia* páramo in the north, *Neurolepis* bamboo páramo in the east and Rainshadow desert páramo in the west. Furthermore, the grassy páramos, present all over the country, revealed similar regional patterns.

	Frequency	%
Species recorded in only 1 Site	168	48.3
Species recorded in 2 Sites	66	19.0
Species recorded in 3 Sites	26	7.5
Species recorded in 4 Sites	26	7.5
Species recorded in 5 Sites	24	6.9
Species recorded in 6 Sites	16	4.6
Species recorded in 7 Sites	10	2.9
Species recorded in 8 Sites	3	0.9
Species recorded in 9 Sites	5	1.4
Species recorded in 10 Sites	2	0.6
Species recorded in 11 Sites	1	0.3
Species recorded in all 12 Sites	1	0.3
Total	348	100.0

Table 7.2.
Frequency distribution of vascular plant species in the twelve study sites in Ecuador.

Despite these regional differences, altitudinal zonation of plant communities was pronounced. The mid-altitude zones (tussock páramos and lower cushion páramos) were extensive in many of the study areas. By contrast, other communities were restricted to much smaller areas, for a number of reasons. The high altitude desert páramos and cushion páramos were confined by the limited extent of the land at such elevations. The high altitude dwarfshrub páramo communities were restricted to a very narrow altitudinal band for reasons that are not yet clear, but which may be related to humidity (Cleef, 1981). Finally, at the lower end of the páramo range, the shrubby sub-páramo was largely absent because of burning and agriculture.

There is very little information on the degree of intraspecific variation in páramo species. Altitudinal ecotypes may exist in the páramos (Smith, 1980). Buckland & Ramsay (in press) measured morphological parameters for several species along two altitudinal gradients. Some of these species showed distinct morphological responses to altitude. For example, *Lycopodium* sp. demonstrated a decrease in leaf size and plant height with increasing altitude. Other species showed little or no correlation with altitude.

In the greenhouse study described in Chapter 6, *Calamagrostis* sp. tussocks from the highest altitude in the Páramo de Guamaní had a fixed response regardless of the prevailing environmental conditions. Growth was slow compared to *Calamagrostis* spp. from lower altitudes and tussock stature was also small. This implies that, for some species at least, rate of growth, plant form and other features are under genetic control. In other species, however, the plant form is partially controlled by the environment. For example, cultivated *Plantago rigida* at Kew has a very different habit to the dense cushion observed in nature.

Thus, the zonal Ecuadorian páramos are relatively species-rich (possibly with significant intra-specific variation) and exhibit strong regional variations in composition. Many of the communities are restricted to small areas, while their sensitivity to disturbance is high because of extreme environmental conditions.

The main threat to this diversity comes from agriculture. Although the high Andes have been populated for thousands of years (Eckholm, 1975), there are two to three times as many people living in the highlands now than were there immediately before the arrival of the first Europeans (Baker, 1978). In Ecuador, approximately 50% of the population live in the Andean Highlands (Luteyn, 1992) and population growth is among the highest in South America.

Traditionally, highland peoples of the Andes have achieved sufficiency by their ability to exploit several distinct life zones simultaneously. Murra (1972) termed this system "vertical control". A highland community would farm a number of geographically separated areas, deriving different products from each and at different times of the year.

The arrival of the Spanish modified this lifestyle, through the introduction of new crops and livestock and the widespread resettlement of peoples (Brush, 1976). However, despite these changes, Murra's model of vertical control remains the basis for the subsistence economies of many Andean communities.

The valley of Daldal, surveyed in Chapter 2 and the main site for Chapter 5's productivity studies, is a good example of how such a system operates even at a local scale. Farmers living in the settlement of Daldal (3,100 m) have a number of fields nearby in which they grow crops such as maize, quinoa (*Chenopodium*), peas and a range of other produce for domestic use and for sale at the local market. These farmers may also possess land at higher altitudes. Many farmers have land at 3,400 m, which is used to cultivate tubers (potatoes, oca) and beans, and another more extensive holding in the pǎramo zone used for the rearing of livestock (mostly cattle and horses). In the nearby settlement of Alao, some farmers occasionally visit the montane forest on the eastern slopes of the Andes to supplement their produce by hunting and fishing.

Since the land-use of extensive highland haciendas was changed by the 1964 Law of Agrarian Reform and Colonisation, smaller, more intensive farms have become common (Cabarle *et al.,* 1989). As the population grows and as communities become less isolated and part of the wider economy, many farmers are unable to operate vertical control. Instead, they are forced to survive with smaller plots or land of lower quality (usually at higher altitudes). Thus, in the valley of Daldal, there were farmers living at 3,400 m with only nearby plots on which to grow food. This requires the intensive use of this land. It is also less resilient than the traditional lifestyle. Cropping at this altitude is less dependable and requires more land for the same crop. Since these people are no longer able to meet all of their food demands, they are forced to sell part of their harvest and trade for other necessities (including fuel, now that most of the montane forest has gone). As a result of these pressures, conversion of natural or semi-natural habitats to agriculture has proceeded very rapidly in recent times, and the sub-pǎramo has completely disappeared in the Daldal valley.

This trend is mirrored in most other highland settlements and the sub-pǎramo has been destroyed in many areas by conversion to arable land. Much of the remainder of the pǎramo has also been affected by its widespread utilisation as grazing pasture. As reported in Chapters 2 and 4, the poor herbage quality of mature tussocks leads farmers to burn tussock páramos every two to four years. The effect of this practice on the Andean environment has led to speculation that the Ecuadorian páramos (covering an area of approximately 20,000 km^2 – Bonifaz, 1981; Encalada, 1986) may not be the true climax vegetation, but a secondary type maintained by burning. Scattered throughout the páramo zone, there are woodlands of varying sizes, mostly consisting of the genus *Polylepis* (Rosaceae) but often in association with *Gynoxys* (Compositae). It has been argued that high-altitude forests, similar to these woodlands, once covered much of today's páramos, but have been destroyed over many years by man-induced fires and replaced by the grasslands present today. Evidence for this view includes:

- the regular practice of burning in many páramo grasslands as a management tool for improving pasture quality (Ellenberg, 1958; Laegaard, 1992);
- the presence of woodlands and small patches of trees growing in areas unlikely to sustain fires, for example, scree slopes and beside rivers (Laegaard, 1992);
- the ability of certain tree species to survive in the grassland zone, some 400-500 m above the present forest limit (Ellenberg, 1958; Brandbyge & Holm-Nielsen, 1986);
- observations that páramo fires erode the edges of adjacent forests (Laegaard, 1992);
- the lack of a transition zone from trees to grassland at the present treeline and observations of such transitions at higher elevations (Laegaard, 1992); and
- biogeographical information relating to birds endemic to high-altitude woodlands (Fieldså, 1992).

Counter to these arguments, other authors believe the páramos to be a largely natural phenomenon, representing the true climax vegetation of high altitudes in the northern Andes. Observations used to support such a view include:

- the apparent restriction of high altitude forests to specific microclimates in sites such as rocky slopes, river courses, valley bottoms, *etc.* (Troll, 1959);
- the common occurrence of trees characteristic of the high altitude forests around dwellings which replicate the microhabitats described above (Simpson, 1979), supported by evidence from Brandbyge (1992) that *Polylepis incana* growth near walls is twice that in the open;

- experimental investigations carried out by Smith (1978) in Venezuela showed convincingly that *Polylepis sericea* was restricted to microsites by poor establishment elsewhere.
- biogeographical evidence relating to the tree species themselves (Simpson, 1979) and fauna associated with them (Simpson, 1979); and
- palaeohistorical data on *Polylepis* suggesting wide expansions and contractions with climatic changes without man (Simpson, 1979).

Clearly, both sides of the debate have drawn upon powerful support for their case. Without doubt, the current extent of páramo grassland is considerably greater than would naturally exist in the absence of man. However, as Balslev & Luteyn (1992) put it, "the question is not whether man has cut the Andean forest and continues to maintain and increase páramo area, but rather whether he alone has been responsible for wiping out the high-elevation forests up to the presently observed timberline or if natural forces have controlled this."

The biogeographical evidence is confused, and has been used to support both views. Owing to the complex climatic history of this region, with periods of speciation and radiation, it is difficult to assess whether species patterns observed today reflect current forest limits or are the consequence of previous isolations and expansions. Similarly, palaeological data have not yet provided sufficient information to determine the former extents of forest cover in this regard.

The ability of some tree species to survive at higher elevations than they are found in nature is undisputed. However, this does not mean that they could colonise grassland if burning were halted. Simpson (1979) suggests *Polylepis* seeds are dispersed by birds and germination rates of *P. incana* are low (Brandbyge, 1992). Brandbyge & Holm-Nielsen (1986) suggested that natural regeneration of *Polylepis* might depend on favourable microclimatic conditions not offered by tussock páramo, and Smith (1978) found *Polylepis sericea* unable to establish in Venezuelan páramo vegetation or on bare soil. The author has not observed *Polylepis* seedlings growing in open grass páramo in Ecuador, only within woodlands or at their edges, on scree or beside water near existing woods.

From this evidence, even without burning, *Polylepis* would invade páramo grassland at a very slow rate, gradually encroaching into the páramo from its current woodland edges. In view of the relatively recent climatic changes (with the last warm period ending about 3,000 years BP – Van der Hammen & Cleef, 1986), in order for *Polylepis* to cover most of today's páramos, it would have been necessary for it to colonise new areas at a relatively fast rate. The means by which such a rate of spread would have been accomplished has not been demonstrated.

Furthermore, the lack of relict traces of former forests in the grassland demands further explanation. Particularly at the highest altitudes (Laegaard, 1992, suggests a true timberline between 4,100-4,350 m in Ecuador) decomposition of charred trees would be slow, and remnants might be expected in some places at least. There are no reports of such finds.

Laegaard (1992) noted that transition zones from forest to grassland are largely absent from the present treeline, and that they have been observed at the upper limit of the high altitude woodlands. However, *Polylepis* woodlands usually have sharp upper boundaries and transitions are not found in the majority of cases. In addition, the present treeline does occasionally present a transition zone, where human disturbance is absent. Therefore, these observations do not favour a higher or lower treeline, but merely confirm the effects of burning on the boundary between forest and grassland, especially in the most accessible areas.

Laegaard (1992) states that "all grass páramos are more or less regularly burned". This seems unlikely. Although great areas of páramo are frequently burned, many remote areas are not. The question then becomes, how frequently must fires occur to prevent woodland establishment? When tussock grasses have not been burned for a long time, fires can be both intense and far-reaching. Natural fires could occur under certain circumstances and have been recorded in similar situations elsewhere (Givnish, McDiarmid & Buck, 1986). Such fires could cover very large areas if climatic and topographic conditions allow. Therefore, if very occasional burning could prevent woodland establishment, natural explanations may be forthcoming.

If only the forest edges are destroyed by a neighbouring grass fire, very many fires would be required to isolate pockets of woodland in the manner that has been proposed. It is unlikely that the frequency of natural fires could account for such a number.

Patches of páramo may be found which are isolated from other grasslands by efficient fire breaks (islands in lakes, land isolated by cliffs and watercourses, *etc.*) and are almost certainly not burned by man. If *Polylepis* woodland was the natural climax vegetation, then these areas would be forested. In many cases, they are not. According to Siltanen, Thurland & Casanova (1987), *Polylepis* trees can grow on a wide range of soil types and depths. It exists on wet and dry soils and even on rocky scree slopes. Therefore, an inappropriate substrate is not a viable explanation for the trees' absence in these sites.

It is generally accepted that human populations only became a significant influence on the vegetation of the high Andes in the last few thousand years (Eckholm, 1975). The apparent capacity of certain plant species to survive fires demands explanation of how such ability evolved if fires are such a recent phenomenon in the páramos. Laegaard (1992) suggests that the ability to survive burning is a fortuitous side-effect of selection for other traits, such as drought tolerance and resistance to UV radiation. Although these features may confer a degree of fire resistance, it is perhaps cold temperature avoidance that offers a more plausible explanation, since insulation from cold temperatures is equally effective against heat.

One possible explanation for the current distribution of *Polylepis* woodlands is that they are relict populations from the warm period some 3,000 years BP that are able to regenerate within the self-perpetuating environment of the forest interior, but are unable to expand much beyond the limits of the current woodlands.

Exactly where the natural timberline lies is difficult to judge on current information. However, it seems likely that it will vary considerably from region to region in a similar way to the vegetation zones described in Chapter 2. Furthermore, local topographic features will alter its distribution at a finer scale.

To answer the fundamental question of high altitude forests requires a great deal of further effort. However, even if the páramos are secondary vegetation types, this does not alter the fact that they now cover large areas of the Andes. They are economically valuable and their sustainable management depends upon an understanding of how the grassland functions.

Páramo fires are important determinants of plant communities. In Chapter 4, the survival of páramo plants following burning was related to fire temperatures. Radiated heat and flames were responsible for the loss of aboveground leaves and stems and the majority of regrowth was from belowground parts. However, high rates of leaf and shoot mortality were observed in surviving plants in subsequent weeks and recovery was a slow process, especially at high altitudes.

Despite these slow growth rates, the productivity experiments in the páramo (Chapter 5) suggested that tussock productivity reaches equilibrium in 3-5 years, which corresponds well to the observed practice of burning every 2-4 years. Furthermore, cutting the plots (to simulate burning) resulted in a higher yield in the páramo plots. In agricultural terms, therefore, the practice of burning appears well founded.

In areas subjected to regular fires, plants which are poorly adapted to burning might be displaced. Other species, able to survive fires or to colonise bare ground after burning, might increase. It is likely, then, that páramo fires might be responsible for the loss of biodiversity. However, regularly burned páramo grassland is not subject to the very high temperatures reached by unburned vegetation. Infrequent fires, therefore, may result in more losses than frequent fires because of their higher intensity.

In some páramos, burning can cause long term damage to the soil. Over-frequent burning appears to be most prevalent at higher altitudes, where the process of recovery takes longer. Thus, burning every 2-4 years does not allow enough time for complete recovery. Over-burning does occur at lower altitudes too, if the frequency of fires is high. Where over-burning is practised, erosion can result (Portsch & Hicks, 1980; Ponce, 1984). The humus content of the soil can be lost during the fire, and the lack of vegetation to bind the remaining soil material can lead to its loss during the runoff events associated with heavy rainfall. Eventually, a sparse plant community remains, growing on a largely mineral substrate. The productivity of the land is lost, in complete contrast to the original aim of the burning.

Grazing and trampling also affect the páramo vegetation. They are strongly associated with burning, since recently burned areas are preferred for foraging (Verweij & Kok, 1992). To meet their nutritional requirements in the páramo, cattle must travel long-distances and forage for long hours (Schmidt & Verweij, 1992). Diet selection does occur (short grasses and sedges are preferred rather than tussock grasses – Schmidt & Verweij, 1992), but the effect of this on the composition of plant communities is still unclear. Widespread trampling effects include the creation of micro-terracing (an intimate series of cattle paths following the hillside contours) and the compaction of wet ground by poaching of livestock hooves. Intertussock plants are damaged by trampling, which may favour tussock species and tough rosette plants capable of surviving trampling.

Occasionally, small patches of highly modified páramo are found, which represent the sheltering sites for livestock. Usually, they are dominated by short herbs (particularly, *Lachemilla orbiculata*) often with thistles (*Sonchus oleraceus*). None of the páramos in this study were grazed by sheep and none showed the extreme modifications in response to heavy grazing described by Grubb, Lloyd & Pennington (unpublished) for the páramo of Volcán Antisana. In addition to the usual tussock grassland, they found large areas of short turf and other areas dominated by tough mats of *Azorella pedunculata.*

However, at lower altitudes in the Daldal valley, in the ceja andina zone, heavy grazing and trampling had resulted in the dominance of *Azorella pedunculata* mats (Chapter 5). These mats reduced the herbage production to levels comparable to desert conditions. In such circumstances, the addition of fertilizers produced minimal effect.

Population pressure is not only reflected in increased agricultural impacts. Fuel requirements have resulted in the widespread destruction of montane forests. In some areas, shrubs from the sub-páramo are now used as the principal source of fuel (personal observation). In other areas, particularly around Volcán Chimborazo, shrubs of *Chuquiraga jussieui* are collected from altitudes of 4,300 m and above. This corresponds to the use of Llareta cushions (*Azorella* spp.) for fuel in Perú (Hodge, 1946, 1960). Efforts are underway to resolve the 'poor man's energy crisis' by planting the highlands with native species (Brandbyge & Holm-Nielsen, 1986; Brandbyge, 1992). The páramo zone between 3,600-3,700 m has been proposed for aforestation with *Pinus radiata* (Miller, 1976).

A number of Ecuadorian National Parks and other protected areas include large areas of páramo (Sangay, Podocarpus, Cotopaxi, Cajas, Cayambe-Coca, Cotacachi-Cayapas). One of the fundamental roles of these areas is to foster contact with the natural environment for urban populations (Ponce, 1984). Of course, this has lead to conflicts with one of the other roles of these areas – to promote nature conservation. For example, in Cajas, with more than 25,000 visitors per year, fishermen are responsible for a high proportion of páramo fires, spread from campfires. In Sangay National Park, hunters of deer and tapir set fires to flush out their prey. Other threats come from trampling and the collection of shrubs and trees for fuel. As the number of visitors to páramos increases, it is important to protect the ecosystems from a corresponding rise in environmental degradation.

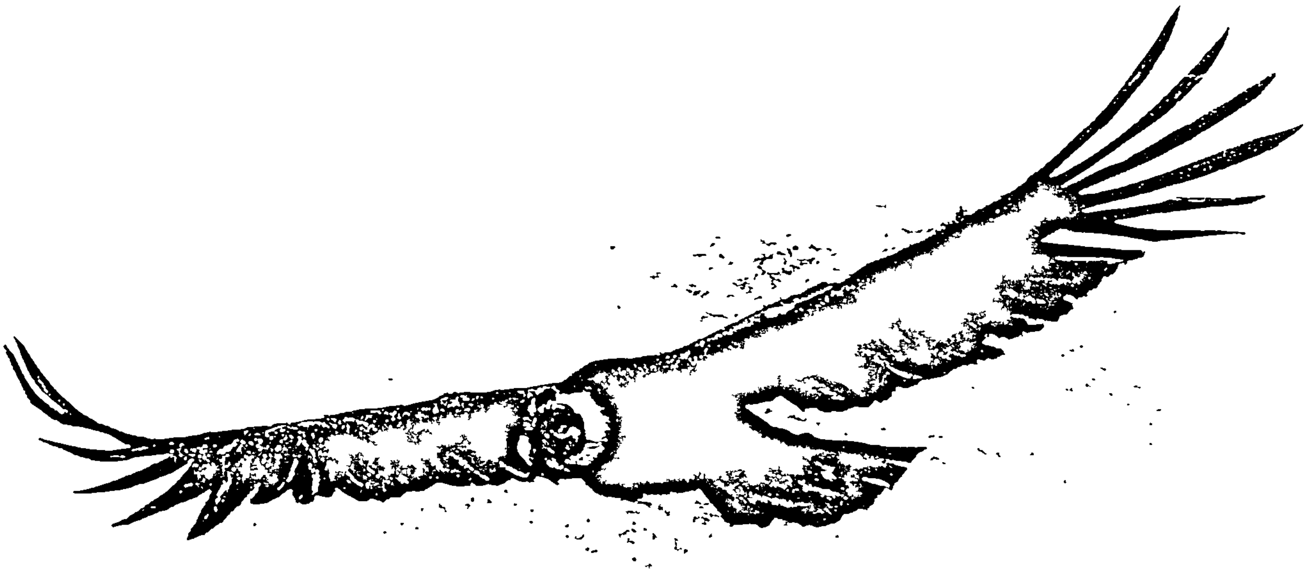
Clearly, the páramo ecosystem is under threat from many sources, the main one being an increase in agriculture within the páramo zone. The páramo is a valuable resource in biological terms (with high biodiversity and significant regional and altitudinal variation), but is also an important resource for major centres of human population. Most highland towns and cities depend upon páramo regions for their water supplies and increasingly for leisure activities and tourism. Furthermore, there is a long history of medicinal uses for páramo species. The best-known páramo plant is Chuquiragua (*Chuquiraga jussieui*) which, among a wide range of uses, has been advocated for the treatment of malaria (Paredes, 1962). Concern over these issues has led to public pressure to conserve and manage these regions in a sustainable manner.

Practices of burning may be sustainable within certain limits, though an increase in the frequency and extent of burning should be considered cautiously. Wherever possible, the conversion of páramo into arable land and pasture should be avoided. It appears from the results of the productivity studies that lower altitude pastures may be substantially under-productive and attention here may negate the requirement for more land in the páramo zone.

Although a strong political commitment and improved social standards are important elements in the long-term conservation of the páramos and the maintenance of their biological diversity, the understanding and participation of the rural poor in the planning, design and management of such strategies are essential. Before this can occur, one major difficulty needs to be resolved. The precarious existence of highland families makes the adoption of new methods and management practices a high risk enterprise. One cannot expect people to venture their very lives on new management models, even if they have been demonstrated scientifically, without adequate financial and social backing.

A great deal of research is currently being carried out in Colombia and Venezuela on the issues of páramo biodiversity, management and community dynamics. While much of this work will be directly relevant to Ecuador, it is clear from this study that the Ecuadorian páramos differ from those further north and more research is needed in Ecuador itself. Researchers who follow this path will find it both challenging and rewarding.

References



Acosta-Solís, M. (1937). Excursión botanica al páramo del Angel. *Flora (Quito),* **1**: 103-118.

Acosta-Solís, M. (1960). Los pastizales naturales del Ecuador: conservación y approvechamiento de los páramos y sabanas. *Revista Geografica (Rio de Janeiro),* **53**: 87-99.

Acosta-Solís, M. (1966). Las divisiones fitogeográficas y las formaciones geobotanicas del Ecuador. *Revista de la Acadamia Colombiana de Ciencias Exactas, Fisicas y Naturales,* **12**: 401-47.

Acosta-Solís, M. (1984). *Los Páramos Andinos del Ecuador.* Quito: Publicaciones Científicas M.A.S.

Acosta-Solís, M. (1985). El Arenal del Chimborazo, ejemplo de puna en el Ecuador. *Revista Geográfica (Quito),* **22**: 115-122.

Alliende, M.C. & Hoffmann, A.J. (1985). Plants intruding *Laretia acaulis* (Umbelliferae), a high Andean cushion plant. *Vegetatio,* **60**: 151-156.

Armesto, J.J., Arroyo, M.T.K. & Villagran, C. (1980). Altitudinal distribution, cover and size structure of umbelliferous cushion plants in the high Andes of Central Chile. *Oecologia Generum,* **1**: 327-332.

Azócar, A. & Monasterio, M. (1979). Variabilidad ambiental en el páramo de Mucubají. In, M.L. Salgado-Labouriau (ed.), *El Medio Ambiente Páramo.* Mérida (Venezuela): Ediciones de Estudios Avanzados.

Azócar, A. & Monasterio, M. (1980). Estudio de la variabilidad meso y microclimática en el Páramo de Mucubají. In, M. Monasterio (ed.), *Estudios Ecológicos en los Páramos Andinos.* Mérida (Venezuela): Ediciones de la Universidad de los Andes.

Azócar, A., Rada, F. & Goldstein, G. (1988). Freezing tolerance in *Draba chionophila*, a 'miniature' caulescent rosette species. *Oecologia,* **75**: 156-160.

Baker, P. (1978). *The Biology of High Altitude Peoples.* Cambridge: Cambridge University Press.

Baldock, J.W. (1982). *Geology of Ecuador. Explanatory Bulletin of the National Geological Map of the Republic of Ecuador, 1:1,000,000 Scale.* Joint publication. London: Natural Environmental Research Council. Quito: Ministerio de Recursos Naturales y Energéticos.

Balslev, H. (1988). Distribution patterns of Ecuadorean plant species. *Taxon,* **37**: 567-577.

Balslev, H. & De Vries, T. (1982). Diversidad de la vegetación en cuatro cuadrantes en el páramo arbustivo del Cotopaxi, Ecuador. *Publicaciones del Museo Ecatoriano de Ciencias Naturales, Año 3,* **3**: 20-32.

Balslev, H. & Luteyn, J.L. (1992). *Páramo: An Andean Ecosystem under Human Influence.* London: Academic Press.

Banco Central del Ecuador (1990). *Invierta en el Ecuador.* Quito: Banco Central del Ecuador.

Barkman, J.J. (1988). New systems of plant growth forms and phenological plant types. In: M.J.A. Werger, P.J.M. van der Aart, H.J. During & J.T.A. Verhoeven (eds.), *Plant Form and Vegetation Structure.* The Hague: SPB Academic Publishing.

Barnes, P.W., Flint, S.D. & Caldwell, M.M. (1987). Photosynthesis damage and protective pigments in plants from a latitudinal arctic/alpine gradient exposed to supplemental UV-B radiation in the field. *Arctic and Alpine Research,* **19**: 21-27.

Barnett, A. & Gordon, C. (1985). Mammal Report. In, A. Barnett (ed.), *U.C.N.W. Exploration Club Expedition to CAJAS National Park, Ecuador, 1984: Preliminary Report.* Privately published.

Barry, R.G. & Van Wie, C.C. (1974). Topo- and microclimatology in alpine areas. In, J.D. Ives & R.G. Barry (eds.), *Arctic and Alpine Environments.* London: Methuen.

Barthélémy, D., Edelin, C. & Hallé, F. (1989). Architectural concepts for tropical trees. In, L.B. Holm-Nielsen, I.C. Nielsen & H. Balslev (eds.), *Tropical Forests: Botanical Dynamics, Speciation and Diversity.* London: Academic Press.

Baruch, Z. (1979). Elevational differentiation in *Espeletia schultzii* (Compositae), a giant rosette plant, from the Venezuelan páramos. *Ecology,* **60**: 85-98.

Baruch, Z. (1982). Patterns of energy content in plants from the Venezuelan páramos. *Oecologia,* **55**: 47-52.

Baruch, Z. (1984). Ordination and classification of vegetation along an altitudinal gradient in the Venezuelan páramos. *Vegetatio,* **55**: 115-126.

Baruch, Z. & Smith, A.P. (1979). Morphological and physiological correlates of niche breadth in two species of *Espeletia* (Compositae) in the Venezuelan Andes. *Oecologia,* **38**: 71-82.

Beck, E., Scheibe, R. & Schulze, E.D. (1986). Recovery from fire: observations in the alpine vegetation of western Mt. Kilimanjaro (Tanzania). *Phytocoenologia,* **14**: 55-77.

Beek, K.J. & Bramao, D.L. (1968). Soil map of South America. In, E.J. Fittkau, J. Illies, H. Klinge, G.H. Schwabe & H. Sioli (eds.), *Biogeography and Ecology in South America, Vol. 1.* The Hague: Dr. W. Junk.

Benoist, R. (1935). Le *Plantago rigida* H.B.K., sa structure, sa biologie. *Bulletin de la Société Botanique Francais,* **82**: 462-466; and **82**: 604-609.

Billings, W.D. (1973). Arctic and alpine vegetations: similarities, differences and susceptibility to disturbance. *Bioscience,* **23**: 697-704.

Billings, W.D. & Mooney, H.A. (1968). The ecology of arctic and alpine plants. *Biological Reviews,* **43**: 481-529.

Black, J. (1982). Los páramos del Antisana. *Revista Geográfica (Quito),* **17**: 25-52.

Bliss, L.C. (1971). Arctic and alpine plant life cycles. *Annual Review of Ecology and Systematics,* **2**: 405-438.

Bonifaz, E. (1981). Agricultura y población de los Andes. *Revista Geográfica (Quito),* **14**: 31-42.

Boza, M.A. (1978). Parque Nacional Chirripó. In, M.A. Boza (ed.), *Los Parques Nacionales de Costa Rica.* Madrid: Instututo de la Caza Fotográfica y Ciencias de Naturaleza.

Brandbyge, J. (1992). Planting of local woody species in the páramo. In, H. Balslev & J.L. Luteyn (eds.), *Páramo: An Andean Ecosystem under Human Influence.* London: Academic Press.

Brandbyge, J. & Holm-Nielsen, L.B. (1986). *Reforestation of the High Andes with Local Species.* Reports from the Botanical Institute, University of Aarhus, No. 13.

Breedlove, D.E. (1973). The phytogeography and vegetation of Chiapas (Mexico). In, A. Graham (ed.), *Vegetation and Vegetational History of Northern Latin America.* Amsterdam: Elsevier.

Bromley, R.J. (1971). *Neurolepis* as a sensitive indicator of human activity in the High Andes. *American Antiquity,* **36**: 475.

Brush, S.B. (1976). Man's use of an Andean ecosystem. *Human Ecology,* **4**: 147-166.

Buckland, S.M. & Ramsay, P.M. (in press). An investigation of intra-specific variation in plant morphology along altitudinal gradients in the Ecuadorian páramos. In, P.M. Ramsay, *Ecological Studies in Parque Nacional Sangay, Ecuador: a Report on the Sangay '89 Expedition.*

Cabarle, B.J., Crespi, M., Dodson, C.H., Luzuriaga, C., Rose, D. & Shores, J.N. (1989). An assessment of biological diversity and tropical forests for Ecuador. Washington: The Center for International Development and Environment of the World Resources Institute.

Cabrera, A.L. (1957). La vegetación de la Puna Argentina. *Revista de las Investigaciones Agricolas de Buenos Aires,* **11**: 317-412.

Cabrera, A.L. (1968). Ecología vegetal de la puna. In, *Geo-ecology of the Mountainous Regions of the Tropical Americas.* Proceedings of the UNESCO Mexico symposium, Aug. 1966. *Colloquium Geographicum,* **9**: 91-116.

Cambridge Llanganati Expedition 1969 (1970). Cambridge Llanganati Expedition 1969. *Cambridge Expeditions Journal,* **1969-70**.

Carlquist, S. (1974). *Island Biology.* New York: Columbia University Press.

Carlquist, S. (1987). Anatomy of tropical alpine plants. In, P. Rundel, F. Meinzer & A.P. Smith (eds.), *Tropical Alpine Environments: Plant Form and Function.* Berlin: Springer-Verlag.

Cerón, C.E. (1985). Los páramos de Pisayambo. *Revista Geográfica (Quito),* **22**: 7-24.

Clapperton, C.M. & McEwan, C. (1985). Late Quaternary moraines in the Chimborazo area, Ecuador. *Arctic and Alpine Research,* **17**: 135-142.

Clark, F.E. & Paul, E.A. (1970). The microflora of grassland. *Advances in Agronomy,* **22**: 375-435.

Cleef, A.M. (1978). Characteristics of neotropical páramo vegetation and its subantarctic relations. In, C. Troll & W. Lauer (eds.), *Geoecological Relations Between the Southern Temperate Zone and the Tropical Mountains, Erdwissenschaftliche Forschung,* **11**: 365-390.

Cleef, A.M. (1979). The phytogeographical position of the neotropical vascular páramo flora with special reference to the Colombian Cordillera Oriental. In, K. Larsen & L.B. Holm-Nielsen (eds.), *Tropical Botany.* New York: Academic Press.

Cleef, A.M. (1981). *The Vegetation of the Colombian Cordillera Oriental.* University of Utrecht: Proefschrift.

Cleef, A.M. (1983). Fitogeografía y composición de la flora vascular de los páramos de la Cordillera Oriental Colombiana (estudio comparativo con otras altas montañas del trópico). *Revista de la Academia Colombiana de Ciencias Exactas, Fisicas y Naturales,* **58**: 23-29.

Clements, F.E. (1916). *Plant Succession: An Analysis of the Development of Vegetation.* Washington (DC): Carnegie Institution.

Clements, F.E. (1920). Plant indicators: the relation of plant communities to process and practice. *Ibid,* **290.**

Coe, M.J. (1967). *The Ecology of the Alpine Zone of Mount Kenya. Monogr. Biol. 17.* The Hague: Junk.

Connolly, J. (1986). On difficulties with replacement series methodology in mixture experiments. *Journal of Applied Ecology,* **23**: 125-137.

Coupland, R.T. (1975). Productivity of grassland ecosystems. In, *Productivity of World Ecosystems: Proceedings of a Symposium.* International Biological Program. Washington, D.C.: National Academy of Sciences.

Crawford, R.M.M., Wishart, D. & Campbell, R.M. (1970). A numerical analysis of high altitude scrub vegetation in relation to soil erosion in the eastern Cordillera of Peru. *Journal of Ecology,* **58**: 173-191.

Cuatrecasas, J. (1934). Observaciones geobotanicas en Colombia. *Trabajos del Museo Nacional de Ciencias Naturales Madrid, Serie Botanica,* **27**.

Cuatrecasas, J. (1958). Aspectos de la vegetación natural de Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Fisicas y Naturales,* **10**: 221-264.

Cuatrecasas, J. (1968). Páramo vegetation and its life forms. *Colloquium Geographicum,* **9**: 163-186.

Cuatrecasas, J. (1979). Growth forms of the Espeletiinae and their correlation to vegetation types of the high tropical Andes. In, K. Larsen & L.B. Holm-Nielsen (eds.), *Tropical Botany.* New York: Academic Press.

Cuatrecasas, J. (1986). Speciation and radiation of the Espeletiinae in the Andes. In, F. Vuilleumier & M. Monasterio (eds.), *High Altitude Tropical Biogeography.* Oxford: Oxford University Press.

Descimon, H. (1986). Origins of the Lepidopteran faunas of the high tropical Andes. In, F. Vuilleumier & M. Monasterio (eds.), *High Altitude Tropical Biogeography.* Oxford: Oxford University Press

Diels, L. (1934). Die páramo der Äquatorial Hoch-Anden. *Sitzungsberichte der Preussischen Akademie der Wissenschaften,* **1934**: 57-68.

Dobzhansky, T. (1950). Evolution in the tropics. *American Scientist,* **38**: 209-221.

Drew, W.B. (1944). Algunas observaciones hechas en mi segunda excursión por las cercanias del Cayambe. *Flora (Quito),* **4**: 77-80.

Du Rietz, G.E. (1931). Life Forms of Terrestrial Flowering Plants. I. *Acta Phytogeographic Suecica,* **3**: 1-95.

Eckholm, E. (1975). The deterioration of mountain environments. *Science,* **189**: 764-770.

Eidt, R.C. (1968). The climatology of South America. In, E.J. Fittkau, J. Illies, H. Klinge, G.H. Schwabe & H. Sioli (eds.), *Biogeography and Ecology in South America, Vol. 2.* The Hague: Junk.

Ellenberg, H. (1958). Wald oder Steppe? Die natürliche Pflanzendecke der Anden Perus. I. *Umschau Heft,* **21**: 645-648.

Ellenberg, H. (1979). The Tansley Lecture: Man's Influence on tropical mountain ecosystems in South America. *Journal of Ecology,* **67**: 401-416.

Ellenberg, H. & Müller-Dombois, D. (1967). Tentative physiognomic-ecological classification of plant formations of the earth. *Bericht des Geobotanischen Instituts der E.T.H., Stiftung Rübel in Zürich,* **37**: 21-55.

Encalada, M. (1986). *Evidencias del Deterioro Ambiental en el Ecuador.* Quito: Gangotena & Ruiz Editores S.A.

Fariñas, M. & Monasterio, M. (1980). La vegetación del Páramo de Mucubají. Analisis de ordanamiento y su interpretación ecológica. In, M. Monasterio (ed.), *Estudios Ecológicos en los Páramos Andinos.* Mérida (Venezuela): Ediciones de la Universidad de los Andes.

Fieldså, J. (1992). Biogeography of the birds of the *Polylepis* woodlands of the Andes. In, H. Balslev & J.L. Luteyn (eds.), *Páramo: An Andean Ecosystem under Human Influence.* London: Academic Press.

Fisher, R.A. (1930). *The Genetical Theory of Natural Selection.* Oxford: Clarendon Press.

Flohn, H. (1974). Contribution to a comparative meteorology of mountain areas. In, J.D. Ives & R.G. Berry (eds.), *Arctic and Alpine Environments.* London: Methuen.

Forster, N.R. (1989). Minifundistas in Tungurahua, Ecuador: survival on the agricultural ladder. In, W.C. Thiesenheusen, *Searching for Agrarian Reform in Latin America.* London: Unwin Hyman.

Fosberg, F.R. (1944). El Páramo de Sumapaz, Colombia. *Journal of the New York Botanical Garden,,* **45**: 226-234.

Fosberg, F.R. (1967). A classification of vegetation for general purposes. In, G.F. Peterken (ed.), *Guide to the Check Sheet for IBP Areas, IBP Handbook No. 4.* Oxford: Blackwell Scientific Publications.

Franco, P., Rangel, O. & Lozano, G. (1986). Estudios ecológicos en la Cordillera Oriental. II. Las comunidades vegetales de los alrededores de la Laguna de Chingaza (Cundinamarca). *Caldasia,* **15**: 219-248.

Frei, E. (1958). Eine Studie über den Zusammenhang zwischen Bodentyp, Klima und Vegetation in Ecuador. *Plant and Soil,* **9**: 215-236.

Furrer, G. & Graf, K. (1978). Die subnivale Höhenstrufe am Kilimandjaro und in den Anden Boliviens und Ecuadors. *Erdwissenschaftliche Forschung,* **11**: 441-457.

Garnett, A. (1937). *Insolation and Relief. Transactions (Institute of British Geographers),* **5**.

Geiger, R. (1966). *The Climate Near the Ground.* Cambridge (Massachussets): Harvard University Press.

Geiger, R. (1969). Topoclimates. In, H. Flohn (ed.), *General Climatology.* Amsterdam: Elsevier.

Givnish, T.J., McDiarmid, R.W. & Buck, W.R. (1986). Fire adaptation in *Neblinaria celiae* (Theaceae), a high elevation rosette shrub endemic to a wet equatorial tepui. *Oecologia,* **70**: 481-483.

Gleason, H.A. (1917). The structure and development of the plant association. *Bulletin of the Torrey Botanical Club,* **44**: 463-481.

Gleason, H.A. (1976). Delving into the history of American ecology. *Bulletin of the Ecological Society of America,* **56**: 7-10.

Godley, E.J. (1978). Cushion Bogs. In: C. Troll & W. Lauer (eds.), *Geoecological Relations Between the Southern Temperate Zone and the Tropical Mountains.* Wiesbaden: Franz Steiner.

Goldstein, G. & Meinzer, F. (1983). Influence of insulating dead leaves and low temperatures on water balance in an Andean giant rosette plant. *Plant Cell and Environment,* **6**: 649-656.

Goldstein, G., Meinzer, F. & Monasterio, M. (1984). The role of capacitance in the water balance of Andean giant rosette species. *Plant Cell and Environment,* **7**: 179-186.

Goldstein, G., Meinzer, F. & Monasterio, M. (1985). Physiological and mechanical factors in relation to size-dependent mortality in an Andean giant rosette species. *Acta Oecologia/Oecologia Plantarum,* **6**: 263-275.

Gómez-Pampa, A. (1973). Ecology of the vegetation of Veracruz. In, A. Graham (ed.), *Vegetation and Vegetational History of Northern Latin America.* Amsterdam: Elsevier.

Gondard, P. (1988). Land use in the Andean region of Ecuador: from inventory to analysis. *Land Use Policy,* **5**: 341-348.

Grace, J. (1988). The functional significance of short stature in montane vegetation. In: M.J.A. Werger, P.J.M. van der Aart, H.J. During & J.T.A. Verhoeven (eds.), *Plant Form and Vegetation Structure.* The Hague: SPB Academic Publishing.

Gradstein, S.R., Cleef, A.M. & Fulford, M.H. (1977). Studies on Colombian cryptogams. II. Hepaticae—oilbody structureand ecological distribution of selected species of tropical Andean Jungermanniales. *Proceedings, Koninklijke Nederlandse Akademie van Wetenschappen, Series C,* **80**: 377-420.

Griesebach, A. (1872). *Die Vegetation der Erde nach ihrer klimatischen Anordnung. Ein Abriss der vergleichende Geographie der Pflanzen,* Leipzig.

Grime, J.P. (1979). *Plant Strategies and Vegetation Processes.* Chichester: Wiley.

Grubb, P.J. (1970). The impact of man on the páramo of Cerro Antisana, Ecuador. *Journal of Applied Ecology,* **58**: 7-8.

Grubb, P.J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews,* **52**: 107-145.

Grubb, P.J., Lloyd, J.R. & Pennington, T.D. (unpublished). *The Páramo of Cerro Antisana in the Ecuadorian Andes: the impact of grazing and burning.*

Hallé, F. & Oldeman, R.A.A. (1970). *Essai sur l'Architecture et la Dynamique de Croissance des Arbres Tropicaux.* Paris: Masson.

Hallé, F., Oldeman, R.A.A. & Tomlinson, P.B. (1978). *Tropical Trees and Forests: An Architectural Analysis.* Berlin: Springer-Verlag.

Halloy, S. (1983). Some ecological data on *Nototriche caesia*, the high Andean Malvaceae in the Cumbres Calchaquies Tucuman, Argentina. *Lilloa,* **36**: 85-104.

Haney, E.B. & Haney, W.G. (1989). The agrarian transition in highland Ecuador. In, W.C. Thiesenheusen, *Searching for Agrarian Reform in Latin America.* London: Unwin Hyman.

Hanselman, D.P. (1975). *Species Diversity in Tundra Environments along a Latitudinal Gradient from the Andes to the Arctic.* M.Sc. thesis, Duke University, Durham, USA.

Harling, G. (1979). The vegetation types of Ecuador—a brief survey. In, K. Larsen & L.B. Holm-Nielsen (eds.), *Tropical Botany.* Academic Press.

Harling, G. & Sparre, B. (1973-). *Flora of Ecuador.* Department of Systematic Botany, University of Göteborg, and the Section of Botany, Riksmuseum, Stockholm.

Harper, J.L. (1977). *Population Biology of Plants.* London: Academic Press

Hedberg, O. (1957). Afroalpine Vascular Plants: a Taxonomic Revision. *Symbolae Botanicae Upsaliensis,* **15**: 1-411.

Hedberg, O. (1964). Features of Afroalpine Plant Ecology. *Acta Phytogeographic Suecica,* **49**: 0-0.

Hedberg, O. (1992). Afroalpine vegetation compared to páramo: convergent adaptations and divergent differentiation. In, H. Balslev & J.L. Luteyn (eds.), *Páramo: An Andean Ecosystem under Human Influence.* London: Academic Press.

Hedberg, I. & Hedberg, O. (1979). Tropical-alpine life-forms of vascular plants. *Oikos,* **33**: 297-307.

Heilborn, O. (1925). Contributions to the ecology of the Ecuadorian páramos with special reference to the cushion plants and osmotic pressure. *Svensk Botanisk Tidskrift,* **19**: 153-170.

Herrera, N. (1987). La racionalidad campesina andina y la alimentatción: el caso de la comuna de Yanaturo en la Sierra Central del Ecuador. *Agricultura y Sociedad,* **45**: 183-227.

Hill, M.O. (1979). *TWINSPAN: a FORTRAN Program for Arranging Multivariate Data in an Ordered Two-way Table by Classification of the Individuals and Attributes.* Cornell Ecology Programs Series. Ithaca, (N.Y.): Cornell University.

Hnatiuk, R.J. (1978). The growth of tussock grasses on an equatorial high mountain and on two Sub-Antarctic islands. In: C. Troll & W. Lauer (eds.) *Geoecological Relations Between the Southern Temperate Zone and the Tropical Mountains.* Wiesbaden: Franz Steiner.

Hobbs, R.J. & Legg, C.J. (1983). Markov models and initial floristic composition in heathland vegetation dynamics. *Vegetatio,* **56**: 31-43.

Hodge, W.H. (1946). Cushion plants of the Peruvian puna. *Journal of the New York Botanical Garden,* **47**: 133-141.

Hodge, W.H. (1960). Yareta—fuel umbellifer of the Andean puna. *Economic Botany,* **14**: 113-118.

Hoffstetter, R. (1986). High Andean mammalian faunas during the Plio-Pleistocene. In, F. Vuilleumier & M. Monasterio (eds), *High Altitude Tropical Biogeography.* Oxford: Oxford University Press.

Holdridge, L.R. (1967). *Life Zone Ecology.* San Jose (Costa Rica): Tropical Science Center.

Holland, P.G. & Steyn, D.G. (1975). Vegetational responses to latitudinal variations in slope angle and aspect. *Journal of Biogeography,* **2**: 179-184.

Hope, A.C.A. (1968). A simplified Monte Carlo significance test procedure. *Journal of the Royal Statistical Society, Series B,* **30**: 582-598.

Horn, H.S. (1974). The ecology of secondary succession. *Annual Review of Ecology and Systematics,* **5**: 25-37.

Horn, H.S. (1975). Markovian properties of forest succession. In, M.L. Cody & J.M. Diamond (eds.), *Ecology and Evolution of Communities.* Cambridge (Massachussets): Belknap, Harvard University Press.

Huber, O. (1987). Neotropical savannas: their flora and vegetation. *Trends in Ecology and Evolution,* **2**: 67-71.

Huey, R. (1978). Latitudinal pattern of between-altitude faunal similarity: mountain passes may be 'higher' in the tropics. *American Naturalist,* **112**: 225-229.

Inouye, R.S. & Schaffer, W.M. (1981). On the ecological meaning of ratio (de Wit) diagrams in plant ecology. *Ecology,* **62**: 1679-1681.

James, D.E. (1973). The evolution of the Andes. *Scientific American,* **229**: 60-67.

Janzen, D.H. (1967). Why mountain passes are higher in the tropics. *American Naturalist,* **101**: 233-249.

Jenny, H. (1948). Great soil groups in the equatorial regions of Colombia, South America. *Soil Science,* **66**: 5-28.

Johnson, A.M. (1976). The climate of Peru, Bolivia and Ecuador. In, W. Schwerdtfeger (ed.), *World Survey of Climatology, Vol. 12: Climates of Central and South America.* Amsterdam: Elsevier Scientific Publishing.

Jolliffe, P.A., Minjas, A.N. & Ruenckles, V.C. (1984). A reinterpretation of yield relationships in replacement series experiments. *Journal of Applied Ecology,* **21**: 277-243.

Jones, H.G. (1983). *Plants and Microclimate.* Cambridge: Cambridge University Press.

Kaufmann (1977). Soil temperature and drying cycle effects on water relations of *Pinus radiata. Canadian Journal of Botany,* **55**: 2413-2418.

Körner, Ch. (1989). The nutritional status of plants from high altitudes: a worldwide comparison. *Oecologia,* **81**: 379-391.

Körner, Ch. & Renhardt, U. (1987). Dry matter partitioning and root length/leaf area ratios in herbaceous perennial plants with diverse altitudinal distribution. *Oecologia,* **74**: 411-418.

Küppers, M. (1989). Ecological significance of above-ground architectural patterns in woody plants: a question of cost-benefit relationships. *Trends in Ecology and Evolution,* **4**: 375-379.

Laegaard, S. (1992). Influence of fire in the grass páramo vegetation of Ecuador. In, H. Balslev & J.L. Luteyn (eds.), *Páramo: An Andean Ecosystem under Human Influence.* London: Academic Press.

Lamotte, M., Garay, I. & Monasterio, M. (1989). Les grands traits du functionnement d'un ecosysteme tropical d'altitude. In: G. Montalenti *et al.* (eds), *Ecologia (Atti 3 congresso della Societa Italiana di Ecologia, Siena, 1987),* **1**: 61-66.

Larcher, E. (1975). Pflanzenokologische Beobachtungen in die Paramostufe der Venezolanische Anden. *Anzeiger der Österreichischen Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Klasse,* **11**: 194-213.

Larcher, W. (1981). Physiological basis of evolutionary trends in low temperature resistance in vascular plants. *Plant Systematics and Evolution,* **137**: 145-180.

Larcher, W. & Bauer, H. (1981). Ecological significance of resistance to low temperature. In, O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegler (eds.) *Physiological Plant Ecology. I. Responses to the Physical Environment.* Berlin: Springer.

Lauer, W. (1976). Zur Hygrischen Hohenstufung Tropischer Gebirge. In, F. Schmithüsen (ed.), *Neotropische Oekosysteme. Biogeographica 7.* The Hague: Junk.

Lauer, W. (1979). La posición de los páramos en la estructura del paisaje de los Andes tropicales. In, M.L. Salgado-Labouriau (ed.), *El Medio Ambiente Páramo.* Mérida (Venezuela): Ediciones Centro de Estudios Avanzados.

Leggett, J. (1990). *Global Warming—The Greenpeace Report.* Oxford: Oxford University Press.

Li, P.H. & Palta, J.P. (1978). Frost hardening and freezing stress in tuber bearing *Solanum* species. In, P.H. Li & A. Sakai (eds.), *Plant Cold Hardiness and Freezing Stress.* London: Academic Press.

Lieth, H. (1975). Primary production of the major vegetation units of the world. In, H. Lieth & R.H. Whittaker, *Primary Productivity of the Biosphere.* Berlin: Springer-Verlag.

Liley, M. (1986). Study of *Polylepis incana.* In, *Report of the Cambridge Ecuadorian Andes Expedition 1985.* Cambridge: Cambridge University.

Lind, E.M. & Morrison, M.E.S. (1974). *East African Vegetation.* London: Longman.

Lojtnant, B. & Molau, U. (1982). Analysis of a virgin páramo plant community on Volcán Sumaco, Ecuador. *Nordic Journal of Botany,* **2**: 567-574.

Lough, T.J., Wilson, J.B., Mark, A.F. & Evans, A.C. (1987). Succession in a New Zealand alpine cushion community: a markovian model. *Vegetatio,* **71**: 129-138.

Lozano, G. & Schnetter, R. (1976). Estudios ecológicos en el Páramo de Cruz Verde, Colombia. II. Las communidades vegetales. *Caldasia,* **11**: 54-68.

Luteyn, J.L. (1992). Páramos: why study them? In, H. Balslev & J.L. Luteyn (eds.), *Páramo: An Andean Ecosystem under Human Influence.* London: Academic Press.

Luteyn, J.L., Cleef, A.M. & Rangel, O. (1992). Plant diversity in páramo: towards a checklist of páramo plants and a generic flora. In, H. Balslev & J.L. Luteyn (eds.), *Páramo: An Andean Ecosystem under Human Influence.* London: Academic Press.

Mabberley, D.J. (1986). Adaptive syndromes of Afroalpine species of *Dendrosenecio.* In, F. Vuilleumier & M. Monasterio (eds.), *High Altitude Tropical Biogeography.* Oxford: Oxford University Press.

MacArthur, R.H. (1965). Patterns of species diversity. *Biological Reviews,* **40**: 510-533.

MacArthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography.* Princeton (N.J.): Princeton University Press.

Malloch, A.J.C. (1988). *Vespan II: A Computer Package to Handle and Analyse Multivariate Species Data and Handle and Display Species Distribution Data.* Lancaster: University of Lancaster.

Mann, G. (1966). Bases ecológicas de la explotación agropecuaria en la América Latina. *Serie Biológica Monográfica No. 2.* Washington: Departamento de Asuntos Científicos de la Secretaría General de la Organización de Estados Americanos.

Mark, A.F. & Adams, N.M. (1973). *New Zealand Alpine Plants.* Wellington: A.H. & A.W. Reed.

Meinzer, F. & Goldstein, G. (1985). Some consequences of leaf pubescence in the Andean giant rosette plant *Espeletia timotensis. Ecology,* **66**: 512-520.

Meinzer, F. & Goldstein, G. (1986). Adaptations for water and thermal balance in Andean giant rosette plants. In, T.J. Givnish (ed.), *On the Economy of Plant Form and Function.* Cambridge: Cambridge University Press.

Mena, P. & Balslev, H. (1986). *Comparación Entre la Vegetación de los Páramos y el Cinturón Afroalpino.* Reports from the Botanical Institute, University of Aarhus, No. 12.

Miller, A. (1976). *Proyecto de Forestación de los Páramos en el Ecuador.* Informe del Proyecto Conjunto ODA-Servico Forestal, 1972-76. Quito: Ministerio de Agricultura y Ganadería.

Miller, E.V. & Coleman, N.T. (1952). Colloidal properties of soils from western equatorial South America. *Soil Science Society of America, Proceedings,* **16**: 239-244.

Miller, G.A. (1987a). The functional significance of inflorescence pubescence in tropical alpine species of *Puya*. In, Rundel, P., Meinzer, F. & Smith, A.P. (eds.), *Tropical Alpine Environments: Plant Form & Function.* Berlin: Springer-Verlag.

Miller, G.A. (1987b). *The Population Biology and Physiological Ecology of Species of Puya (Bromeliaceae) in the Ecuadorian Andes.* Ph.D. Thesis, University of Connecticut.

Miller, G.A. & Silander Jr., J.A. (1991). Control of the distribution of giant rosette species of *Puya* (Bromeliaceae) in the Ecuadorian páramos. *Biotropica,* **23**: 124-133.

Mills, K. (1975). Flora de la Sierra, un estudio en el Parque Nacional Cotopaxi 1974/75. *Ciencia y Naturaleza (Quito),* **16**: 23-43.

Monasterio, M. (1980a). El Páramo de Mucubají dentro del cuadro general de los páramos Venezolanos. In, M. Monasterio (ed.), *Estudios Ecológicos en los Páramos Andinos.* Mérida (Venezuela): Ediciones de la Universidad de los Andes.

Monasterio, M. (1980b). Las formaciones vegetales de los páramos de Venezuela. In, M. Monasterio (ed.), *Estudios Ecológicos en los Páramos Andinos.* Mérida (Venezuela): Ediciones de la Universidad de los Andes.

Monasterio, M. (1980c). Los Páramos Andinos como región natural: Caracteristicas biogeograficas generales y afinidades con otras regiones andinas. In, M. Monasterio (ed.), *Estudios Ecológicos en los Páramos Andinos.* Mérida (Venezuela): Ediciones de la Universidad de Los Andes.

Monasterio, M. (1986). Adaptive strategies of *Espeletia* in the Andean desert paramo. In, F. Vuilleumier & M. Monasterio (eds.), *High Altitude Tropical Biogeography.* Oxford: Oxford University Press.

Monasterio, M. & Reyes, S. (1980). Diversidad ambiental y variación de la vegetación en los páramos de los Andes Venezolanos. In, M. Monasterio (ed.), *Estudios Ecológicos en los Páramos Andinos.* Mérida (Venezuela): Ediciones de la Universidad de los Andes.

Monasterio, M. & Vuilleumier, F. (1986). High tropical mountain biota of the world. In, F. Vuilleumier & M. Monasterio, (eds.), *High Altitude Tropical Biogeography.* Oxford: Oxford University Press.

Mooney, H.A. (1974). Plant forms in relation to environment. In, B.R. Strain & W.D. Billings (eds.), *Handbook of Vegetation Science. Part VI. Vegetation and Environment.* The Hague: Junk.

Muñoz, L., Balslev, H. & De Vries, Tj. (1985). Diversidad de la vegetación en cuatro cuadrantes en el páramo pajonal del Antisana, Ecuador. *Publicaciones del Museo Ecuatoriano de Ciencias Naturales, Año 6,* **4**: 21-33.

Murra, J.V. (1972). El "Control Vertical" de un maximo de pisos ecológicos en la economia de las sociedades Andinas. In, Ortiz, I., *Vista de la Provincia de Leon Huánuco (1562), Vol. II.* Huánuco (Perú): Universidad Hermillo Valdizan.

Nathaniel, P. (1985). *Cambridge Ecuador Geological Expedition 1984.* Cambridge: published by author.

Nishikawa, Y. (1990). Role of rhizomes in tussock formation by *Carex thunbergii* var. *appendiculata. Ecological Research,* **5**: 261-269.

Noble, I.R. & Slatyer, R.O. (1981). Concepts and models of succession in vascular plant communities subject to recurrent fires. In, A.M. Gill, R.H. Groves & I.R. Noble (eds.), *Fire and the Australian Biota.* Canberra: Australian Academy of Science.

Norrington-Davies, J. (1967). Application of diallel analysis to experiments in plant competition. *Euphytica,* **16**: 391-406.

Øllgaard, B. & Balslev, H. (1979). *Report on the 3rd Danish Botanical Expedition to Ecuador.* Reports from the Botanical Institute, University of Aarhus. No. 4.

Paredes, A.C. (1962). Esquema fisiográfico de la vegetación en el Ecuador. *Ciencias y Naturaleza (Quito),* **5**: 21-30.

Peet, R.K. (1978). Forest vegetation of the Colorado Front Range: patterns of species diversity. *Vegetatio,* **37**: 65-78.

Pels, B. & Verweij, P.A. (1992). Burning and grazing in a bunchgrass páramo ecosystem: vegetation dynamics described by a transition model. In, H. Balslev & J.L. Luteyn (eds.), *Páramo: An Andean Ecosystem under Human Influence.* London: Academic Press.

Penland, C.W.T. (1941). The alpine vegetation of the southern Rockies and the Ecuadorian Andes. *Colorado College Publications, Studies Series,* **32**: 4-30.

Pérez, F.L. (1987). Soil moisture and the upper altitudinal limit of growth of giant rosettes. *Journal of Biogeography,* **14**: 173-186.

Pfitsch, W.A. (1988). Microenvironment and the distribution of two species of *Draba* (Brassicaceae) in a Venezuelan páramo. *Arctic and Alpine Research,* **20**: 333-341.

Polunin, O. & Stainton, A. (1987). *Concise Flowers of the Himalayas.* Oxford: Oxford University Press

Ponce, A. (1984). Ecuadorian Strategy for the Conservation of Wildlands and Wildlife. In, J.A. McNeely & K.R. Miller (eds.), *National Parks, Conservation and Development: the Role of Protected Areas in Sustaining Society.* Washington (DC): Smithsonian Institution Press.

Portsch, S. & Hicks, J.L. (1980). A soil conservation program for Ecuador. *Journal of Soil & Water Conservation,* **35**: 243-244.

Quintanilla, V. (1983). Comparación entre dos ecosistemas tropoandinas: la puna chilena y el páramo ecuatoriano. *Informaciones Geográficas , Universidad de Chile,* **30**: 25-45.

Rada, F., Goldstein, G., Azócar, A. & Meinzer, F. (1985). Freezing avoidance in Andean giant rosette plants. *Plant Cell and Environment,* **8**: 501-507.

Ramsay, P.M. (unpublished). *A Field and Experimental Study of an Environmental Moisture Gradient.* B.Sc. Biology Dissertation, University of Wales, Bangor

Ramsay, P.M. (1988). *University College of North Wales El 'CAJAS' Expedition, Ecuador, 1985—Scientific Report.* Bangor: P.M. Ramsay.

Rangel, O. & Aguirre, J. (1987). Estudios ecológicos en la Cordillera Oriental de Colombia. III. La vegetación de la cuenca lacustre de Tota (Boyaca). *Caldasia,* **15**: 263-312.

Rangel, O. & Franco, P. (1985). Observaciones fitoecologicas en varias regiones de vida de la Cordillera Central de Colombia. *Caldasia,* **14**: 211-249.

Rangel, O. & Lozano, G. (1986). Un perfil de vegetación entre La Plata (Huila) y el Volcán del Puracé. *Caldasia,* **14**: 503-547.

Rauh, W. (1939). Über polsterförmingen Wuchs. *Nova Acta Leopoldina N.F. 7,* **49**: 267-508.

Raunkiaer, C. (1907). *Planterigeta livsformer og deres betydning for geografien.* Copenhagen: Kjobenhavn & Kristiania.

Raunkiaer, C. (1908). Livsformernes statistik som grundlag for biologisk plantegeografi. *Botanisk Tidsskrift,* **29**: 42-83.

Raunkiaer, C. (1934). *The Life Forms of Plants and Statistical Plant Geography.* Oxford: Oxford University Press.

Ricardi, M., Briceño, B. & Adamo, G. (1987). Sinopsis de la flora vascular del páramo de Piedras Blancas, Venezuela. *Ernstia,* **44**: 4-14.

Robberecht, R., Caldwell, M.M. & Billings, W.D. (1980). Leaf ultraviolet optical properties along a latitudinal gradient in the arctic-alpine life zone. *Ecology,* **61**: 612-619.

Rossenaar, A.J.G.A. & Hofstede, R.G.M. (1992). Effects of burning and grazing on root biomass in the páramo ecosystem. In, H. Balslev & J.L. Luteyn (eds.), *Páramo: An Andean Ecosystem under Human Influence.* London: Academic Press.

Ruthsatz, B. (1978). Las plantas en cojín de los semi-desiertos andinos del Noroeste Argentino. *Darwiniana,* **21**: 491-539.

Sakai, A. & Larcher, W. (1987). *Frost survival of plants: Responses and Adaptations to to Freezing Stress.* Berlin: Springer.

Sandwith, N.Y. (1926). Humboldt and Bonpland's itinery in Ecuador and Peru. *Kew Bulletin,* **4**: 181-190.

Sarmiento, F. (1987). *Desde la Selva... Hasta el Mar: Antologia Ecológica del Ecuador. Serie Monografía Año 7 (Número 2).* Quito: Ediciones Casa de la Cultura Ecuatoriana.

Sarmiento, G. (1986). Ecological features of climate in high tropical mountains. In, F. Vuilleumier & M. Monasterio (eds.), *High Altitude Tropical Biogeography.* Oxford University Press.

Schimper, A.F.W. (1898). *Pflanzengeographie auf physiologischer Grundlage.* Jena.

Schmidt, A.M. & Verweij, P.A. (1992). Forage intake and secondary production in extensive livestock systems in páramo. In, H. Balslev & J.L. Luteyn (eds.), *Páramo: An Andean Ecosystem under Human Influence.* London: Academic Press.

Schulze, E.-D. (1982). Plant life forms and their carbon, water and nutrient relations. In, O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegler (eds.). *Physiological Plant Ecology II: Water Relations and Carbon Assimilation.* Berlin: Springer-Verlag.

Schulze, E.-D., Beck, E., Scheibe, R. & Ziegler, P. (1985). Carbon dioxide assimilation and stomatal response of afroalpine giant rosette plants. *Oecologia,* **65**: 207-213.

Schwabe, G.H. (1968). Towards an ecological characterization of the South American continent. In, E.J. Fittkau, J. Illies, H. Klinge, G.H. Schwabe & H. Sioli (eds.), *Biogeography and Ecology in South America, Vol. 1.* The Hague: Junk.

Seibert, P. (1983). Human impact on landscape and vegetation in the Central high Andes. In, W. Holzner, M.J.A. Werger & I. Ikusima (eds.), *Man's Impact on Vegetation.* The Hague: Junk.

Sewell, T.G. (1954). The high-altitude snow-tussock grassland in South Island, New Zealand. *New Zealand Journal of Science and Technology (Section A),* **36**: 335-364.

Shugart, H.H. & Hett, J.M. (1973). Succession: similarities of species turnover rates. *Science,* **180**: 1379-1381.

Sick, W. (1969). Geographical substance. In, E.J. Fittkau, J. Illies, H. Kling, G.H. Schwabe & H. Sioli (eds.), *Biogeography and Ecology in South America, Vol. 2.* The Hague: Junk.

Silander Jr., J.A. & Pacala, S.W. (1985). Neighbourhood predictors of plant performance. *Oecologia,* **66**: 256-263.

Siltanen, M., Thurland, M. & Casanova, J. (1987). Evaluación de biomasa en función al suelo en cinco rodales de *Polylepis incana.* Proyecto Arbolandino (Puno, Perú).

Silvertown, J.W. (1981). Microspatial heterogeneity and seedling demography in species rich grassland. *New Phytologist,* **88**: 117-128.

Silvertown, J.W. (1987). *Introduction to Plant Population Ecology.* Harlow: Longman Scientific & Technical.

Simpson, B.B. (1974). Glacial migrations of plants: island biogeographical evidence. *Science,* **185**: 698-700.

Simpson, B.B. (1975). Pleistocene changes in the flora of the high tropical Andes. *Paleobiology,* **1**: 273-294.

Simpson, B.B. (1979). A revision of the genus *Polylepis* (Rosaceae: Sanguisorbeae). *Smithsonian Contributions to Botany, No. 43.*

Sims, P.L. & Singh, J.S. (1978). The structure and function of ten western North American grasslands. III. Net primary production, turnover and efficiencies of energy capture and water use. *Journal of Ecology,* **66**: 573-597.

Smith, A.P. (1972). Notes on wind-related growth patterns of páramo plants in Venezuela. *Biotropica,* **4**: 10-16.

Smith, A.P. (1974). Bud temperature in relation to nyctinastic leaf movement in an Andean giant rosette plant. *Biotropica,* **6**: 263-266.

Smith, A.P. (1978). Establishment of seedlings of *Polylepis sericea* in the páramo (alpine) zone of the Venezuelan Andes. *Bartonia,* **45**: 11-14.

Smith, A.P. (1979). Function of dead leaves in *Espeletia schultzii* (Compositae), an Andean caulescent rosette species. *Biotropica,* **13**: 39-48.

Smith, A.P. (1980). The paradox of plant height in an Andean giant rosette species. *Journal of Ecology,* **68**: 63-73.

Smith, A.P. (1981). Growth and population dynamics of *Espeletia* (Compositae) in the Venezuelan Andes. *Smithsonian Contributions to Botany, No. 48.*

Smith, A.P. (1987). Does the correlation of elevation with plant taxonomic richness vary with latitude? *Biotropica,* **20**: 259-261.

Smith, A.P. & Young, T.P. (1987a). Population biology of *Senecio keniodendron*, an afroalpine giant rosette plant. [Cited by Smith & Young (1987b)] In, P. Rundel, F. Meinzer & A.P. Smith (eds.), *Tropical Alpine Environments: Plant Form and Function.* Berlin: Springer Verlag.

Smith, A.P. & Young, T.P. (1987b). Tropical alpine plant ecology. *Annual Review of Ecology and Systematics,* **18**: 137-158.

Smith, J.M.B. (1975). Mountain grasslands of New Guinea. *Journal of Biogeography,* **2**: 27-44.

Smith, J.M.B. (1977). An ecological comparison of two tropical high mountains. *Journal of Tropical Geography,* **44**: 71-80.

Smith, J.M.B. (1978). Relationship of slope aspect to deforestation in highland Papua New Guinea. *Queensland Geographical Journal,* **4**: 69-75.

Smith, J.M.B. & Cleef, A.M. (1988). Composition and origins of the world's tropicalpine floras. *Journal of Biogeography,* **15**: 631-645.

Smith, J.M.B. & Klinger, L.F. (1985). Aboveground: belowground phytomass ratios in Venezuelan páramo vegetation and their significance. *Arctic and Alpine Research,* **17**: 189-198.

Snaydon, R.W. (1991). Replacement or additive designs for competition studies? *Journal of Applied Ecology,* **28**: 930-946.

Snaydon, R.W. & Satorre, E.H. (1989). Bivariate diagrams for plant competition data: modifications and interpretation. *Journal of Applied Ecology,* **26**: 1043-1057.

Solbrig, O.T. (1960). The South American sections of *Erigeron* and their relation to *Celmisia*. *Contributions to the Gray Herbarium,* **188**: 85.

Stadel, C. (1989). The perception of stress by campesinos: a profile from the Ecuadorian Sierra. *Mountain Research and Development,* **9**: 35-49.

Sturm, H. (1978). Zur Ökologie der andinen Paramoregion. *Biogeographica,* **14**: 1-121.

Sturm, H. & Abouchaar, A. (1981). Observaciones sobre la ecología del páramo andino de Monserrate. *Caldasia,* **13**: 223-256.

Sturm, H. & Rangel, O. (1985). *Ecología de los Páramos Andinos: una Visión Preliminar Integrada.* Bogota: Universidad Nacional de Colombia.

Svenson, H.K. (1945). The vegetation of Ecuador, a brief review. In, F. Verdoorn (ed.), *Plants and Plant Sciences in Latin America.* New York.

Tamm, C.O. (1975). Plant nutrients as limiting factors in ecosystem dynamics. In, *Productivity of World Ecosystems: Proceedings of a Symposium.* Washington (D.C.): National Academy of Sciences.

Tansley, A.G. & Chipp, T.F. (1926). *Aims and Methods in the Study of Vegetation.* London.

Ter Braak, C.J.F. (1988). *Canoco—a Fortran program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (Version 2.1).* Report LWA-88-02. Wageningen: Agricultural Mathematics Group.

Thórhallsdóttir, T.E. (1983). *The Dynamics of a Grassland Community with Special Reference to Five Grasses and White Clover.* Ph.D. Thesis, University of Wales.

Thórhallsdóttir, T.E. (1990). The dynamics of a grassland community: a simultaneous investigation of spatial and temporal heterogeneity at various scales. *Journal of Ecology,* **78**: 884-908.

Tieszen, L.L. & Detling, J.K. (1983). Productivity of grassland and tundra. In, O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegler (eds.), *Physiological Plant Ecology IV. Ecosystem Processes: Mineral Cycling, Productivity and Man's Influence.* Berlin: Springer-Verlag.

Tol, G.J. & Cleef, A.M. (1992). Nutrient status of a *Chusquea tessellata* bamboo páramo. In, H. Balslev & J.L. Luteyn (eds.), *Páramo: An Andean Ecosystem under Human Influence.* London: Academic Press.

Tomlinson, P.B. (1987). Architecture of tropical plants. *Annual Review of Ecology and Systematics,* **18**: 1-21.

Troll, C. (1959). Die tropische Gebirge. *Bonner Geographische Abhandlungen,* **25**: 1-93.

Troll, C. (1968). The Cordilleras of the tropical Americas: aspects of climatic, phytogeographical and agrarian ecology. In, C. Troll (ed.), *Geo-ecology of the Mountainous Regions of the Tropical Americas.* Bonn: Ferd. Dümmlers Verlag.

Usher, M.B. (1979). Markovian approaches to ecological succession. *Journal of Animal Ecology,* **48**: 413-426.

Usher, M.B. (1981). Modelling ecological succession, with particular reference to Markovian models. *Vegetatio,* **46**: 11-18.

Van Royen, P. (1967). Some observations on the alpine vegetation of Mount Biota (Papua). *Acta Botanica Neerlandica,* **15**: 530-534.

Van Steenis, C.G.G.J. (1935). On the origin of the Malaysian mountain flora, 2. Altitudinal zones, general considerations and renewed statement of the problem. *Bulletin Jardin Botanique Buitenzorg,* **13**: 129-257.

Van Steenis, C.G.G.J. (1939). Ecological observations on the genus *Pleiocraterium* in Gajoland, Sumatra. *Recueil des Travaux Botaniques Néerlandais,* **36**: 446-448.

Van der Hammen, T. & Cleef, A.M. (1986). Development of the high Andean páramo flora and vegetation. In, F. Vuilleumier & M. Monasterio (eds.), *High Altitude Tropical Biogeography.* Oxford: Oxford University Press.

Vareschi, V. (1970). *Flora de los Páramos de Venezuela.* Mérida (Venezuela): Universidad de Los Andes.

Velásquez, A. (1992). Grazing and burning in grassland communities of high volcanoes in México. In, H. Balslev & J.L. Luteyn (eds.), *Páramo: An Andean Ecosystem under Human Influence.* London: Academic Press.

Vera, R. & Lopez, R. (1986). El origen de la cangahua. *Paisajes Geográficos (Quito),* **16**: 21-28.

Verweij, P.A. & Beukema, H. (1992). Aspects of human influence on upper-Andean forest line vegetation. In, H. Balslev & J.L. Luteyn (eds.), *Páramo: An Andean Ecosystem under Human Influence.* London: Academic Press.

Verweij, P.A. & Budde, P.E. (1992). Burning and grazing gradients in páramo vegetation: initial ordination analyses. In, H. Balslev & J.L. Luteyn (eds.), *Páramo: An Andean Ecosystem under Human Influence.* London: Academic Press.

Verweij, P.A. & Kok, K. (1992). Effects of fire and grazing on *Espeletia hartwegiana* populations. In, H. Balslev & J.L. Luteyn (eds.), *Páramo: An Andean Ecosystem under Human Influence.* London: Academic Press.

Von Humboldt. F.H.A. (1806). *Ideen zu einer Physiognomik der Gewäsche.* Stuttgart: Cotta.

Vuilleumier, F. (1970). Insular biogeography in continental regions. I. The northern Andes of South America. *American Naturalist,* **104**: 373-388.

Walter, H. (1973). *Vegetation of the Earth in Relation to Climate and the Eco-physiological Conditions.* London: English Universities Press.

Walter, H. & Medina, F. (1969). La temperatura del suelo como factor determinante para la caracterización de los pisos subalpino y alpino en los Andes de Venezuela. *Boletin Venezolana de Ciencias Naturales,* **115/116**: 201-210.

Wardlaw, I.F. (1969). The effect of water stress on translocation in relation to photosynthesis and growth. II. Effect during leaf development in *Lolium temulentum* L. *Australian Journal of Biological Sciences,* **22**: 1-16.

Warming, E. (1884). *Om Skudbygning, Overvintring og Foryngelse.* Copenhagen: Naturhistorisk Forenings Festskrift.

Warming, E. (1909). *Oecology of Plants: An Introduction to the Study of Plant Communities.* Oxford.

Watson, M.A. & Cook, C. (1982). The development of spatial pattern in clones of an aquatic plant, *Eichhornia crassipes* Solms. *American Journal of Botany,* **69**: 248-253.

Watt, A.S. (1947). Pattern and process in the plant community. *Journal of Ecology,* **35**: 1-22.

Weberbauer, A. (1945). *El Mundo Vegetal de los Andes Peruanos.* Lima: Ministerio de Agricultura.

Weiner, J. (1982). A neighbourhood model of annual plant interference. *Ecology,* **63**: 1237-1241.

Weischet, W. (1969). Klimatologische Regeln zur Vertical-verteilung der Niederschlage in den Tropengebirgen. *Die Erde,* **100**: 287-306.

West, T.L. (1987). The burning bush: exploitation of native shrubs for fuel in Bolivia. In, D.L. Browman, *Arid Land Use Strategies and Risk Management in the Andes: a Regional Anthropological Perspective.* Boulder: Westview Press.

Whittaker, R.H. (1975). *Communities and Ecosystems*, 2nd Edn. New York: Macmillan.

Whymper, E. (1892). *Travels Amongst the Great Andes of the Equator.* London: Murray.

Wilcox, B.P., Bryant, F.C., Wester, D. & Allen, B.L. (1986). Grassland communities and soils of a high elevation grassland of Central Peru. *Phytologia,* **61**: 231-250.

Williams, E.J. (1962). The analysis of competition experiments. *Australian Journal of Biological Science,* **15**: 509-525.

Williams, L. (1941). The phytogeography of Peru. *Chronica Botanica,* **6**: 406-410.

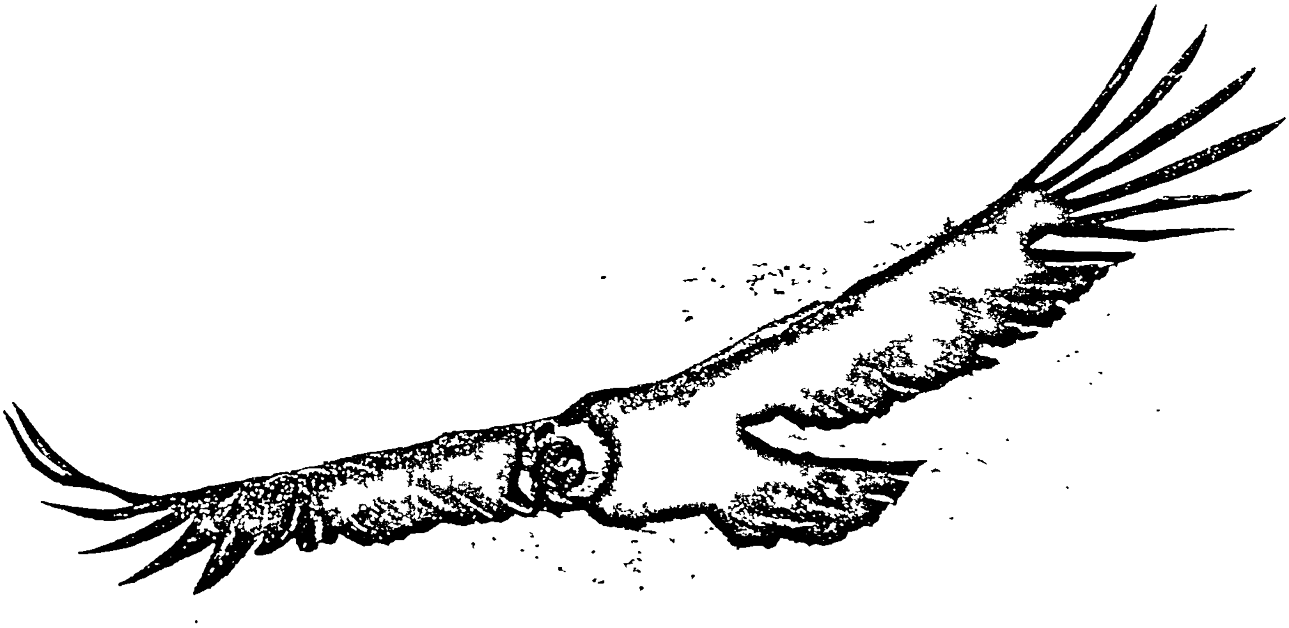
Wilson, M.V. & Smida, A. (1984). Measuring beta diversity with presence-absence data. *Journal of Ecology,* **72**: 1055-1064.

de Wit, C.T. (1960). On competition. *Verslagen van Landouwkundige Onderzoekingen,* **66**: 1-82.

Young, T.P. & Van Orden Robe, S. (1986). Microenvironmental role of a secreted aqueous solution in the Afro-alpine plant *Lobelia keniensis. Biotropica,* **18**: 189-194.

Zar, H. (1984). *Biostatistical Analysis.* London: Prentice-Hall.

Photographic Plates



Key to Plates on pages 249-254.

Plate 1. The extensive páramo plateau of Cajas, with Laguna Luspa. Note the large, grass-covered island in the lake. 24 August, 1985.

Plate 2. The Páramo de Guamaní, another extensive páramo region. 8 October, 1987.

Plate 3. The páramo of Volcán Cotacachi, an example of an isolated páramo region surrounding a volcanic peak. 10 October 1987.

Plate 4. The Collanes valley beneath the crater of El Altar, part of the larger páramo system on the Altar massif. Note the burning at the far end of the valley. The El Altar (west) sampling transect was situated on the slopes to the left. 3 September, 1987.

Plate 5. Cushion bog of *Distichia muscoides*, 4,200 m, Páramo de Guamaní. 9 August, 1987.

Plate 6. *Blechnum loxense* Shrub Páramo (BS), 3,900 m, Volcán Tungurahua. 29 August, 1987.

Plate 7. Humid Desert Páramo (HD), 4,200 m, Volcán Tungurahua. 28 August, 1987.

Plate 8. *Calamagrostis* sp. [251] and *Chuquiraga jussieui* Desert Páramo with *Cerastium* sp. [200] (CCCD), 4,600 m, Volcán Chimborazo. 25 October, 1987.

Plate 9. *Werneria humilis* & *Plantago rigida* Cushion Páramo (WPC), 4,200 m, Volcán Cotacachi. 11 October, 1987.

Plate 10. Transition between *Calamagrostis* sp. [251] Tussock Grassland with *Hypochaeris sonchoides, Halenia* sp. [189] and *Satureja nubigena* (HHCT) and *Werneria humilis* and *Plantago rigida* Cushion Páramo (WPC), 4160 m, Volcán Cotacachi. 11 October, 1987.

Plate 11. *Calamagrostis* sp. [251] Tussock Grassland with *Viola humboldtii* (VCT), 3,700 m, Páramo de Daldal. 25 September, 1987.

Plate 12. *Neurolepis elata* Bamboo Páramo (NB), 3,800 m, eastern slopes of El Altar. 10 August, 1989.

Plate 13. *Calamagrostis* sp. [251] and *Espeletia pycnophylla* Tussock Grassland with *Viola* sp. [192] (PCE), 3,700 m, Volcán Chiles. 22 October, 1987.

Plate 14. *Calamagrostis* sp. [251] Tussock Grassland with *Paspalum tuberosum* and *Chrysactinium acaule* (PCCT), 3,100 m, Oña. 16 September, 1987.

Plate 15. *Calamagrostis* sp. [251] and *Chuquiraga jussieui* Desert Páramo (CCD), 4,150 m, Volcán Chimborazo. 25 October, 1987.

Plate 16. Stem Rosette growth form: *Espeletia pycnophylla* ssp. *angelensis*, 3,700 m, Volcán Chiles. 22 October, 1987.

Plate 17. Basal Rosette growth form: *Puya* sp., 3,500 m, Cajas. 11 September, 1987.

Plate 18. Tussock growth form: *Cortaderia sericantha*, 4,100 m, Páramo de Daldal. 19 August, 1987.

Plate 19. Acaulescent Rosette growth form: *Senecio repens*, 4,050 m, Páramo de Guamaní. 8 August, 1987.

Plate 20. Cushion growth form: *Azorella corymbosa*, 4,300 m, Páramo de Daldal. 18 August, 1987.

Plate 21. Upright Shrub growth form: *Pentacalia andicola*, 4,050 m, Volcán Chiles. 21 October, 1987.

Plate 22. Prostrate Shrub growth form: *Disterigma empetrifolium,* 4,100 m, Volcán Chiles. 21 October, 1987.

Plate 23. Erect Herb growth form: *Bartsia laticrenata*, 4200 m, Volcán Cotacachi. 11 October, 1987.

Plate 24. Prostrate Herb growth form: *Satureja nubigena*, 3,900 m, Páramo de Guamaní. 8 August, 1987.

Plate 25. Trailing Herb growth form: *Lobelia tenera,* 3,600 m, Páramo de Daldal. 16 July, 1987.

Plate 26. Páramo fire near Laguna Luspa, Cajas. 27 August, 1985.

Plate 27. Páramo fire near Laguna Luspa, Cajas. 27 August, 1985.

Plate 28. Result of overburning: the loss of soil. Páramo near Laguna Yantahuayco, Cajas. 18 August, 1985.

Plate 29. Fire in *Espeletia* Páramo, 3,700 m, Volcán Chiles. 22 October, 1987.

Plate 30. Thermochrom crayons and pyrometers used in the experimental fire at Cajas. 13 September, 1985.

Plate 31. Recently burned páramo at 3,750 m in the Daldal valley. This area was mapped and the transition experiment transects located in the areas between the tussocks (Figure 4.4). 4 July 1987.

Plate 32. Burned *Calamagrostis* tussock with recently germinated seedlings of *Rumex acetosella,* approximately 15 weeks after the fire. 3,750 m, Páramo de Daldal. 25 September, 1987.

Plate 33. Intertussock regeneration at 3,750 m, approximately 15 weeks after the fire. Páramo de Daldal. 25 September, 1987.

Plate 34. Burned páramo at 3,950 m, 123 days after a fire. The transition experiment transects at this altitude were located in this area. Páramo de Daldal. 30 October, 1987.

Plate 35. Transition zone between *Plantago rigida* cushions and *Calamagrostis* tussocks after a recent fire, 4,000 m, Páramo de Daldal. 30 October, 1987.

Plate 36. *Plantago rigida* cushion smothering a *Calamagrostis* tussock. Note the moss growing on the top of the cushion, where the *Plantago* has already begun to break down. Páramo de Daldal. 3 July, 1987.

Plate 37. *Werneria humilis* cushion growing over *Calamagrostis* sp. [251] tussock. 4200 m, Volcán Cotacachi. 11 October, 1987.

Plate 38. The upper Daldal valley, showing the location of the four productivity study exclosures (B-E). 22 August, 1987.

Plate 39. Part of the Alao valley. Exclosure A of the productivity study was located on the valley floor, near the Río Alao at 3,100 m. 19 August, 1987.

Plate 40. Exclosure B of the productivity study, 3,250 m, Daldal valley. 5 July, 1987.

Plate 41. Exclosure C of the productivity study, 3,450 m, Daldal valley. 22 August, 1987.

Plate 42. Exclosure D of the productivity study, 3,750 m, Páramo de Daldal. 5 July, 1987.

Plate 43. Exclosure E of the productivity study, 3,950 m, Páramo de Daldal. 20 August, 1987.

Plate 44. Tussock and Cushion Páramo, 4,150 m, Páramo de Guamaní. The collection area for *Calamagrostis* sp. tussock material for the greenhouse competition experiments. Small tussocks of *Calamagrostis* A can be seen amongst the mats of *Plantago rigida*. Shrubby vegetation of *Loricaria ilinissae* and *Diplostephium rupestre* can be seen in the background. 12 November, 1987.

Plate 45. Tussock Páramo, 4,000 m, Páramo de Guamaní. The collection area for *Calamagrostis* sp. tussock material for the greenhouse competition experiments. Large tussocks of *Calamagrostis* B dominate the landscape. Other prominent plants are *Puya clava-herculis* and *Senecio chionageton*. 12 November, 1987.

Plate 46. Cattle grazing on the upper part of the Cajas sampling transect on Soldados, Cajas. Note the typical location of the *Polylepis* woodland at 3,800 m: beneath a cliff on a rocky substrate. 12 September, 1987.

Plate 47. Local farmer collecting *Chuquiraga jussieui* for fuelwood (the load shown lasts approximately five days), 4,300 m, Volcán Chimborazo.

Plate 48. Severe soil erosion, 4,150 m, Volcán Cotacachi. 11 October, 1987.

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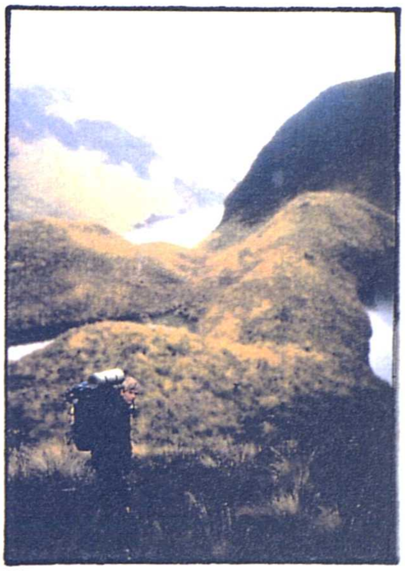

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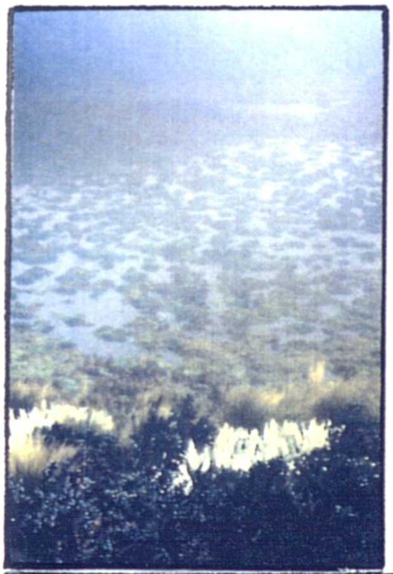

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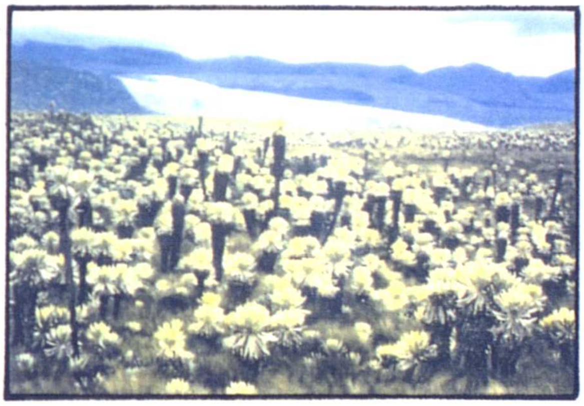

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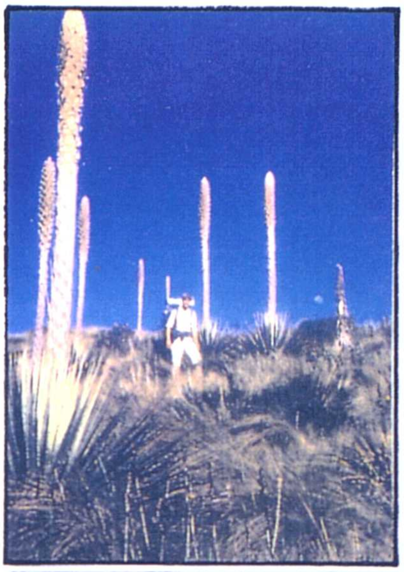

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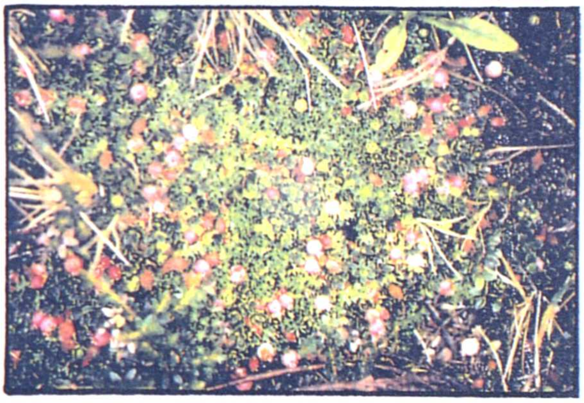

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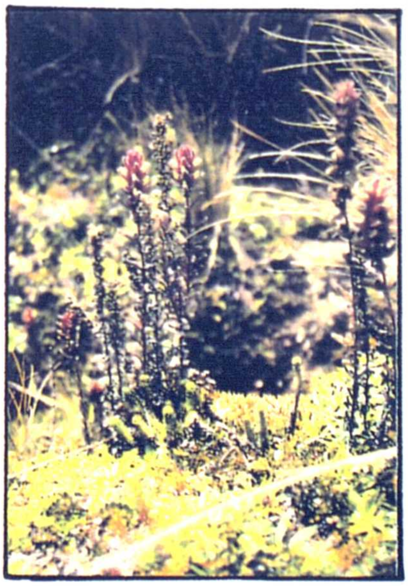

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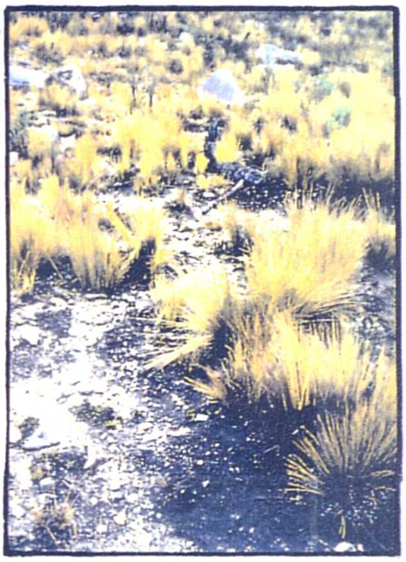

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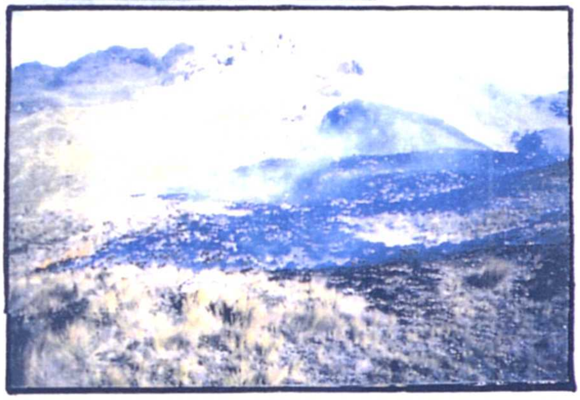

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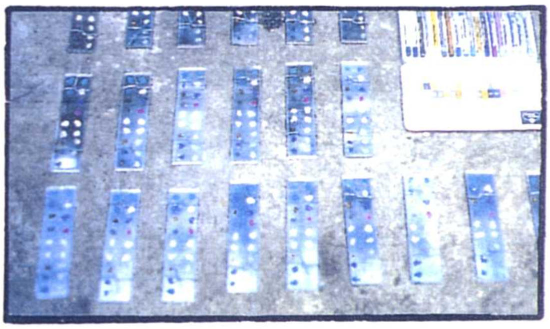

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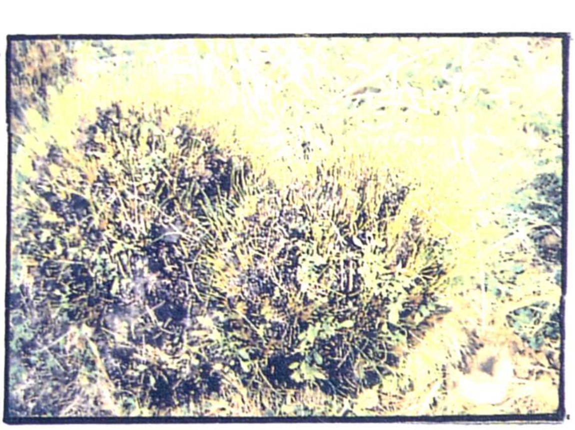

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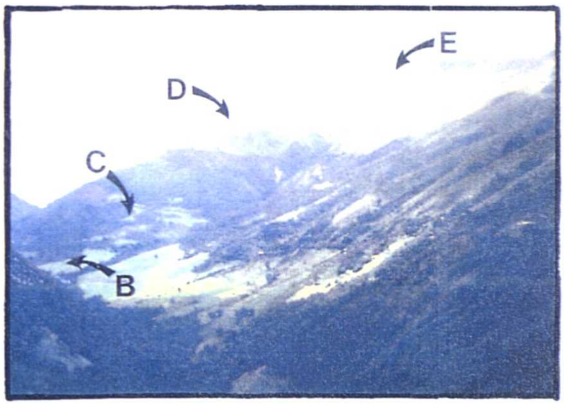

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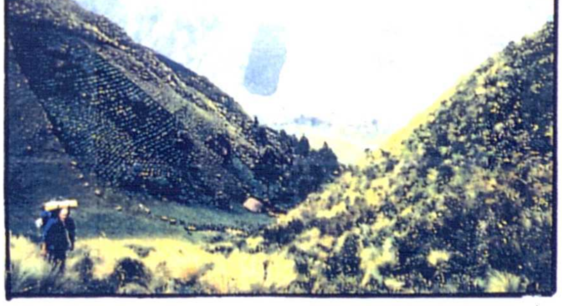

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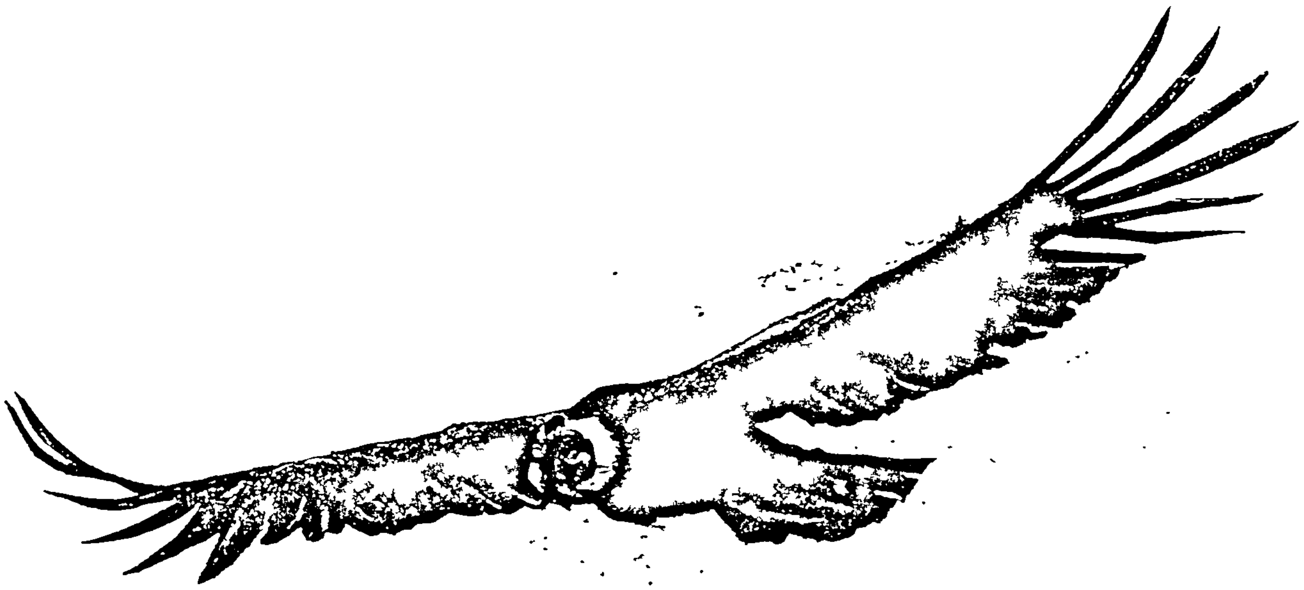
Appendix 1.

Vascular Plant Species



The species referred to in the text have been cross-referenced with voucher material deposited in herbaria in the UK and in Ecuador (as described in the text). The following list allows the species names and codes used in the text to be linked to the pressed specimens in the herbaria. The voucher collection numbers relate to those of the Páramos '87 collection by P.M. Ramsay & P.J. Merrow-Smith, 1987, unless otherwise stated. A small number of species were only found in sterile form and were not collected. Some of the code numbers were not used.

Code	**Scientific Name, Family, Voucher Collection Numbers and Growth Form**
1	*Bomarea caldasii* (H.B.K.) Willd. (Alstroemeriaceae). Voucher Collection Nº 68, 827. Growth form: Trailing Herb.
2	*Bomarea glaucescens* Baker (Alstroemeriaceae). Voucher Collection Nº 231, 348, 648, 778. Growth form: Erect Herb.
3	*Blechnum loxense* (H.B.K.) Hieron. (Blechnaceae). Voucher Collection Nº 74, 272. Growth form: Stem Rosette.
4	*Lobelia tenera* H.B.K. (Campanulaceae). Voucher Collection Nº 22, 838. Growth form: Trailing Herb.
5	*Cerastium danguyi* Macbr. (Caryophyllaceae). Voucher Collection Nº 801. Growth form: Trailing Herb.
6	*Cerastium floccosum* Benth. (Caryophyllaceae). Voucher Collection Nº 253, 811. Growth form: Prostrate Herb.
7	*Cerastium mollissimum* Poir. (Caryophyllaceae). Voucher Collection Nº 395, 732, 1060. Growth form: Prostrate Herb.
8	*Stellaria leptopetala* Benth. (Caryophyllaceae). Voucher Collection Nº 294, 366, 532, 733. Growth form: Trailing Herb.
9	*Baccharis alaternoides* H.B.K. (Compositae). Voucher Collection Nº 669. Growth form: Upright Shrub.
10	*Baccharis alpina* H.B.K. (Compositae). Voucher Collection Nº 138, 256, 363, 499, 977. Growth form: Prostrate Shrub.
11	*Baccharis genistelloides* H.B.K. (Compositae). Voucher Collection Nº 633, 993. Growth form: Erect Herb.
12	*Baccharis genistelloides* H.B.K. (Compositae). Voucher Collection Nº 556. Growth form: Erect Herb.
13	*Baccharis genistelloides* H.B.K. (Compositae). Voucher Collection Nº 84, 288. Growth form: Erect Herb.
14	*Baccharis humifusa* H.B.K. (Compositae). Voucher Collection Nº 215. Growth form: Prostrate Shrub.
15	*Bidens andicola* H.B.K. (Compositae). Voucher Collection Nº 46, 560, 612. Growth form: Prostrate Herb.
16	*Chrysactinium acaule* (H.B.K.) Wedd. (Compositae). Voucher Collection Nº 452, 565, 609. Growth form: Acaulescent Rosette.
17	*Chuquiraga jussieui* Gmel. (Compositae). Voucher Collection Nº 442. Growth form: Upright Shrub.
18	*Conyza uliginosa* (Benth.) Cuatr. (Compositae). Voucher Collection Nº 467, 923. Growth form: Upright Shrub.

19 *Culcitium adscendens* Benth. (Compositae). Voucher Collection Nº 382, 1000. Growth form: Erect Herb.

20 *Culcitium nivale* H.B.K. (Compositae). Voucher Collection Nº 252. Growth form: Acaulescent Rosette.

21 *Culcitium ovatum* (Sch.) Blake (Compositae). Voucher Collection Nº 148, 276, 969. Growth form: Erect Herb.

22 *Culcitium rufescens* H. & B. (Compositae). Voucher Collection Nº 754, 934. Growth form: Basal Rosette.

23 *Diplostephium hartwegii* Hieron. (Compositae). Voucher Collection Nº 490. Growth form: Upright Shrub.

24 *Diplostephium oblanceolatum* Blake (Compositae). Voucher Collection Nº 624. Growth form: Upright Shrub.

25 *Diplostephium rupestre* (H.B.K.) Wedd. (Compositae). Voucher Collection Nº 152, 757, 966. Growth form: Upright Shrub.

26 *Erigeron pinnatus* Turcz. (Compositae). Voucher Collection Nº 988. Growth form: Acaulescent Rosette.

27 *Espeletia pycnophylla* Cuatr. ssp. *angelensis* Cuatr. (Compositae). Voucher Collection Nº 849. Growth form: Stem Rosette.

28 *Gnaphalium ? luteo-album* L. (Compositae). Voucher Collection Nº 640, 836, 1064. Growth form: Erect Herb.

29 *Gnaphalium pensylvanicum* Willd. (Compositae). Voucher Collection Nº 112, 268, 365, 918, 1043. Growth form: Erect Herb.

30 *Gnaphalium antennarioides* DC. (Compositae). Voucher Collection Nº 947. Growth form: Erect Herb.

31 *Gnaphalium coarctatum* Willd. (Compositae). Voucher Collection Nº 538, 823. Growth form: Erect Herb.

32 *Gnaphalium dysodes* Spreng. (Compositae). Voucher Collection Nº 116. Growth form: Erect Herb.

33 *Gnaphalium gnaphaloides* (Kunth.) Beauv. (Compositae). Voucher Collection Nº 737. Growth form: Erect Herb.

34 *Gynoxys baccharoides* (H.B.K.) Cass. (Compositae). Voucher Collection Nº 312. Growth form: Upright Shrub.

35 *Gynoxys buxifolia* (H.B.K.) Cass. (Compositae). Voucher Collection Nº 674. Growth form: Upright Shrub.

36 *Gynoxys cuicochensis* Cuatr. (Compositae). Voucher Collection Nº 647. Growth form: Upright Shrub.

37 *Gynoxys fuliginosa* (H.B.K.) Cass. (Compositae). Voucher Collection Nº 1124. Growth form: Upright Shrub.

38 *Gynoxys miniphylla* Cuatr. (Compositae). Voucher Collection Nº 504. Growth form: Upright Shrub.

39 *Hieracium frigidum* Wedd. (Compositae). Voucher Collection Nº 80, 305, 352, 643, 673, 685, 799. Growth form: Erect Herb.

40 *Hypochaeris sessiliflora* H.B.K. (Compositae). Voucher Collection Nº 306, 955, 960, 985. Growth form: Acaulescent Rosette.

41 *Hypochaeris sonchoides* H.B.K. (Compositae). Voucher Collection Nº 126, 714, 764, 995. Growth form: Acaulescent Rosette.

42 *Loricaria complanata* (Sch.Bip.) Wedd. (Compositae). Voucher Collection Nº 489. Growth form: Upright Shrub.

43 *Loricaria thuyoides* (Lam.) Sch.Bip. (Compositae). Voucher Collection Nº 304, 340. Growth form: Upright Shrub.

44 *Lucilia lehmanii* Hieron. (Compositae). Voucher Collection Nº 200. Growth form: Acaulescent Rosette.

45 *Lucilia radians* (Benth.) Cuatr. (Compositae). Voucher Collection Nº 989. Growth form: Cushion.

46 *Oritrophium hieracioides* (Wedd.) Cuatr. (Compositae). Voucher Collection Nº 334. Growth form: Acaulescent Rosette.

47 *Oritrophium limnophilum* (Sch.Bip.) Cuatr. (Compositae). Voucher Collection Nº 233, 333, 994, 1030. Growth form: Acaulescent Rosette.

48 *Oritrophium peruvianum* (Lam.) Cuatr. (Compositae). Voucher Collection Nº 163, 260, 347, 765, 846. Growth form: Acaulescent Rosette.

49 *Oritrophium peruvianum* (Lam.) f. intermedium Cuatr. (Compositae). Voucher Collection Nº 458, 564, 620. Growth form: Acaulescent Rosette.

50 *Perezia pungens* (H.B.K.) Less. (Compositae). Voucher Collection Nº 850. Growth form: Erect Herb.

51 *Pentacalia* aff. *andicola* Turcz. (Compositae). Voucher Collection Nº 779, 891, 1067. Growth form: Upright Shrub.

52 *Pentacalia arbutifolius* H.B.K. (Compositae). Voucher Collection Nº 220, 285. Growth form: Upright Shrub.

53 *Senecio chionageton* Wedd. (Compositae). Voucher Collection Nº 150, 436, 948. Growth form: Erect Herb.

54 *Senecio lingulatus* (Schlechtd.) Cuatr. (Compositae). Voucher Collection Nº 493. Growth form: Erect Herb.

55 *Senecio pimpinellifolia* H.B.K. (Compositae). Voucher Collection Nº 65, 286, 394. Growth form: Acaulescent Rosette.

56 *Senecio repens* DC. (Compositae). Voucher Collection Nº 183, 329. Growth form: Acaulescent Rosette.

57 *Pentacalia stuebellii* Hieron. (Compositae). Voucher Collection Nº 883, 921. Growth form: Upright Shrub.

58 *Senecio teretifolius* (H.B.K.) DC. (Compositae). Voucher Collection Nº 1005. Growth form: Upright Shrub.

59 *Sonchus ? oleraceus* L. (Compositae). Voucher Collection Nº 44. Growth form: Erect Herb.

60 *Stevia* sp. (Compositae). Voucher Collection Nº 634. Growth form: Erect Herb.

61 *Taraxacum officinale* Weber (Compositae). Voucher Collection Nº 70. Growth form: Acaulescent Rosette.

62 *Vernonia* sp. (Compositae). Voucher Collection Nº 902. Growth form: Upright Shrub.

63 *Werneria ? crassa* Blake (Compositae). Voucher Collection Nº 999. Growth form: Acaulescent Rosette.

64 *Werneria humilis* H.B.K. (Compositae). Voucher Collection Nº 186, 362, 726, 759, 866. Growth form: Cushion.

65 *Werneria nubigena* H.B.K. (Compositae). Voucher Collection Nº 177, 780. Growth form: Acaulescent Rosette.

66 *Werneria pumila* H.B.K. (Compositae). Voucher Collection Nº 869. Growth form: Cushion.

67 *Diplostephium glutinosum* Blake (Compositae). Voucher Collection Nº 219, 322, 583. Growth form: Upright Shrub.

68 *Lepidium* sp. (Cruciferae). Voucher Collection Nº 736, 838. Growth form: Erect Herb.

69 *Carex crinalis* Boott (Cyperaceae). Voucher Collection Nº 359, 476, 525, 607, 644, 1026, 1058. Growth form: Acaulescent Rosette.

70 *Carex lemanniana* Boott (Cyperaceae). Voucher Collection Nº 747. Growth form: Tussock.

71 *Carex pichinchensis* H.B.K. (Cyperaceae). Voucher Collection Nº 125, 419, 491, 876. Growth form: Tussock.

72 *Carex tristicha* Boott (Cyperaceae). Voucher Collection Nº 161, 360, 385, 533, 815, 959, 1025. Growth form: Acaulescent Rosette.

73 *Oreobolus goeppingeri* K. Svessenguth (Cyperaceae). Voucher Collection Nº 327, 632, 688, 702, 926. Growth form: Cushion.

74 *Oreobolus obtusangulus* Gaud. (Cyperaceae). Voucher Collection Nº 225. Growth form: Cushion.

75 *Rhynchospora macrochaeta* Steud. (Cyperaceae). Voucher Collection Nº 508, 699, 859. Growth form: Tussock.

76 *Rhychospora* cf. *ruiziana* Boeck. (Cyperaceae). Voucher Collection Nº 550, 617, 906, 1056. Growth form: Basal Rosette.

77 *Uncinia* cf. *hamata* (Sw.) Urb. (Cyperaceae). Voucher Collection Nº 378. Growth form: Acaulescent Rosette.

78 *Uncinia phleoides* Pers. (Cyperaceae). Voucher Collection Nº 739. Growth form: Tussock.

79 *Disterigma empetrifolium* (H.B.K.) Drude (Ericaceae). Voucher Collection Nº 85, 287, 342, 417, 694, 774, 958. Growth form: Prostrate Shrub.

80 *Gentiana sedifolia* H.B.K. (Gentianaceae). Voucher Collection Nº 120, 280, 316, 569, 629, 867. Growth form: Prostrate Herb.

81 *Gentianella ? corallina* Gilg. (Gentianaceae). Voucher Collection Nº 622. Growth form: Erect Herb.

82 *Gentianella ? foliosa* (H.B.K.) Fabris (Gentianaceae). Voucher Collection Nº 862. Growth form: Erect Herb.

83 *Gentianella cernua* (H.B.K.) Fabris (Gentianaceae). Voucher Collection Nº 991. Growth form: Erect Herb.

84 *Gentianella gracilis* (H.B.K.) Fabris (Gentianaceae). Voucher Collection Nº 554. Growth form: Erect Herb.

85 *Gentianella hirculus* (Griseb.) Fabris (Gentianaceae). Voucher Collection Nº 449. Growth form: Erect Herb.

86 *Gentianella hyssopifolia* (H.B.K.) Fabris (Gentianaceae). Voucher Collection Nº 464, 637, 671. Growth form: Erect Herb.

87 *Gentianella nummalarifolia* Griseb. (Gentianaceae). Voucher Collection Nº 713, 766. Growth form: Erect Herb.

88 *Halenia weddelliana* Gilg. (Gentianaceae). Voucher Collection Nº 335, 892. Growth form: Erect Herb.

89 *Geranium multipartitum* Benth. (Geraniaceae). Voucher Collection Nº 123, 319. Growth form: Prostrate Herb.

90 *Geranium reptans* Kunth. (Geraniaceae). Voucher Collection Nº 18, 299, 364, 730. Growth form: Prostrate Herb.

91 *Geranium sibbaldioides* Benth. (Geraniaceae). Voucher Collection Nº 122, 318, 625, 687, 775, 925. Growth form: Prostrate Herb.

92 *Aciachne flagellifera* Laegaard (Gramineae). Voucher Collection Nº 719, 762, 863. Growth form: Cushion.

93 *Anthoxanthum odoratum* L. (Gramineae). Voucher Collection Nº 249, 540. Growth form: Erect Herb.

94 *Bromus lanatus* Kunth (Gramineae). Voucher Collection Nº 291, 320, 523, 524, 591, 720. Growth form: Erect Herb.

95 *Cortaderia nitida* (Kunth) Pilger (Gramineae). Voucher Collection Nº 105. Growth form: Tussock.

96 *Holcus lanatus* L. (Gramineae). Voucher Collection Nº 248. Growth form: Erect Herb.

97 *Paspalum tuberosum* Mez. (Gramineae). Voucher Collection Nº 103, 325. Growth form: Prostrate Herb.

98 *Orthrosanthus chimboracensis* (H.B.K.) Baker (Iridaceae). Voucher Collection Nº 83, 593, 1069. Growth form: Erect Herb.

99 *Sisyrinchium jamesoni* Baker (Iridaceae). Voucher Collection Nº 167, 267, 323, 802, 932, 1023. Growth form: Tussock.

100 *Sisyrinchium tinctorium* H.B.K. (Iridaceae). Voucher Collection Nº 547, 559, 619, 695. Growth form: Tussock.

101 *Luzula gigantea* Desv. (Juncaceae). Voucher Collection Nº 301, 964. Growth form: Tussock.

102 *Luzula racemosa* Desv. (Juncaceae). Voucher Collection Nº 251, 341, 721, 793. Growth form: Acaulescent Rosette.

103 *Satureja nubigena* (Kunth.) Briq. (Labiatae). Voucher Collection Nº 121, 300, 795, 885. Growth form: Prostrate Herb.

104 *Stachys elliptica* Kunth. (Labiatae). Voucher Collection Nº 66, 380. Growth form: Erect Herb.

105 *Lupinus ? purdieanus* C.P. (Leguminosae). Voucher Collection Nº 273. Growth form: Prostrate Shrub.

106 *Lupinus ? sarmentosus* Desr. (Leguminosae). Voucher Collection Nº 328, 492, 641, 788, 924, 1041. Growth form: Prostrate Herb.

107 *Lupinus microphyllus* Desr. (Leguminosae). Voucher Collection Nº 798. Growth form: Prostrate Shrub.

108 *Lupinus ramosissimus* Benth. (Leguminosae). Voucher Collection Nº 106. Growth form: Upright Shrub.

109 *Lupinus smithianus* Kunth. (Leguminosae). Voucher Collection Nº 987. Growth form: Prostrate Herb.

110 *Trifolium repens* L. (Leguminosae). Voucher Collection Nº 89. Growth form: Prostrate Herb.

111 *Vicia ? andicola* H.B.K. (Leguminosae). Voucher Collection Nº 144, 738. Growth form: Trailing Herb.

112 *Vicia ? setifolia* H.B.K. (Leguminosae). Voucher Collection Nº 841. Growth form: Trailing Herb.

113 *Pinguicula calyptrata* H.B.K. (Lentibulariaceae). Voucher Collection Nº 628, 684, 913. Growth form: Acaulescent Rosette.

114 *Tofieldia sessiliflora* Hook (Melanthiaceae). Voucher Collection Nº 621, 670. Growth form: Erect Herb.

115 *Brachyotum alpinum* Cogn. (Melastomataceae). Voucher Collection Nº 434. Growth form: Upright Shrub.

116 *Brachyotum* cf. *confertum* (Bonpl.) Triana (Melastomataceae). Voucher Collection Nº 611. Growth form: Upright Shrub.

117 *Brachyotum ledifolium* (Desr.) Triana (Melastomataceae). Voucher Collection Nº 825. Growth form: Upright Shrub.

118 *Plantago major* L. (Plantaginaceae). Voucher Collection Nº 63. Growth form: Acaulescent Rosette.

119 *Plantago rigida* H.B.K. (Plantaginaceae). Voucher Collection Nº 213, 379, 526. Growth form: Cushion.

120 *Monnina crassifolia* H.B.K. (Polygalaceae). Voucher Collection Nº 905. Growth form: Upright Shrub.

121 *Rumex acetosella* L. (Polygonaceae). Voucher Collection Nº 216, 935. Growth form: Prostrate Herb.

122 *Anemone jamesonii* Hook. (Ranunculaceae). Voucher Collection Nº 487. Growth form: Prostrate Herb.

123 *Ranunculus peruvianus* Pers. (Ranunculaceae). Voucher Collection Nº 338, 450, 848, 1018. Growth form: Prostrate Herb.

124 *Lachemilla ? rupestris* (H.B.K.) Rothm. (Rosaceae). Voucher Collection Nº 337, 686, 929, 1045. Growth form: Prostrate Herb.

125 *Lachemilla andina* (Perry) Rothm. (Rosaceae). Voucher Collection Nº 227. Growth form: Prostrate Herb.

126 *Lachemilla galioides* Benth. (Rosaceae). Voucher Collection Nº 1046. Growth form: Acaulescent Rosette.

127 *Lachemilla hispidula* (Perry) Rothm. (Rosaceae). Voucher Collection Nº 257, 361, 717. Growth form: Acaulescent Rosette.

128 *Lachemilla holosericea* (Perry) Rothm. (Rosaceae). Voucher Collection Nº 718. Growth form: Acaulescent Rosette.

129 *Lachemilla nivalis* H.B.K. (Rosaceae). Voucher Collection Nº 506, 768, 877, 878. Growth form: Acaulescent Rosette.

130 *Lachemilla orbiculata* R. & P. (Rosaceae). Voucher Collection Nº 303, 368. Growth form: Prostrate Herb.

131 *Lachemilla pinnata* R. & P. (Rosaceae). Voucher Collection Nº 884. Growth form: Prostrate Herb.

132 *Nertera granadensis* (Lf.) Druce (Rubiaceae). Voucher Collection Nº 262, 522, 963. Growth form: Prostrate Herb.

133 *Relbunium hypocarpium* (L.) Hemsl. (Rubiaceae). Voucher Collection Nº 289, 293, 638, 741, 1063. Growth form: Trailing Herb.

134 *Bartsia laticrenata* Benth. (Scrophulariaceae). Voucher Collection Nº 330, 771, 855. Growth form: Erect Herb.

135 *Calceolaria ferruginea* Cav. (Scrophulariaceae). Voucher Collection Nº 307. Growth form: Upright Shrub.

136 *Ourisia chamaedryfolia* Benth. (Scrophulariaceae). Voucher Collection Nº 881. Growth form: Acaulescent Rosette.

137 *Pedicularis incurva* Benth. (Scrophulariaceae). Voucher Collection Nº 513, 631. Growth form: Acaulescent Rosette.

138 *Veronica serpyllifolia* L. (Scrophulariaceae). Voucher Collection Nº 534. Growth form: Erect Herb.

139 *Azorella aretoides* H.B.K. (Umbelliferae). Voucher Collection Nº 210, 353, 783, 944. Growth form: Acaulescent Rosette.

140 *Azorella corymbosa* (R. & P.) Pers. (Umbelliferae). Voucher Collection Nº 376. Growth form: Cushion.

141 *Azorella crenata* (R. & P.) Pers. (Umbelliferae). Voucher Collection Nº 887, 1053. Growth form: Acaulescent Rosette.

142 *Azorella pedunculata* (Spreng.) M. & C. (Umbelliferae). Voucher Collection Nº 134, 271. Growth form: Cushion.

143 *Eryngium humile* Cav. (Umbelliferae). Voucher Collection Nº 228, 266, 566, 613, 837, 937, 980. Growth form: Acaulescent Rosette.

144 *Hydocotyle bonplandii* A. Rich (Umbelliferae). Voucher Collection Nº 250. Growth form: Prostrate Herb.

145 *Niphogeton dissecta* (Benth.) F. Macbr. (Umbelliferae). Voucher Collection Nº 119, 709, 787, 879, 890. Growth form: Acaulescent Rosette.

146 *Oreomyrrhis andicola* (Kunth.) Hook f. (Umbelliferae). Voucher Collection Nº 141, 297, 357, 729, 819. Growth form: Acaulescent Rosette.

147 *Valeriana aretioides* H.B.K. (Valerianaceae). Voucher Collection Nº 756, 763. Growth form: Cushion.

148 *Valeriana rigida* R. & P. (Valerianaceae). Voucher Collection Nº 808, 1040. Growth form: Cushion.

149 *Valeriana adscendens* Turcz. (Valerianaceae). Voucher Collection Nº 711. Growth form: Acaulescent Rosette.

150 *Valeriana bonplandiana* Wedd. (Valerianaceae). Voucher Collection Nº 218, 275, 389, 561, 616, 691, 745, 880. Growth form: Upright Shrub.

151 *Valeriana bracteata* Benth. (Valerianaceae). Voucher Collection Nº 332, 494. Growth form: Acaulescent Rosette.

152 *Valeriana alypifolia* ssp. *alypifolia* (Valerianaceae). Voucher Collection Nº 971. Growth form: Prostrate Shrub.

153 *Valeriana microphylla* H.B.K. (Valerianaceae). Voucher Collection Nº 355, 446, 809, 998, 1029. Growth form: Upright Shrub.

154 *Valeriana plantaginea* H.B.K. (Valerianaceae). Voucher Collection Nº 952. Growth form: Basal Rosette.

155 *Viola humboldtii* Tr. & Fl. (Violaceae). Voucher Collection Nº 29. Growth form: Prostrate Herb.

156 *Viola nivalis* Benth. (Violaceae). Voucher Collection Nº 414, 1037. Growth form: Acaulescent Rosette.

157 *Astragalus geminiflorus* H.B.K. (Leguminosae). Voucher Collection Nº 982. Growth form: Cushion.

158 *Geranium* sp. (Geraniaceae). Voucher Collection Nº 472. Growth form: Prostrate Herb.

159 *Geranium* sp. (Geraniaceae). Voucher Collection Nº 1004. Growth form: Prostrate Herb.

160 *Geranium* sp. (Geraniaceae). Voucher Collection Nº 716, 888. Growth form: Prostrate Herb.

161 *Hypericum* sp. (Guttiferae). Voucher Collection Nº 314, 495, 562, 661, 676, 941, 1021. Growth form: Erect Herb.

162 Unidentified species (Melastomataceae). Voucher Collection Nº 462, 664. Growth form: Prostrate Herb.

163 Unidentified species (Melastomataceae). Voucher Collection Nº 639. Growth form: Prostrate Herb.

164 *Oxalis* sp. (Oxalidaceae). Voucher Collection Nº 521. Growth form: Prostrate Herb.

165 *Bartsia* sp. (Scrophulariaceae). Voucher Collection Nº 498, 615, 690, 936, 1022, 1051. Growth form: Erect Herb.

166 *Bartsia* sp. (Scrophulariaceae). Voucher Collection Nº 816. Growth form: Erect Herb.

167 *Bartsia* sp. (Scrophulariaceae). Voucher Collection Nº 263. Growth form: Erect Herb.

168 *Castilleja* sp. (Scrophulariaceae). Voucher Collection Nº 222, 331, 772, 981. Growth form: Erect Herb.

169 *Castilleja* sp. (Scrophulariaceae). Voucher Collection Nº 946. Growth form: Erect Herb.

170 *Castilleja* sp. (Scrophulariaceae). Voucher Collection Nº 265, 672. Growth form: Erect Herb.

171 *Castilleja* sp. (Scrophulariaceae). Voucher Collection Nº 354, 460, 553, 817, 1019. Growth form: Erect Herb.

172 *Veronica* sp. (Scrophulariaceae). Voucher Collection Nº 535. Growth form: Erect Herb.

173 *Aphanactis jamesonia* Wedd. (Compositae). Voucher Collection Nº 189, 317, 938. Growth form: Acaulescent Rosette.

174 *Cotula ? mexicana* (DC.) Cabr. (Compositae). Voucher Collection Nº 17, 370, 939. Growth form: Acaulescent Rosette.

175 Unidentified species (Alliaceae). Voucher Collection Nº 810. Growth form: Erect Herb.

176 *Nototriche jamesonii* A.W. Hill (Malvaceae). Voucher Collection Nº 997. Growth form: Cushion.

177 As for Code Nº 157.

178 Unidentified species (Family not known). Voucher Collection Nº 984. Growth form: Cushion.

179 *Puya clava-herculis* Mez & Sodiro (Bromeliaceae). Voucher Collection Nº 516. Growth form: Basal Rosette.

180 *Puya* cf. *pygmaea* L.B. Smith (Bromeliaceae). Voucher Collection Nº 655. Growth form: Basal Rosette.

181 *Puya* sp. (Bromeliaceae). Voucher Collection Nº 662. Growth form: Basal Rosette.

182 Unidentified species (Cruciferae). Voucher Collection Nº 735. Growth form: Erect Herb.

183 Not used.

184 *Cardamine* sp. (Cruciferae). Voucher Collection Nº 367. Growth form: Erect Herb.

185 *Pemettya* sp. (Ericaceae). Voucher Collection Nº 814, 953. Growth form: Prostrate Shrub.

186 *Gentianella* sp. (Gentianaceae). Voucher Collection Nº 1017. Growth form: Erect Herb.

187 *Halenia* sp. (Gentianaceae). Voucher Collection Nº 570. Growth form: Erect Herb.

188 *Halenia* sp. (Gentianaceae). Voucher Collection Nº 642, 689. Growth form: Erect Herb.

189 *Halenia* sp. (Gentianaceae). Voucher Collection Nº 712, 760. Growth form: Erect Herb.

190 Not used.

191 Unidentified species (Umbelliferae). Voucher Collection Nº 731. Growth form: Erect Herb.

192 *Viola* sp. (Violaceae). Voucher Collection Nº 927. Growth form: Acaulescent Rosette.

193 *Ribes* sp. (Grossulariaceae). Voucher Collection Nº 854. Growth form: Upright Shrub.

194 *Valeriana* sp. (Valerianaceae). Voucher Collection Nº 990. Growth form: Cushion.

195 *Azorella* sp. (Umbelliferae). Voucher Collection Nº 868. Growth form: Cushion.

196 *Sibthorpia repens* (Mutis) Kuntze (Scrophulariaceae). Voucher Collection Nº 511, 961. Growth form: Prostrate Herb.

197 *Cerastium* sp. (Caryophyllaceae). Voucher Collection Nº 454, 536. Growth form: Trailing Herb.

198 *Cerastium* sp. (Caryophyllaceae). Voucher Collection Nº 728. Growth form: Prostrate Herb.

199 *Cerastium* sp. (Caryophyllaceae). Voucher Collection Nº 743, 871. Growth form: Prostrate Herb.

200 *Cerastium* sp. (Caryophyllaceae). Voucher Collection Nº 979. Growth form: Prostrate Herb.

201 *Vicia* sp. (Leguminosae). Voucher Collection Nº 381. Growth form: Trailing Herb.

202 *Lupinus* sp. (Leguminosae). Voucher Collection Nº 146. Growth form: Prostrate Herb.

203 *Lupinus* sp. (Leguminosae). Voucher Collection Nº 824. Growth form: Upright Shrub.

204 Unidentified species (Compositae). Voucher Collection Nº 746. Growth form: Prostrate Herb.

205 Unidentified species (Umbelliferae). Voucher Collection Nº 527. Growth form: Prostrate Herb.

206 *Cotula* sp. (Compositae). Voucher Collection Nº 1001. Growth form: Acaulescent Rosette.

207 *Sisyrinchium* sp. aff. *alatum* Hook. (Iridaceae). Voucher Collection Nº 481. Growth form: Tussock.

208 *Monnina* sp. (Polygalaceae). Voucher Collection Nº 830. Growth form: Upright Shrub.

209 *Lachemilla* sp. (Rosaceae). Voucher Collection Nº 336. Growth form: Prostrate Herb.

210 *Lachemilla* sp. (Rosaceae). Voucher Collection Nº 653. Growth form: Prostrate Herb.

211 *Viola* sp. (Violaceae). Voucher Collection Nº 557. Growth form: Prostrate Herb.

212 *Neurolepis elata* (Kunth) Pilger (Gramineae). Voucher Nº 436 from Ramsay, Evans & Buckland 1989 Collection. Growth form: Tussock.

213 *Ranunculus guzmanii* H.B.K. (Ranunculaceae). Voucher Collection Nº 856. Growth form: Prostrate Herb.

214 *Carex* sp. (Cyperaceae). Voucher Collection Nº 542. Growth form: Acaulescent Rosette.

215 *Distichia muscoides* Nees & Meyen (Juncaceae). Voucher Collection Nº 179. Growth form: Cushion.

216 *Equisetum bogotense* H.B.K. (Equisetaceae). Voucher Collection Nº 813, 1052. Growth form: Erect Herb.

217 *Ophioglossum crotalophoroides* Walt. (Ophioglossaceae). Voucher Collection Nº 133, 255, 943, 1156. Growth form: Acaulescent Rosette.

218 *Plantago linearis* H.B.K. (Plantaginaceae). Voucher Collection Nº 58, 558, 812, 1028, 1059. Growth form: Acaulescent Rosette.

219 *Baccharis caespitosa* (R. & P.) Pers. (Compositae). Voucher Collection Nº 1224. Growth form: Prostrate Shrub.

220 *Poa cucullata* Hack. (Gramineae). Voucher Collection Nº 1225. Growth form: Erect Herb.

221 Not used.

222 *Huperzia hypogoea* B. Ollg. (Lycopodiaceae). Voucher Collection Nº 1231. Growth form: Erect Herb.

223 Unidentified species (Family not known). Voucher Collection Nº 520. Growth form: Acaulescent Rosette.

224 Unidentified species (Family not known). Voucher Collection Nº 623. Growth form: Upright Shrub.

225 *Eudema nubigena* H.B.K. (Cruciferae). Voucher Collection Nº 727, 1185. Growth form: Cushion.

226 Unidentified species (Family not known). Voucher Collection Nº 734. Growth form: Erect Herb.

227 Unidentified species (Family not known). Voucher Collection Nº 1061. Growth form: Erect Herb.

228 *Eriosorus* sp. (Filicopsida). Voucher Collection Nº 264, 872. Growth form: Basal Rosette.

229 *Thelypteris* sp. (Thelypteridaceae). Voucher Collection Nº 292, 1066. Growth form: Basal Rosette.

230 *Asplenium* sp. (Aspleniaceae). Voucher Collection Nº 270. Growth form: Acaulescent Rosette.

231 *Lysipomia montioides* H.B.K. (Campanulaceae). Voucher Collection Nº 212. Growth form: Prostrate Herb.

232 Unidentified species (Compositae). Voucher Collection Nº 873. Growth form: Prostrate Herb.

233 *Diplostephium* sp. (Compositae). Voucher Collection Nº 933. Growth form: Upright Shrub.

234 *Draba* sp. (Cruciferae). Voucher Collection Nº 715. Growth form: Erect Herb.

235 *Draba* sp. (Cruciferae). Voucher Collection Nº 1062. Growth form: Erect Herb.

236 *Agrostis* sp. (Gramineae). Voucher Collection Nº 548, 940. Growth form: Erect Herb.

237 *Agrostis* sp. (Gramineae). Voucher Collection Nº 537. Growth form: Erect Herb.

238 *Agrostis* sp. (Gramineae). Voucher Collection Nº 411. Growth form: Erect Herb.

239 *Agrostis* sp. (Gramineae). Voucher Collection Nº 864. Growth form: Erect Herb.

240 *Agrostis* sp. (Gramineae). Voucher Collection Nº 530, 551, 660, 679, 680, 698, 931, 1047. Growth form: Erect Herb.

241 *Agrostis* sp. (Gramineae). Voucher Collection Nº 910. Growth form: Erect Herb.

242 *Agrostis* sp. (Gramineae). Voucher Collection Nº 377, 416, 501, 531, 659, 822, 992, 1008. Growth form: Erect Herb.

243 *Agrostis* sp. (Gramineae). Voucher Collection Nº 261, 284, 326, 514, 700. Growth form: Erect Herb.

244 *Agrostis nigritella* Pilg. (Gramineae). Voucher Collection Nº 254, 344, 421, 722, 786, 865, 986. Growth form: Erect Herb.

245 Not used.

246 *Calamagrostis* sp. (Gramineae). Voucher Collection Nº 707, 761. Growth form: Erect Herb.

247 *Calamagrostis* sp. (Gramineae). Voucher Collection Nº 1031. Growth form: Erect Herb.

248 Not used.

249 *Calamagrostis* sp. (Gramineae). Voucher Collection Nº 549, 692, 696. Growth form: Erect Herb.

250 *Calamagrostis* sp. (Gramineae). Voucher Collection Nº 384. Growth form: Erect Herb.

251 *Calamagrostis* sp. (Gramineae). Voucher Collection Nº 321, 509, 580, 657, 697, 724, 725, 777, 893, 894, 920, 954, 956, 972, 1007, 1036, 1057. Growth form: Tussock.

252 Not used.

253 *Elymus attenuatum* (H.B.K.) R. & S. (Gramineae). Voucher Collection Nº 740. Growth form: Erect Herb.

254 *Festuca* sp. (Gramineae). Voucher Collection Nº 343, 442, 1035. Growth form: Tussock.

255 *Festuca* sp. (Gramineae). Voucher Collection Nº 502, 896. Growth form: Tussock.

256 *Festuca* sp. (Gramineae). Voucher Collection Nº 510, 742. Growth form: Tussock.

257 *Muhlenbergia angustata* (Presl.) Kunth (Gramineae). Voucher Collection Nº 834. Growth form: Tussock.

258 *Muhlenbergia ligularis* (Hack.) Hitchc. (Gramineae). Voucher Collection Nº 369, 541. Growth form: Erect Herb.

259 *Paspalum* sp. Mez. (Gramineae). Voucher Collection Nº 568. Growth form: Prostrate Herb.

260 *Paspalum* sp. Mez. (Gramineae). Voucher Collection Nº 908. Growth form: Prostrate Herb.

261 *Poa* sp. (Gramineae). Voucher Collection Nº 345, 356, 723, 1033. Growth form: Erect Herb.

262 *Poa* sp. (Gramineae). Voucher Collection Nº 346, 500, 505, 744, 821, 875, 1032. Growth form: Erect Herb.

263 *Poa* sp. (Gramineae). Voucher Collection Nº 383. Growth form: Erect Herb.

264 *Poa* sp. (Gramineae). Voucher Collection Nº 390, 889. Growth form: Erect Herb.

265 *Poa* sp. (Gramineae). Voucher Collection Nº 425. Growth form: Erect Herb.

266 *Poa* sp. (Gramineae). Voucher Collection Nº 543. Growth form: Erect Herb.

267 *Poa* sp. (Gramineae). Voucher Collection Nº 544. Growth form: Erect Herb.

268 *Poa* sp. (Gramineae). Voucher Collection Nº 807. Growth form: Erect Herb.

269 *Poa* sp. (Gramineae). Voucher Collection Nº 820. Growth form: Erect Herb.

270 *Stipa* sp. (Gramineae). Voucher Collection Nº 586, 658. Growth form: Tussock.

271 *Trisetum spicatum* (L.) Richt. (Gramineae). Voucher Collection Nº 1034. Growth form: Erect Herb.

272 *Hypericum* sp. (Guttiferae). Voucher Collection Nº 840. Growth form: Prostrate Herb.

273 *Hypericum* sp. (Guttiferae). Voucher Collection Nº 313, 486, 748, 915, 1050. Growth form: Upright Shrub.

274 Not used.

275 *Hypericum* sp. (Guttiferae). Voucher Collection Nº 474, 475, 587, 957. Growth form: Prostrate Herb.

276 *Hypericum* sp. (Guttiferae). Voucher Collection Nº 826. Growth form: Upright Shrub.

277 *Jamesonia* sp. (Hemionitidaceae). Voucher Collection Nº 1176. Growth form: Erect Herb.

278 *Jamesonia alstonii* A.F. Tryon (Hemionitidaceae). Voucher Collection Nº 388, 497, 627, 1049. Growth form: Erect Herb.

279 *Jamesonia pulchra* Hook. & Grev. (Hemionitidaceae). Voucher Collection Nº 907, 930. Growth form: Erect Herb.

280 *Jamesonia robusta* Karst. (Hemionitidaceae). Voucher Collection Nº 675. Growth form: Erect Herb.

281 *Elaphaglossum* sp. (Lomariopsidaceae). Voucher Collection Nº 805, 1048. Growth form: Erect Herb.

282 *Elaphaglossum* sp. (Lomariopsidaceae). Voucher Collection Nº 269. Growth form: Erect Herb.

283 *Elaphaglossum* sp. (Lomariopsidaceae). Voucher Collection Nº 1065. Growth form: Erect Herb.

284 *Huperzia compacta* (Hook.) B. Ollg. (Lycopodiaceae). Voucher Collection Nº 515. Growth form: Erect Herb.

285 *Lycopodium* sp. (Lycopodiaceae). Voucher Collection Nº 803. Growth form: Erect Herb.

286 *Lycopodium* sp. (Lycopodiaceae). Voucher Collection Nº 942. Growth form: Erect Herb.

287 *Lycopodium* sp. (Lycopodiaceae). Voucher Collection Nº 1038. Growth form: Erect Herb.

288 *Lycopodium* sp. (Lycopodiaceae). Voucher Collection Nº 258. Growth form: Erect Herb.

289 *Lycopodium* sp. (Lycopodiaceae). Voucher Collection Nº 373, 758, 860. Growth form: Erect Herb.

290 *Huperzia columnaris* B. Ollg. (Lycopodiaceae). Voucher Collection Nº 484. Growth form: Erect Herb.

291 *Lycopodium* sp. (Lycopodiaceae). Voucher Collection Nº 635. Growth form: Prostrate Herb.

292 *Lycopodium clavatum* L. ssp. *contiguum*(Kl.) B. Ollg. (Lycopodiaceae). Voucher Collection Nº 545, 555, 903, 636. Growth form: Erect Herb.

293 *Lycopodium* sp. (Lycopodiaceae). Voucher Collection Nº 463, 804. Growth form: Prostrate Herb.

294 As for Code Nº 292.

295 *Lycopodium* sp. (Lycopodiaceae). Voucher Collection Nº 278. Growth form: Prostrate Herb.

296 *Lycopodium magallanicum* (P. Beauv.) Sw. (Lycopodiaceae). Voucher Collection Nº 315, 517, 1044. Growth form: Prostrate Herb.

297 *Lycopodium* sp. (Lycopodiaceae). Voucher Collection Nº 350, 909, 1054. Growth form: Prostrate Herb.

298 *Epilobium denticulatum* R. & P. (Onagraceae). Voucher Collection Nº 296. Growth form: Erect Herb.

299 *Altensteinia ?fimbriata* H.B.K. (Orchidaceae). Voucher Collection Nº 277, 351, 962, 1068. Growth form: Acaulescent Rosette.

300 *Myrosmodes* sp. (Orchidaceae). Voucher Collection Nº 708, 1024. Growth form: Erect Herb.

301 *Plantago* sp. (Plantaginaceae). Voucher Collection Nº 1010. Growth form: Acaulescent Rosette.

302 *Plantago* sp. (Plantaginaceae). Voucher Collection Nº 978. Growth form: Cushion.

303 *Ranunculus* sp. (Ranunculaceae). Voucher Collection Nº 339, 832, 1020. Growth form: Prostrate Herb.

304 *Ranunculus* sp. (Ranunculaceae). Voucher Collection Nº 283, 710. Growth form: Prostrate Herb.

305 *Arcytophyllum* sp. (Rubiaceae). Voucher Collection Nº 916. Growth form: Cushion.

306 *Arcytophyllum aristatum* Standley (Rubiaceae). Voucher Collection Nº 519. Growth form: Prostrate Shrub.

307 *Arcytophyllum filiforme* (R. & P.) Standley (Rubiaceae). Voucher Collection Nº 496. Growth form: Cushion.

308 *Arcytophyllum vernicosum* Standley (Rubiaceae). Voucher Collection Nº 630, 665. Growth form: Upright Shrub.

309 *Galium* sp. (Rubiaceae). Voucher Collection Nº 1039. Growth form: Trailing Herb.

310 *Relbunium croceum* (R. & P.) Sch. (Rubiaceae). Voucher Collection Nº 806, 983. Growth form: Trailing Herb.

311 *Relbunium hirsutum* (R. & P.) Schum. (Rubiaceae). Voucher Collection Nº 466, 1055. Growth form: Trailing Herb.

312 *Valeriana* sp. (Valerianaceae). Voucher Collection Nº 874. Growth form: Cushion.

313 *Valeriana ? niphobia* Briq. (Valerianaceae). Voucher Collection Nº 870. Growth form: Acaulescent Rosette.

314 *Xyris subulata* R. & P. var. *subulata*(Xyridaceae). Voucher Collection Nº 546, 618, 693. Growth form: Tussock.

315 *Bromus pitensis* H.B.K. (Gramineae). Voucher Collection Nº 797, 895. Growth form: Erect Herb.

316 *Gentianella* sp. (Gentianaceae). Voucher Nº 425 from Ramsay, Evans & Buckland 1989 Collection. Growth form: Erect Herb.

317 As Code Nº 128.

318 *Oreobolus* sp. (Cyperaceae). Voucher Collection Nº 518, 626. Growth form: Cushion.

319 *Carex* sp. (Cyperaceae). Voucher Collection Nº 529. Growth form: Acaulescent Rosette.

320 *Carex* sp. (Cyperaceae). Voucher Collection Nº 358. Growth form: Acaulescent Rosette.

321 *Carex* sp. (Cyperaceae). Voucher Collection Nº 375. Growth form: Acaulescent Rosette.

322 *Carex* sp. (Cyperaceae). Voucher Collection Nº 418. Growth form: Acaulescent Rosette.

323 *Isoëtes* sp. (Isoëtaceae). Voucher not collected. Growth form: Acaulescent Rosette.

324 Not used.

325 Not used.

326 *Viola* sp. (Violaceae). Voucher not collected. Growth form: Prostrate Herb.

327 As for Code Nº 225.

328 *Uncinia* sp. (Cyperaceae). Voucher Collection Nº 349. Growth form: Acaulescent Rosette.

329 *Uncinia* sp. (Cyperaceae). Voucher Collection Nº 386, 800, 1027. Growth form: Acaulescent Rosette.

330 Unidentified species (Family not known). Voucher Collection Nº 681. Growth form: Erect Herb.

331 *Culcitium* sp. (Compositae). Voucher Collection Nº 901. Growth form: Basal Rosette.

332 *Culcitium* sp. (Compositae). Voucher Collection Nº 485. Growth form: Basal Rosette.

333 *Erigeron* sp. (Compositae). Voucher Collection Nº 259. Growth form: Acaulescent Rosette.

334 *Loricaria* sp. (Compositae). Voucher Collection Nº 844. Growth form: Upright Shrub.

335 Unidentified species (Ericaceae). Voucher Collection Nº 281. Growth form: Prostrate Shrub.

336 Unidentified species (Ericaceae). Voucher Collection Nº 552. Growth form: Prostrate Shrub.

337 Unidentified species (Ericaceae). Voucher Collection Nº 666. Growth form: Prostrate Shrub.

338 Unidentified species (Ericaceae). Voucher Collection Nº 667. Growth form: Prostrate Shrub.

339 Unidentified species (Ericaceae). Voucher Collection Nº 678. Growth form: Prostrate Shrub.

340 Unidentified species (Ericaceae). Voucher Collection Nº 828. Growth form: Upright Shrub.

341 Unidentified species (Gramineae). Voucher Collection Nº 528. Growth form: Erect Herb.

342 *Jamesonia* sp. (Hemionitidaceae). Voucher Collection Nº 767, 861. Growth form: Erect Herb.

343 Unidentified species (Juncaceae). Voucher Collection Nº 590. Growth form: Tussock.

344 *Luzula* sp. (Juncaceae). Voucher Collection Nº 1002. Growth form: Acaulescent Rosette.

345 Unidentified species (Orchidaceae). Voucher Collection Nº 1190. Growth form: Erect Herb.

346 *Plantago* sp. (Plantaginaceae). Voucher Collection Nº 274. Growth form: Cushion.

347 *Paspalum* sp. (Gramineae). Voucher Collection Nº 324. Growth form: Prostrate Herb.

348 Unidentified species (Gramineae). Voucher Collection Nº 996. Growth form: Erect Herb.

349 Unidentified species (Gramineae). Voucher Collection Nº 503. Growth form: Erect Herb.

350 *Agrostis* sp. (Gramineae). Voucher Collection Nº 539. Growth form: Erect Herb.

351 *Agrostis* sp. (Gramineae). Voucher Collection Nº 567. Growth form: Erect Herb.

352 *Festuca* sp. (Gramineae). Voucher Collection Nº 1006. Growth form: Erect Herb.

353 *Stipa* sp. (Gramineae). Voucher Collection Nº 1009. Growth form: Tussock.

354 *Relbunium* sp. (Rubiaceae). Voucher not collected. Growth form: Trailing Herb.

355 *Vaccinium* sp. (Ericaceae). Voucher not collected. Growth form: Prostrate Shrub.

356 *Puya* sp. (Bromeliaceae). Voucher not collected. Growth form: Basal Rosette.

357 *Veronica* sp. (Scrophulariaceae). Voucher not collected. Growth form: Erect Herb.

358 *Viola* sp. (Violaceae). Voucher not collected. Growth form: Prostrate Herb.

359 *Oxalis* sp. (Oxalidaceae). Voucher not collected. Growth form: Prostrate Herb.

360 Unidentified species (Family not known). Voucher not collected. Growth form: Erect Herb.

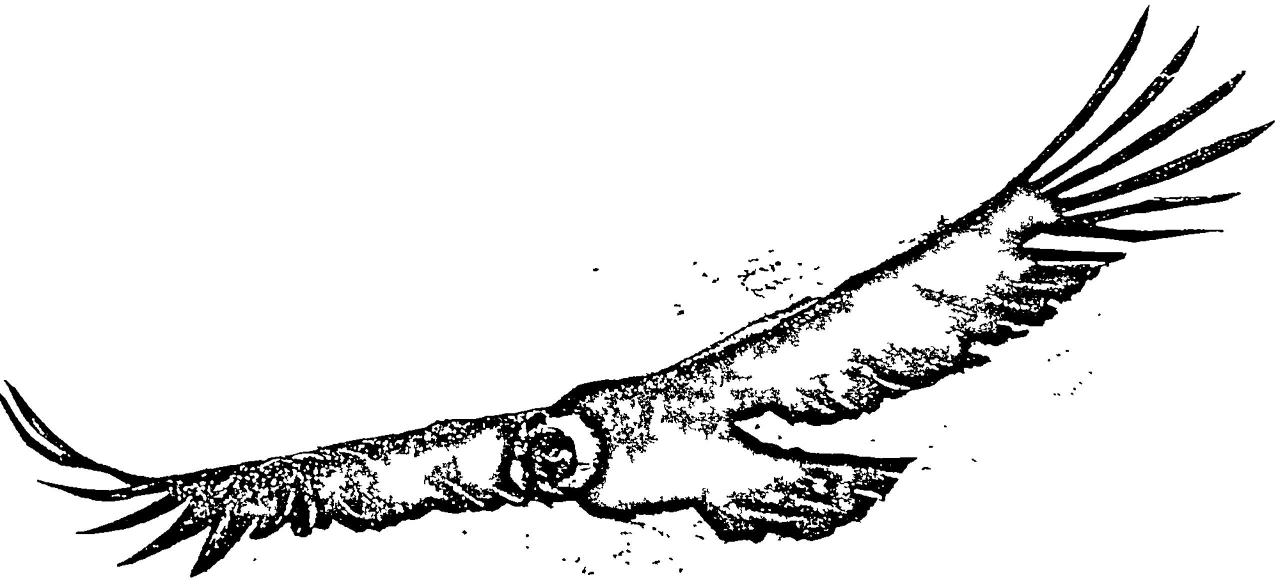
361 *Puya* sp. (Bromeliaceae). Voucher not collected. Growth form: Basal Rosette.

362 Unidentified species (Orchidaceae). Voucher not collected. Growth form: Acaulescent Rosette.

363 Unidentified species (Family not known). Voucher not collected. Growth form: Erect Herb.

Appendix 2.

Example Chi Square Calculation for Transition Probabilities (Chapter 4, p.139)



The χ^2 test will determine the probability that the pattern of replacement observed is completely random. If for each species pair, the species present at time 1 is called the i^{th} species and the species present at time 2 the j^{th} species, then the null hypothesis states that "species i will be replaced by species j in that proportion which the total replacements made by species j contribute to the overall number of changes" or:

$$E_{ij} = \frac{\sum (n_{ir} - n_{ii}) \times (n_{rj} - n_{jj})}{\sum (n_{rj} - n_{jj})}$$

where 'r' represents all species other than i or j, 'n_{ir}' the total number of times species i is followed by all other species, 'n_{ii}' the total number of quadrats occupied by species i at time 1 and time 2, 'n_{rj}' the total number of times species j follows all other species, and 'n_{jj}' the total number of quadrats occupied by species j at time 1 and time 2. Put another way, the expected value is:

$$\mathrm{E_{ij}} = \frac{\begin{array}{c}\text{Total number of quadrats} \\ \text{vacated by } i^{th} \text{ species}\end{array} \times \begin{array}{c}\text{Total number of quadrats} \\ \text{invaded by } j^{th} \text{ species}\end{array}}{\text{Grand Total of All Changes}}$$

provided the diagonal terms (the species replacing themselves) in the matrix are subtracted before making the calculation.

Most of the species involved in the data were rare and to avoid bias in the χ^2 values those species with an expected value less than 5 were not subjected to a χ^2 test. The rarer species were treated as a group to overcome this problem. Yates' correction for continuity was applied.

Using the transition matrix for unburned vegetation at 3,750 m in the Páramo de Daldal given in Table 4.4 (p.149), *Paspalum* sp. replaced *Azorella pedunculata* three times. The total number of quadrats vacated by *Azorella pedunculata* (excluding the diagonal) was 86.75 and the total number of quadrats invaded by Paspalum sp. (excluding the diagonal) was 34. The grand total of all changes (again excluding the diagonals) was 368.75.

Therefore, the expected number of replacements of *Azorella pedunculata* by *Paspalum* sp. is given by:

$$E = \frac{86.75 \times 34}{368.75}$$

$$E = 8.00$$

The Chi Square test requires the following information:

	Azorella pedunculata replaced by *Paspalum* sp.	 Other species	 All Species
Observed	3	83.75	86.75
Expected	8	78.75	86.75

The χ^2 calculation (with Yates' correction applied) is:

$$\chi^2 = \Sigma \frac{(\text{Observed} - \text{Expected} - 0.5)^2}{\text{Expected}}$$

So, for the example given:

$$\chi^2 = \frac{(3 - 8 - 0.5)^2}{8} + \frac{(83.75 - 78.75 - 0.5)^2}{78.75}$$

$$\chi^2 = 3.781 + 0.257$$

$$\chi^2 = \mathbf{4.038}$$

From χ^2 tables, the probability that this result was due to random replacement lies between 0.05 and 0.01. Therefore, the null hypothesis is rejected: *Azorella pedunculata* was replaced by *Paspalum* sp. less frequently than chance would predict.