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Physiological aspects of tillering in barley (Hordeum distichum).

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Physiological Aspects of Tillering in Barley (*Hordeum distichum*)

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SUMMARY

The pattern of production, development and survival of component tillers of spring barley (Hordeum distichum) cv. Triumph was investigated. Tiller appearance followed a well-defined pattern, with the emergence of the main shoot followed by that of primary tillers and by higher order tillers. The earliest emerged tillers survived the longest and contributed the largest percentage to grain yield; many of the higher order tillers died prematurely with those surviving contributing little to the grain yield of the whole plant. Tiller death and suppression of tiller production were coincident with the reproductive phase of main shoot development; some late tillering after anthesis was observed.

The nutritional and hormonal control of tillering was investigated by applying a range of nutrient and plant growth regulator treatments. Pre-tillering applications of the growth retardant, Terpal, rapidly diminished the growth of the main shoot stem, leaves and roots whilst displaying a promotory effect on tillering. Terpal increased the production and early outgrowth of higher order tillers enabling a greater proportion of these to survive and produce ears; this did not result in any overall increase in yield as mean ear size was reduced. Another growth retardant, Cerone, and the auxin-antagonist, TIBA, similarly promoted tillering. The control of apical dominance systems in uniculm and tillering varieties of barley and wheat were compared. Tiller buds were revealed in the leaf axils of young uniculm plants and in barley it was impossible to initiate their outgrowth whereas several treatments, notably Terpal, Cerone and TIBA promoted tiller production in the uniculm wheat plants.

These results are discussed with respect to competition for assimilates/nutrients and the roles of endogenous ethylene, auxin, gibberellins and cytokinins. The possibility of using growth regulators to modify tillering on a commercial scale is discussed and the prospect of seed treatment as a useful method of growth regulator application is also considered.

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CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

In the Gramineae alternately arranged leaf primordia arise in acropetal succession at the apical meristem. Soon after, as a result of meristematic activity in the sub-hypodermal layers of the apex, tiller (lateral, axillary) buds develop in the axil of each leaf on the vegetative plant. Under suitable environmental and internal conditions each tiller bud develops into a tiller of similar morphology and structure to the shoot on which it arises. The tillers themselves also bear buds in their leaf axils and these in turn give rise to tillers. However, only a proportion of tiller buds emerge as tillers, and not all tillers survive to produce ears (Langer, 1963; Jewiss, 1972; Williams et al., 1975; Langer, 1979; Kirby and Appleyard, 1984a). In most higher plants the apical meristem exerts a dominant influence over the growth and development of lateral bud meristems (Sachs and Thimann, 1967; Phillips, 1975) and the degree of this apical dominance may change during development. In cereals and grasses the inhibition of lateral buds tends to be relatively weak during the initial period of vegetative growth but increases greatly during the reproductive phase, especially at the onset of stem elongation (Jewiss, 1972).

Developing buds and emerging elongating tillers are initially dependent on their subtending leaf and parental axis for supplies of raw materials for growth (carbohydrate, organic nitrogen, minerals and water), but as each tiller establishes leaf area and develops nodal roots it will become less dependent on its parental tiller for its nutritional requirements. For example, Quinlan and Sagar (1962) showed that in young wheat (Triticum aestivum) plants, ^{14}C-labelled assimilate was translocated from the main shoot to developing primary tillers, and that this declined with time as the tillers became established. Similar observations have been recorded in young vegetative plants of Lolium perenne (Marshall and Sagar, 1968; Colvill and Marshall, 1981). During the reproductive phase of development the growth of successive stem

internodes and the development of the inflorescence represent major sinks for carbohydrates and minerals and so the availability of materials for tiller development is likely to be reduced. Correspondingly, the production of new tillers is greatly restricted at this time (Bunting and Drennan, 1966) but can be stimulated by removal of the inflorescence or by the addition of nitrogen (Leopold, 1949; Aspinall, 1961, 1963; Bunting and Drennan, 1966). However, the way in which the onset of reproductive growth influences the development of tillers is still a matter of controversy, as hormonal factors as well as increased competition for growth substrates may be centrally involved (Jewiss, 1972; Phillips, 1975; Rubenstein and Nagao, 1976; McIntyre, 1977; Hillman, 1984). The senescence of late-appearing tillers usually begins during the reproductive stage of main shoot development (Rawson, 1971) and as a result many tillers die without producing an ear (Barley and Naidu, 1964; Aufhammer, 1980). Whether such tillers are wasteful of the plant's resources is unclear (Gallagher and Biscoe, 1978; Russelle et al., 1984; Shanahan et al., 1985).

From an economic viewpoint tillering in cereals is important since it aids plant establishment, allows the plant to compensate for low population densities and the effects of pests and diseases, and the tillers themselves make a significant contribution to grain yield (Jewiss, 1972; Isbell and Morgan, 1982). Cereal grain yield can be defined by the following components: number of plants per unit area, number of ear-bearing tillers per plant, number of grains per ear and their mean grain weight (Darwinkel, 1978; Power and Alessi, 1978; Darwinkel, 1979). Tillering is therefore a major yield-determining factor (Friend, 1965) and consequently much attention has been given to the factors influencing the productivity of tillers (Langer, 1963, 1966; Williams, 1970). Such factors are numerous and include light,

temperature, edaphic conditions and resources, sowing rate and chemical applications. The extent to which these factors affect tillering is dependent upon genotype.

It is difficult to separate the effects of environmental factors such as light and temperature in the field as changes in radiation affect temperature. From experiments conducted in controlled environments it is clear that increases in both irradiance and temperature increase tiller production (Ryle, 1964; Friend, 1966). High irradiance increases the levels of available carbohydrate and tiller production is increased relatively more than leaf emergence; that is, a greater proportion of tiller buds grow out reflecting diminished apical dominance (Aspinall and Paleg, 1964). When the temperature is raised leaf emergence and MS development tend to be favoured more than tiller production resulting in increased apical dominance (Friend, 1965, 1966), but nevertheless in absolute terms more tillers are produced as the temperature increases up to around 25°C. Daylength also influences tillering; tiller production is favoured by short days (Leopold, 1949; Ryle, 1966a, 1966b; Langer, 1979). Changes in light quality may also be important in regulating the growth of tiller buds as lateral bud outgrowth is favoured by high red:far red light ratios in tomato (Lycopersicon esculentum) (Tucker, 1977b) and in ryegrass (Lolium perenne and Lolium multiflorum) (Deregibus et al., 1983).

Currently the most direct effect on tillering that can be achieved by the farmer is by the application of nitrogen fertilizer. Nitrogen stimulates the outgrowth of tiller buds (Barley and Naidu, 1964; Spiertz and De Vos, 1983) and increases leaf size (Bunting and Drennan, 1966; Biscoe and Gallagher, 1978). Light interception by the crop may therefore be greatly increased so the assimilate supply to tiller buds may be maximized thus promoting their emergence (Gallagher et al.,

1976a; Gallagher and Biscoe, 1978). The magnitude of this effect is dependent upon the time of N application (Aspinall, 1961; Darwinkel, 1983). For example, to increase tiller production in autumn-sown wheat N fertilizer must be applied before the emergence of the first primary tiller (Fraser et al., 1982). Fraser (1978, in Fraser et al., 1982) found that N applied at floret development had no effect on tiller numbers. Nitrogen fertilizer may also increase tiller survival and yield, by increasing N uptake, tiller leaf area, assimilate production and retention (Power and Alessi, 1978; Fraser et al., 1982).

In general tiller production and survival are inversely related to soil water stress (Langer, 1979). The effects of drought on the growth and yield of field-grown barley (Hordeum spp.) were examined by Legg et al. (1979). The largest effects of drought on yield appeared to be via a reduction in leaf area and hence light interception. In spring wheat, drought during the period of rapid leaf development can reduce the number of fertile tillers (Slavik, 1966).

Another factor which greatly affects tiller production and survival is sowing rate. High seeding rates and subsequently high plant densities restrict tillering; tillering being favoured at low plant densities (Puckeridge and Donald, 1967; Kirby and Faris, 1972; Darwinkel, 1978; Colvill and Marshall, 1981; Fraser et al., 1982). It is considered that some form of interplant competition is operative in reducing tiller number at high density; it is likely that competition is primarily for light since nutrients and water are usually adequately supplied in most studies. Competition begins earlier in denser crops, early competition being expressed by the initiation of fewer tillers and a higher proportion of tiller mortality (Darwinkel, 1978) and by the diminished growth of the MS and ear (Darwinkel, 1979). The ability of sparsely-sown cereals to tiller more freely than densely-sown cereals so that

the total number of shoots per unit area is similar in both cases forms the basis of the phenomenon of yield component compensation. For example, in regions with severe winters many plants may be killed by frost or where plants are destroyed by drought or disease, compensation may be achieved by extensive tillering of the surviving plants (Darwinkel, 1979). Such compensation will not occur to the same extent if seed quality is poor or drilling is uneven (Gallagher and Biscoe, 1978). However, since intraplant competition may become more severe where large numbers of tillers are produced, sowing at low density is unlikely to improve grain yield. High seeding rates usually ensure a high population of dominant MS ears at harvest (Fraser et al., 1982). It is well-known that the yield of the MS surpasses that of tillers (Thorne, 1962; Gallagher et al., 1976a; Power and Alessi, 1978; Darwinkel, 1979). It is for this reason that a plant with a single culm was selected as one of the characters of Donald's (1968) crop ideotype.

Although the effects of various environmental factors on tiller production and survival have been investigated extensively, studies of the part played by hormonal factors in tillering have been neglected. Investigation into hormonal aspects of tillering is particularly difficult in grasses and cereals because of the relative inaccessibility of both the shoot apex (before inflorescence emergence) and tiller buds for experimental manipulation and observation (Langer et al., 1973; Jinks and Marshall, 1982). As such nearly all studies on the hormonal regulation of bud outgrowth have been conducted on dicotyledons, but it seems that there is no reason why these results should not apply also to apical dominance in grasses and cereals. A number of hypotheses have been offered to explain the mechanism of apical dominance in dicotyledonous plants. The earliest, in which there has recently been renewed interest (McIntyre, 1977), proposes that the stem apex inhibits lateral buds by competing with them for a limited

resource supply (carbohydrate, nitrogen and water). This view is known as the "nutritive hypothesis". However, there is much evidence that argues against nutrient availability and supply being the basic mechanism controlling lateral bud growth. For example, it has been shown that the total nutrient content of inhibited buds is no smaller than in buds released from inhibition (Gregory and Veale, 1957) and furthermore that direct applications of nutrients to dormant buds do not release them from inhibition (Goodwin and Cansfield, 1967). Since the discovery of auxin and the demonstration that it could substitute for the stem apex in maintaining bud inhibition (Thimann and Skoog, 1934) much research has concentrated on the action of this growth substance in apical dominance. The "direct inhibitor" hypothesis of apical dominance involves the concept of a direct inhibitor, probably auxin, of lateral bud outgrowth (Thimann and Skoog, 1933). However, this hypothesis has received much criticism (Snow, 1937) and hypotheses in which auxin has a major but indirect influence on buds are now generally preferred. For example, auxin may influence the movement of essential metabolites within the plant (Booth et al., 1962) and so regulate the supply to the buds; this response is known as hormone directed transport (Zeroni and Hall, 1980). Another hypothesis proposes that auxin may deprive buds of nutrients by inhibiting the development of vascular connections with the parent shoot (Gregory and Veale, 1957; Phillips, 1975; McIntyre, 1977). In addition it is now clear that other plant growth substances such as cytokinins, ethylene, gibberellins and abscisic acid (ABA) also exert significant effects on the control of bud outgrowth. Thus, a mechanism of bud inhibition wholly mediated via a direct effect of auxin seems unlikely.

Nevertheless auxin appears to have a primary role in the regulation of tillering in both the vegetative and reproductive phases of growth in grasses and cereals. For example, tillering was stimulated in barley

and teosinte plants in which the apical region was artificially damaged, but when auxin was applied to the damaged apex this was reversed (Leopold, 1949). However, Thorne (1962) and Aspinall (1963) were unable to demonstrate these effects in barley. However, a further line of evidence that points to the importance of auxin in maintaining apical dominance comes from studies using inhibitors of auxin transport such as 2,3,5-triiodobenzoic acid (TIBA). For example, Leopold (1949) found that applications of TIBA to barley were effective in promoting tillering and Jewiss (1972) showed that applications of the auxin antagonist, ACP1 55, to winter wheat resulted in further tillering after inflorescence emergence. Such stimulation of tillering in wheat has also been reported by Langer et al. (1973).

In dicotyledons auxin-induced retardation of lateral buds (Burg and Burg, 1967, 1968; Blake et al., 1983) may be related to the stimulation of ethylene production by indole-3-acetic acid (IAA) (Kang et al., 1971; Evans, 1984). However, Harrison and Kaufman (1982) suggested that IAA-induced ethylene production is not likely to be involved in the maintenance of apical dominance in oat shoots since they found no correlation between ethylene production and lack of tiller bud growth. They further suggested that ethylene may act by promoting the swelling of tiller buds after their release from quiescence or by increasing the sensitivity of tiller buds to kinetin treatment. Applications of ethephon (an ethylene-releaser) have been found to induce axillary bud outgrowth in Phaseolus vulgaris (Yeang and Hillman, 1981) and increase the production of ear-bearing tillers in winter wheat (Hill et al., 1982). In contrast, Burg and Burg (1968) found that continuous application of ethylene to pea (Pisum sativum) plants inhibited lateral bud growth.

Besides auxin, gibberellins are also synthesized in the apex and young

leaves and exported down the stem and as such it has been suggested that gibberellns may have a primary role in maintaining bud inhibition (Phillips, 1975). Increased tiller bud inhibition, reflecting increased apical dominance, has been demonstrated following exogenous applications of gibberellic acid (GA_3) in spring wheat (Jewiss, 1972), in wheat, oat and barley (Johnston and Jeffcoat, 1977) and in sorghum (Sorghum bicolor) (Isbell and Morgan, 1982). However, GA_3 is required for tiller bud growth once buds are released from inhibition (Harrison and Kaufman, 1980).

Abscisic acid (ABA) may also be involved in apical dominance, although it is not thought to play a major role in the control of bud growth (Goodwin and Erwee, 1983). ABA has been implicated in bud dormancy and exogenous applications can inhibit both stem and bud growth in dicotyledons (Bellandi and Dorffling, 1974; Rubenstein and Nagao, 1976) and may inhibit tiller bud release in oat (Harrison and Kaufman, 1980).

In contrast to the above growth substances, applications of cytokinins to leaves, buds and to roots have been found to promote bud outgrowth in grasses and cereals (Langer et al., 1973; Clifford and Langer, 1975; Johnston and Jeffcoat, 1977; Harrison and Kaufman, 1980; Sharif and Dale, 1980a; Isbell and Morgan, 1982). Furthermore, cytokinin application can overcome the inhibitory effects of auxin on lateral buds (Wickson and Thimann, 1958) and of ethylene (Burg and Burg, 1968). It has been proposed that the outgrowth of lateral buds is primarily controlled by both auxin and cytokinins and that the degree of apical dominance is determined by the balance of these two growth substances (Wickson and Thimann, 1958; Sachs and Thimann, 1964; Davies et al., 1966; Leakey et al., 1975; Phillips, 1975; Harrison and Kaufman, 1980; Isbell and Morgan, 1982). The role of all the above mentioned growth substances in the apical dominance phenomenon will be discussed further

in the following chapters.

The use of plant growth regulators (PGRs) to regulate the growth and yield of wheat and barley has assumed an increasingly important role in overall crop management strategy and offers another way in which the farmer can influence tiller productivity. Historically PGRs employed in cereal husbandry have been growth retardants which are applied to prevent lodging thereby allowing the increased use of N fertilizer. The effect of growth retardants is to shorten stem internodes by the inhibition of cell division and cell expansion in the sub-apical region of the stem (Dicks, 1976; Luckwill, 1981). Growth retardants are commonly referred to as antigibberellins since nearly all disrupt the action of endogenous gibberellins; applications of GA_3 can reverse the effects of most growth retardants. There are three ways in which these retardants may exert their effect on endogenous gibberellins: there may be competition for sites of action, inhibition of synthesis, or inactivation (Lang, 1970; Dicks, 1976). There is much direct evidence to show that most retardants are potent inhibitors of gibberellin biosynthesis at various steps in the pathway (Fig. 1.1).

The widely used CCC introduced by Tolbert in 1960, was the first growth retardant to achieve major success on a commercial scale (Garrod, 1982). The chemical name of CCC is 2-chloroethyl trimethylammonium chloride and other names include chlorocholine chloride, chlormequat chloride and Cycocel (Hudson, 1976). The main feature of action of CCC is the inhibition of growth particularly of stem elongation (Bruinsma et al., 1965; Jepson, 1965). This action is probably due to interference by CCC with the biosynthesis of gibberellins in plants (Harada and Lang, 1965; Paleg et al., 1965). GA_3 application can reverse the effects of CCC (Tolbert, 1960; Lockhart, 1962; Bruinsma et al., 1965). There are at least 10 formulations of CCC available

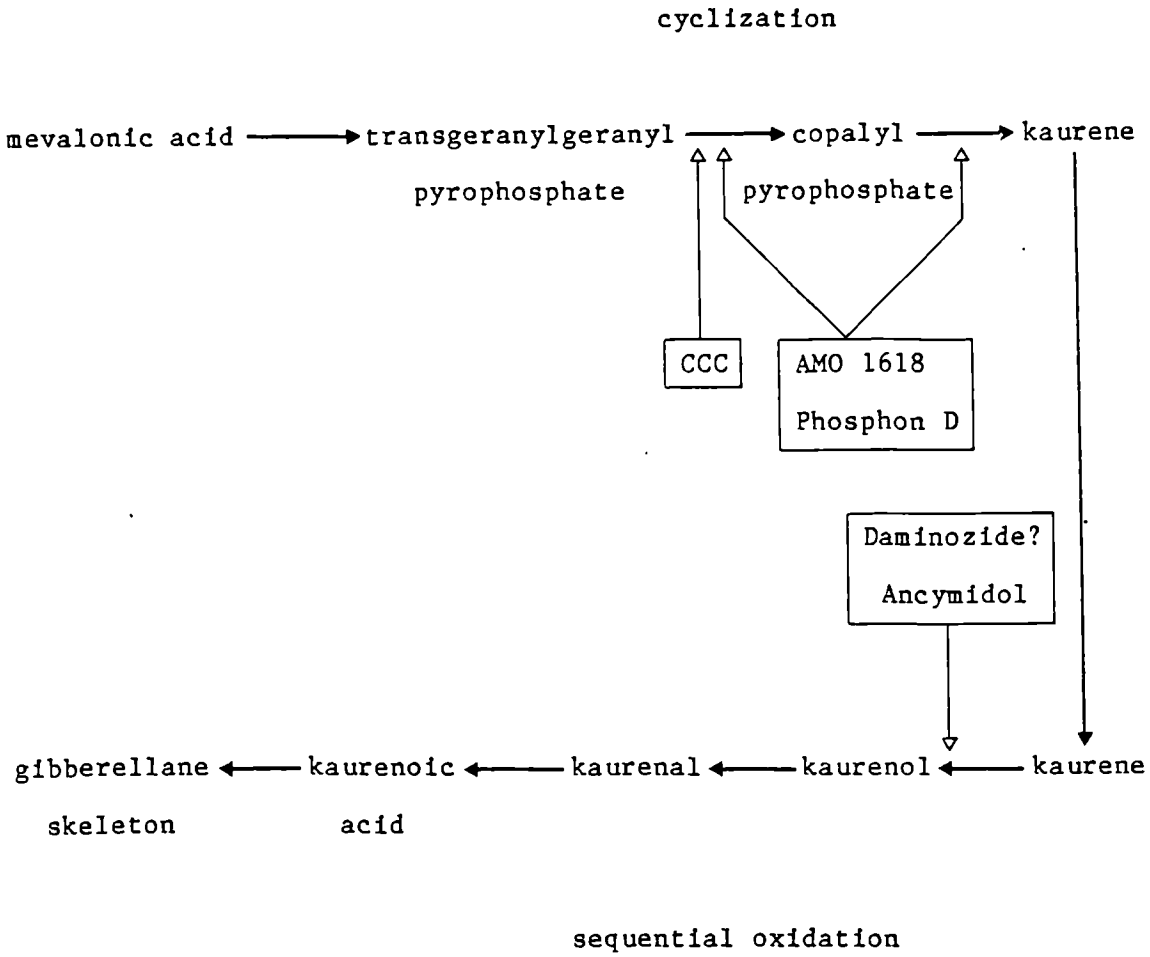


Fig. 1.1 Outline of the gibberellin biosynthetic pathway, showing steps blocked by growth retardants (after Dicks, 1976; Jones and MacMillan, 1984).

commercially for use on cereals to prevent lodging particularly on wheat supplied with high doses of N (Jensen and Andersen, 1981). By decreasing lodging CCC normally promotes an increase in yield (Jepson, 1965). Its effect on barley is less reliable (Humphries, 1968; Garrod, 1982) as CCC moves less readily in this species than in wheat (Lord and Wheeler, 1981). There is, however, a special formulation of CCC available for use on barley, namely Barleyquat B. CCC has a variety of other uses including dwarfing ornamentals and ripening sugar cane (Bruinsma et al., 1965; Garrod, 1982). Other similar chemicals have also been available for 20 years, for example, daminozide (B999, Alar) and AMO 1618 both of which are antagonistic to gibberellin (Child et al., 1983). Mepiquat chloride (1,1-dimethyl-piperidinium chloride; DPC), a more recently produced compound, is currently under experimental use as a cotton growth retardant (Schott and Rittig, 1982; York, 1983a, 1983b) and is thought to also interfere with gibberellin biosynthesis (Chapman et al., 1983).

Another extremely potent growth retardant is Ancymidol (α-cyclopropyl-α-(4 methoxyphenyl)-5-pyrimidine methanol)) which was introduced by Elanco Products in 1971 and has activity on a wide range of plant species including cereals. It is primarily used as a retardant on ornamentals, particularly chrysanthemums and lilies (Garrod, 1982). Ancymidol has recently been shown to have a marked effect on stem elongation in the Gramineae (Hebblethwaite et al., 1980; Jinks and Marshall, 1982). It is known to act by inhibiting GA_3 biosynthesis (Coolbaugh and Hamilton, 1976; Shive and Sisler, 1976; Dicks and Abdel-Kawi, 1979; Isbell and Morgan, 1982). Hebblethwaite et al. (1980) showed that in ryegrass (Lolium perenne) crops grown for seed production the application of Ancymidol increased seed yield by 70%, an effect attributed to the greatly reduced lodging of the crop canopy. The new "anti-gibberellin" retardant, Paclobutrazol (PP333), has

similar general effects on grasses and cereals as Ancymidol. Child et al. (1983) reported that it reduces the extension of the lowest internodes of cereals with less effect on the middle and upper ones. Prevention of lodging, using Paclobutrazol, significantly increased ryegrass seed yields (Hampton et al., 1983; Hampton and Hebblethwaite, 1985) by increasing the number of seeds per spikelet (Hebblethwaite et al., 1982) and by increasing the number of fertile tillers (Hampton and Hebblethwaite, 1985).

One of the most significant introductions of PGRs has been that of ethephon (2-chloroethyl phosphonic acid; Cerone, Ethrel, Cepa), an ethylene-releasing compound. Amchem Products Inc. reported and patented its growth regulatory properties in 1965. Below pH 4.1 ethephon is chemically stable, but on entering plant tissues, which are less acidic, it undergoes a base-catalysed elimination reaction to liberate ethylene into tissues (Yang, 1969; Dicks, 1976; Garrod, 1982). Ethylene has been found to antagonise the action of gibberellins thereby inducing dwarfism (Scott and Leopold, 1967; Valdovinos et al., 1967; Fuchs and Lieberman, 1968), to decrease levels of diffusible auxin (Morgan and Gausman, 1966; Burg and Burg, 1967; Valdovinos et al., 1967; Beyer and Morgan, 1970) and to inhibit longitudinal cell expansion (Lürssen and Konze, 1985). Cerone (Union Carbide) is a formulation of ethephon for use on winter barley to prevent lodging. Ethephon has also been used in mixtures with other growth retardants: Terpal, marketed by BASF in the UK in 1979, for the prevention of lodging in winter barley is the most widely used. It is a mixture of two substances: mepiquat chloride and ethephon in the ratio 2:1. It shortens and stiffens the straw by reducing the length of all stem internodes (BASF advisory pamphlet, 1979).

The use of PGRs to control lodging is therefore well established. In

recent years, however, the introduction of dwarfing genes to current varieties has reduced the need to control lodging with chemicals (Child et al., 1983). As such, research has turned to using PGRs on varieties not susceptible to lodging or on sites where lodging is not a problem; PGR applications have on occasions resulted in yield increases in crops where lodging did not occur (Humphries, 1967). The ability of early applications of growth retardants to influence tiller production and survival has recently been given much attention. In this respect the effects of CCC have been investigated by several workers (Tolbert, 1960; Bruinsma et al., 1965; Humphries, 1967; Jewiss, 1972; Sharif and Dale, 1980b; Hutley-Bull and Schwabe, 1982; Matthews and Thomson, 1984). In particular a greater proportion of tillers produce ears when barley plants exhibit synchronous early emergence of tillers which can result from CCC application (Koranteng, 1981; Koranteng and Matthews, 1982). Application of Ancymidol to sorghum led to the rapid promotion of tiller bud outgrowth (Isbell and Morgan, 1982). Cerone has been found to increase the number of ear-bearing tillers (Hill et al., 1982), and there is some evidence that Terpal also enhances tillering (Jensen and Andersen, 1981). TIBA has also been shown to increase tillering (Jewiss, 1972); there is therefore scope for PGRs other than growth retardants in modifying tiller productivity.

The primary objective of the present thesis was to investigate the pattern of tiller bud emergence, tiller development, survival and yield and their regulation. Fundamental studies of this kind are of practical importance when considering manipulation of grain yield. To obtain a better understanding of the regulation of tillering, modifications to tillering behaviour by PGR treatments were examined. Spring barley (Hordeum distichum) cv. Triumph was mainly used in this study. Triumph, introduced in 1980, is not prone to lodging as it has a short, very stiff straw. Growth retardants, in particular, Terpal, were

nevertheless applied in an attempt to modify tillering pattern. PGRs were generally applied early in this study, before the tillering phase. In contrast, PGRs are conventionally applied late in the life of the crop when many of the plant's morphogenetic features, for example, maximum tiller number, have been determined and little is observed except a reduction in MS growth.

CHAPTER 2

FIELD STUDIES

INTRODUCTION

Most previous studies of field grown cereals have concentrated mainly on crop yield, that is, upon final ear number, grain number per ear and grain size. Relatively few field studies have been concerned with the dynamics of the tiller population. As such, there is little detailed information on the production, growth, longevity and yield of individual tillers. It is considered that an investigation of basic tillering behaviour in crops grown under normal agricultural conditions is fundamental to any understanding of the control of the tillering process. It was with this premise that the following investigation of tillering in the field was undertaken. Some previous studies of tillering under field conditions are those of Cannell (1969a) and Kirby and Faris (1972) on barley, and Darwinkel (1978) and Fraser et al. (1982) on wheat.

A further objective of the present study was to investigate whether any aspect of tillering could be modified by the application of a PGR which might then provide information on the mechanisms governing tillering. PGRs have previously been shown to influence tillering in field grown cereals. For example, early applications of GA_3 and CCC to spring and winter barley (Koranteng, 1981; Matthews et al., 1982) and Cerone to winter wheat (Hill et al., 1982) have been shown to increase the number of ear-bearing tillers and correspondingly result in an increased grain yield. Also applications of mepiquat chloride to spring barley (Cartwright and Waddington, 1982) and various formulations of CCC to winter barley (Williams et al., 1982) have resulted in increased uniformity of ear and grain size as well as increased yields.

Two experiments were conducted; the first, in 1982, provided information on tillering pattern within a spring barley crop. A PGR,

Terpal (BASF), was applied, but there was no obvious modification to growth or development. The second experiment, in 1983, was undertaken to define more specifically the effect of Terpal since it had been found to have profound effects on tillering in spring barley plants grown under glasshouse conditions (Chapter 4).

EXPERIMENTAL

Two field experiments were undertaken at the UCNW farm, Aber, Gwynedd. They were conducted in a field that is routinely used for experiments and trials of a range of spring sown crops. The soil type was a brown-red clay loam of pH 6.5, underlined by an alluvial silt soil. The field had a high stone content and was well drained.

Experiment 2.1

MATERIALS AND METHODS

Six plots, each 10m x 1.2m, were machine sown with spring barley, cv. Triumph, on 25 March, 1982. Each plot was made up of twelve 10m rows. On emergence the plant population was 240 plants m^{-2}, an estimate obtained by quadrat sampling and this corresponds to the normal plant density for field crops of spring barley. The PGR, *Terpal, was applied to 3 of the plots with a knapsack sprayer at the recommended rate for winter barley, that is, 2.5 dm^3 ha^{-1} in 220 dm^3 H_2O ha^{-1} on 5 May, 1982 when the plants were at growth stage (GS) 13 (Zadocks et al., 1974; Tottman and Makepeace, 1979). Fertilizer (72 kg ha^{-1} of P_2O_5 + K_2O) was applied to the seedbed prior to sowing and nitrogen (100 kg ha^{-1} N) was applied immediately after crop emergence. Weeds and diseases were controlled using chemicals applied at the appropriate times. These were Fisons "Springclene" herbicide (Bromoxynil + ioxynil + mecoprop + linuron) applied on 10 May, 1982 at GS 14 and Bayer "Bayleton" fungicide (Triadimefon) applied on 16 June, 1982 at GS 49.

The growth and development of individual plants in each plot was recorded as follows:

a) At the three leaf stage (GS 13) six plants were selected for uniformity from one half of each of the six plots. Plants in the outer

*Terpal contains 46% w/v mepiquat chloride and ethephon in aqueous solution.

two rows of each plot were not selected for study. Each of the 36 selected plants was marked by a small cane with a coloured marker at its tip. This enabled each individual plant to be readily identified in the plot throughout the recording period. Emerging tillers on these plants were ringed with coloured plastic rings, with a different colour identifying the origin of each tiller. Weekly observations were made on the appearance and identity of new tillers, leaf production by the main shoot (MS) and tillers, and on the lifespan of individual leaves and tillers. Only fully expanded leaves were counted, a leaf was classed as fully expanded once its ligule was formed. The degree of leaf senescence was scored on a scale 0 to 3, with 0 representing a fully green leaf and with 1 representing a leaf in which 33% of the area was yellow. A tiller was classed as dying when its newest emerging leaf became yellow and limp, its other leaves were usually green at this time, and a tiller was classed as dead when all of its leaves were yellow or brown.

b) Three plants were sampled at random at weekly intervals from the other half of each plot (but not from the outer two rows). They were transported to the laboratory where observations were made on the growth and development of unemerged tiller buds. The height (measured from ground level to the youngest leaf ligule) of the MS and primary tillers was also recorded together with their dry weights (following oven drying at $60^{o}C$).

c) Final harvest measurements were taken on 11 August, 1982. The 36 marked plants were harvested and the proportion of fertile and infertile tillers recorded. The height of the MS and ear-bearing tillers was measured and the dry weight of individual ears and straw (leaves plus stem) recorded after oven drying. The grain weight and number per ear was also determined for the MS and tillers. In addition

the total grain yield of each plot was obtained following cutting with a combine harvester.

No temperature or rainfall records are available for assessment as the portable automatic recording weather station located in the experimental field was stolen at the time that detailed observations commenced.

Where appropriate results were analysed statistically using analysis of variance, the Student Newman-Keuls test, the Student t test and non-parametric tests following standard procedures (Siegel, 1956; Zar, 1974; Steel and Torrie, 1981). These statistical techniques were also used in the following chapters. Levels of significance are indicated by * or ** representing $p<0.05$ or $p<0.01$ respectively unless otherwise stated.

Tiller nomenclature was the same as that described for wheat and barley by Kirby and Appleyard (1984a) except that the coleoptile tiller was referred to as CT instead of TC. It is usual to designate each tiller by reference to the leaf in the axil of which it occurs. Primary tillers arising from the axils of leaf 1 (L1), L2, L3 and L4 of the main shoot (MS) were described as T1, T2, T3 and T4 respectively. The tiller at the coleoptile node was termed CT. Secondary tillers arising from the prophyll (P) or the axils of L1, L2 and L3 of the primary tillers were described as TnP, Tn,1, Tn,2, and Tn,3 respectively, where n is the primary tiller number. Tertiary tillers were termed according to the leaf of the secondary tiller from which they arose. For example, T1P,1 is the tiller arising from L1 of the prophyll tiller of T1, and T2,1,1 is the tiller arising from L1 of T2,1.

RESULTS

Tillering pattern.

In treated and control plants tillering commenced when the MS had 3 fully expanded leaves, with the emergence of the first primary tiller (T1) from the axil of MS L1, and finally ceased 17 weeks after sowing when all the MS leaves had senesced and grain filling had begun (Fig. 2.1). There was an initial rapid phase of tillering but this declined at the time of ear emergence and by 10 weeks after sowing the production of new tillers had virtually ceased. Dead tillers were also recorded at this time and the death of tillers (mostly non-flowering) continued at a more or less steady rate up to the final harvest. However, after MS anthesis tiller production resumed and this resulted in a second phase of rapid tillering until MS grain filling was well underway (Fig. 2.1). There was no significant effect of Terpal on this overall tillering pattern. The maximum number of live tillers per plant at any one time was about 4.5 and Terpal did not modify this number (Fig. 2.1).

All of the plants produced T1, T2 and T3 tillers and over 65% produced T1P and T2P tillers; T4, other secondary and tertiary tillers were less frequently produced (Fig. 2.2). Nevertheless dissection of buds from the sampled plants showed that all plants produced a T4 bud of healthy appearance and almost 40% of the plants had a tiller bud in the axil of the fifth MS leaf. The buds of the secondary tillers, T1,1 and T2,1, were also evident in all plants. Thus the relatively low frequency of appearance of tillers from these sites (nil for T2,1) was not due to the lack of a viable bud. All buds were observed to commence growth and many reached a length of 10 mm or more before shrivelling and dying in the immediate post-anthesis period, but after the onset of tiller death (Table 2.1). The application of Terpal had very little effect on this overall pattern of bud production and outgrowth.

Fig. 2.1

Effect of Terpal on the mean number of live and dead tillers per plant and total tiller production per plant with time (excluding MS).

○ ● Total tiller number

□ ■ Live " "

△ ▲ Dead " "

Open symbols represent control plants.

Solid symbols represent Terpal treated plants.

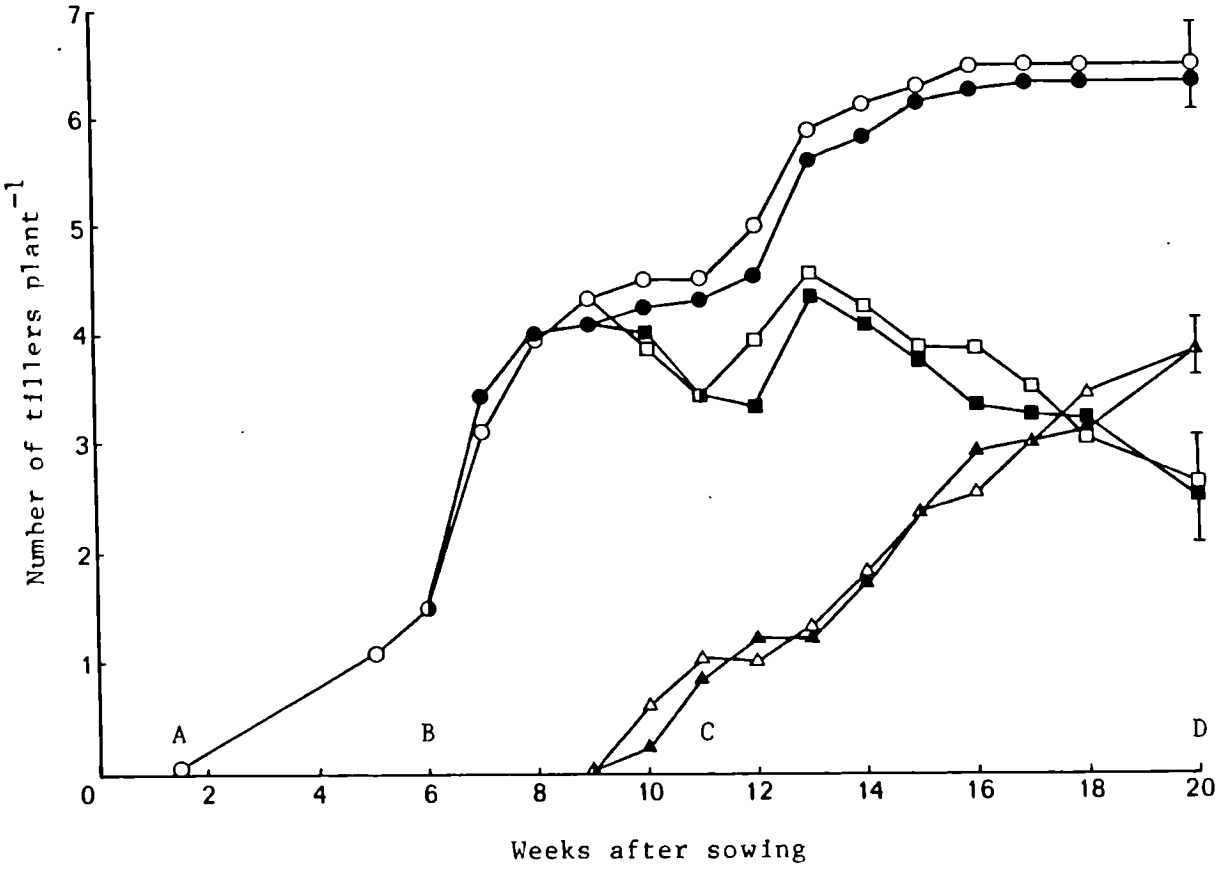
A : Emergence

B : Terpal application

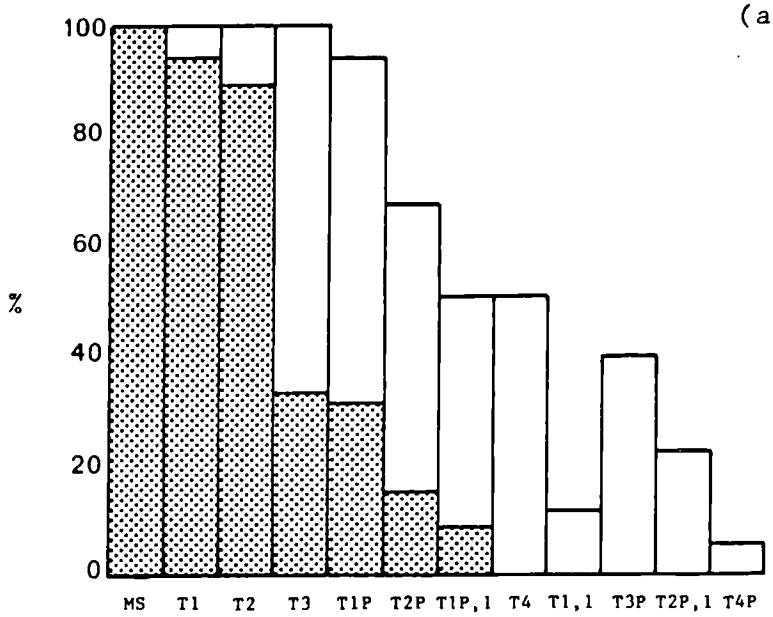
C : MS anthesis

D : Final harvest

Vertical bars represent ±SE.


Number of tillers plant^{-1}
0
1
2
3
4
5
6
7
2
4
6
8
10
12
14
16
18
20
A
B
C
D
Weeks after sowing

(a)


100
80
60
%
40
20
0
MS
T1
T2
T3
T1P
T2P
T1P,1
T4
T1,1
T3P
T2P,1
T4P

(b)

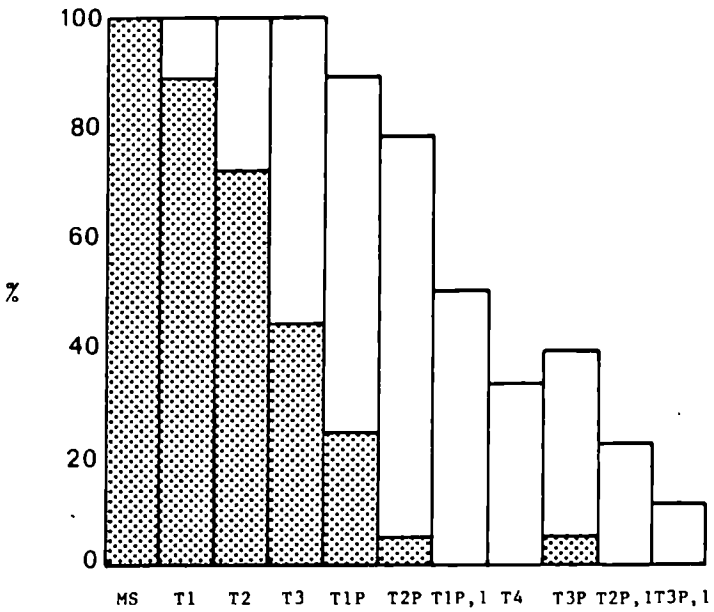

100
80
60
%
40
20
0
MS
T1
T2
T3
T1P
T2P
T1P,1
T4
T3P
T2P,1
T3P,1

Table 2.1 Effect of Terpal on the onset and order of appearance and death of tillers.

Weeks after sowing	Summary of events	Appearance		Death	
		Control	Terpal	Control	Terpal
1					
2	Emergence	MS	MS		
3					
4					
5	Vegetative MS apex	T1	T1		
6	Terpal applied	T2	T2		
7	MS spikelet initiation	T3;T1P	T3;T1P		
8	MS leaf death begins	T2P;T1P,1	T2P;T1P,1		
9	Rapid MS stem elongation				
	Tillering temporarily halted				
10	MS ear emergence				
	Death of non-flowering tillers			T1P;T3	T3;T2P
11	MS anthesis			T1P,1	T1P;T1P,1
12	Grain filling	T4	T4		
13	Bud death begins	T1,1;T3P;	T3P;T2P,1;	T1,1;T4;	T4
		T2P,1	T3P,1	T2P;T3P	
14		T4P		T2P,1	T2P,1;T3P;
					T3P,1
15					
16				T4P	
17					
18					
19					
20	Harvest				

Tillers were produced in a distinct order. The sequence of tiller emergence was the first three primary tillers (T1, T2 and T3) in order with the prophyll tiller of T1 (T1P) apppearing with T3 (Table 2.1). These were immediately followed by T2P and a tertiary tiller T1P,1. Thereafter, there was a period of just over 4 weeks before other tillers appeared (T4 and secondary tillers). During this time some tillers died and these were identified as the most recently produced tillers, that is, a proportion of T3, T1P, and T1P,1 tillers died in their early vegetative phase (Table 2.1). Tillers produced in the second flush of tillering had very short lifespans, for example, T3P tillers appeared in week 13 in control plants and had all died 3 weeks later (Table 2.2). Treatment with Terpal did not greatly affect the order of tiller emergence or death, or the lifespans of tillers.

At the final harvest plants in both treatments had a mean of about 3.5 ears and these were mainly produced by MS, T1, T2 and either T3 or T1P. Terpal did not significantly modify tiller survival or fertility. About half of the tillers produced were infertile (Table 2.3) and the number of component tillers surviving to produce an ear followed a hierarchical sequence. In all of the plants sampled the MS produced an ear and successively less of the later produced tillers survived to ear production (Fig. 2.2).

Leaf production and survival.

The MS produced a total of about 9 leaves and leaf senescence began 8 weeks after sowing when the MS had produced 6 fully expanded leaves (Fig. 2.3). The order of leaf death was the same as the order of leaf production with L1 senescing first. Leaf senescence temporarily halted at anthesis for approximately 2 weeks as grain filling commenced (Fig. 2.3). This increased the lifespan of those leaves that senesced during

Table 2.2 Effect of Terpal on the lifespan of individual tillers ±SE.

Tiller (in order of appearance)	Lifespan (weeks)	
	Control	Terpal
MS	18.0±0.00	18.0±0.00
T1	14.7±0.33	14.4±0.42
T2	13.2±0.54	12.8±0.54
T3	8.9±1.02	9.4±1.12
T1P	7.3±1.20	8.3±1.10
T2P	10.4±0.83	9.6±1.07
T1P,1	7.9±1.60	6.4±1.20
T4	4.7±0.92	3.2±1.20
T1,1	1.0±0.00	
T3P	3.0±1.04	3.3±0.97
T2P,1	3.2±1.20	3.0±1.30
T4P	2.0±0.00	
T3P,1		2.0±1.00

Table 2.3 Effect of Terpal on the mean tiller number per plant (including MS) at final harvest ±SE.

Tillers	Control	Terpal
Ear-bearing	3.61±0.26	3.50±0.27
Infertile	3.83±0.39	3.83±0.29
Total	7.44±0.43	7.33±0.29

Fig. 2.3

Effect of Terpal on the mean number of MS and T1 leaves per plant (solid lines) and on the mean number of senesced or partially senesced leaves per plant (dotted lines).

○ ● MS

△ ▲ T1

Open symbols represent control plants.

Solid symbols represent Terpal treated plants.

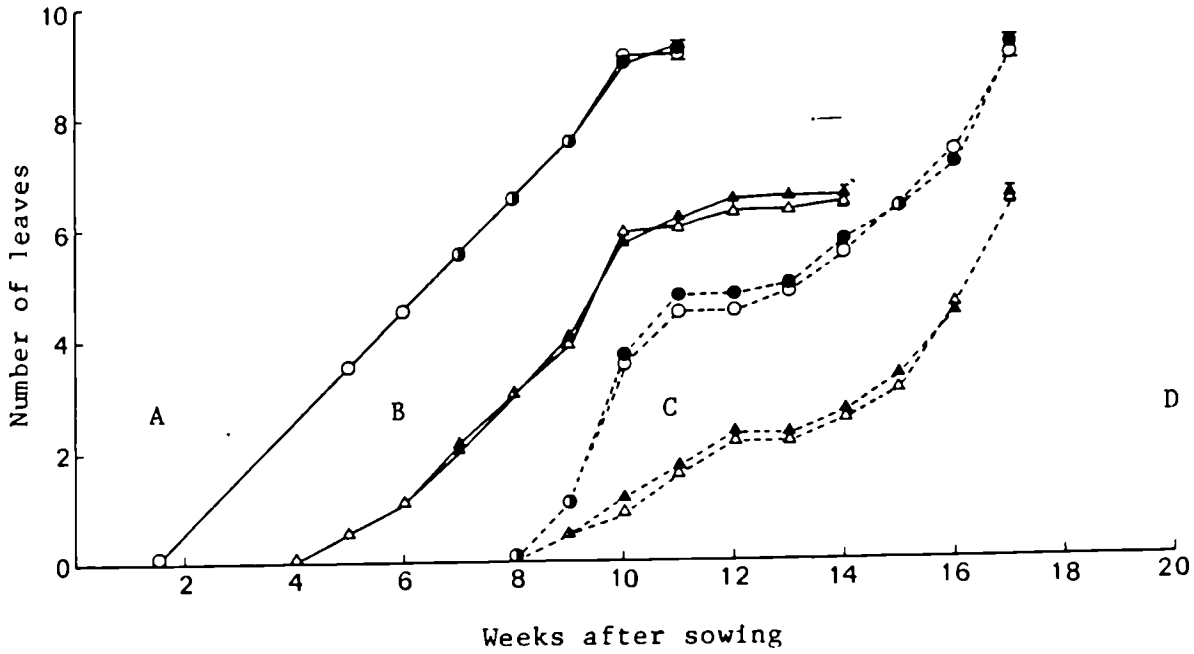
A : Emergence

B : Terpal application

C : MS anthesis

D : Final harvest

Vertical bars represent ±SE.


Number of leaves
Weeks after sowing
A
B
C
D
0
2
4
6
8
10
12
14
16
18
20

grain filling, these were leaves 5 to 9 and 3 to 6 for the MS and T1 respectively. Leaf lifespans of Terpal treated plants are not presented since they differed little from those of control plants (Table 2.4). The period when MS leaf senescence stopped corresponds to the time of increased tillering and decreased tiller mortality (Fig. 2.1). The number of leaves per tiller was related to the time of tiller appearance, the earliest produced tiller, that is, T1, having the highest number of leaves and the later appearing tillers having the least (Table 2.5). Terpal did not significantly modify MS, or tiller, leaf production or senescence.

Stem and ear growth.

Maximum MS height was reached at anthesis, 11 weeks after sowing. By this time the Terpal treated plants were significantly shorter (at $p<0.01$ level) than the control plants (Fig. 2.4). In control plants the height of the MS, T1, T2 and T3 followed a hierarchical sequence related to the order of emergence (Fig. 2.5). Terpal had the effect of reducing this hierarchy slightly, by decreasing the height of the MS and increasing the heights of the other tillers (Fig. 2.5). By the time of the final harvest, differences in the heights of the MS and tillers in control plants were significantly ($p<0.05$) greater than those in Terpal treated plants.

The maximum length of the MS, T1, T2 and T3 inflorescence was also reached by week 11. There was a hierarchical pattern of development with the MS having the largest ear and T3 the smallest (Table 2.6). The Terpal results are not presented as they were not significantly different from those of control plants.

Dry weight and final yield.

There was a hierarchical distribution of dry weight between shoots of

Table 2.4 The mean lifespan of individual leaves of the MS and T1 ±SE.

Leaf number (in order of emergence)	Lifespan (weeks)	
	MS	T1
1	6.5±0.23	4.0±0.17
2	5.9±0.11	4.7±0.22
3	5.6±0.18	6.7±0.29
4	4.9±0.11	6.6±0.29
5	6.6±0.17	6.7±0.17
6	6.9±0.11	6.2±0.11
7	7.3±0.15	
8	7.0±0.17	
9	6.9±0.11	

Table 2.5 Effect of Terpal on mean total leaf production per tiller ±SE.

Tiller (in order of appearance)	Control	Terpal
MS	9.1±0.13	9.2±0.10
T1	6.5±0.20	6.5±0.23
T2	6.0±0.30	5.9±0.21
T3	2.8±0.41	3.5±0.58
T1P	2.1±0.22	2.5±0.36
T2P	1.8±0.48	1.8±0.75
T1P,1	1.0±0.00	1.0±0.00
T4	1.8±0.48	1.4±0.25
T1,1	1.0±0.00	
T3P	1.2±0.20	1.4±0.27
T2P,1	1.0±0.00	1.0±0.00
T4P	1.0±0.00	
T3P,1		2.0±1.00

Fig. 2.4

Effect of Terpal on the mean height of the MS with time.

○ Control

● Terpal treated plants

A : Emergence

B : Terpal application

C : MS anthesis

D : Final harvest

Vertical bars represent ±SE.

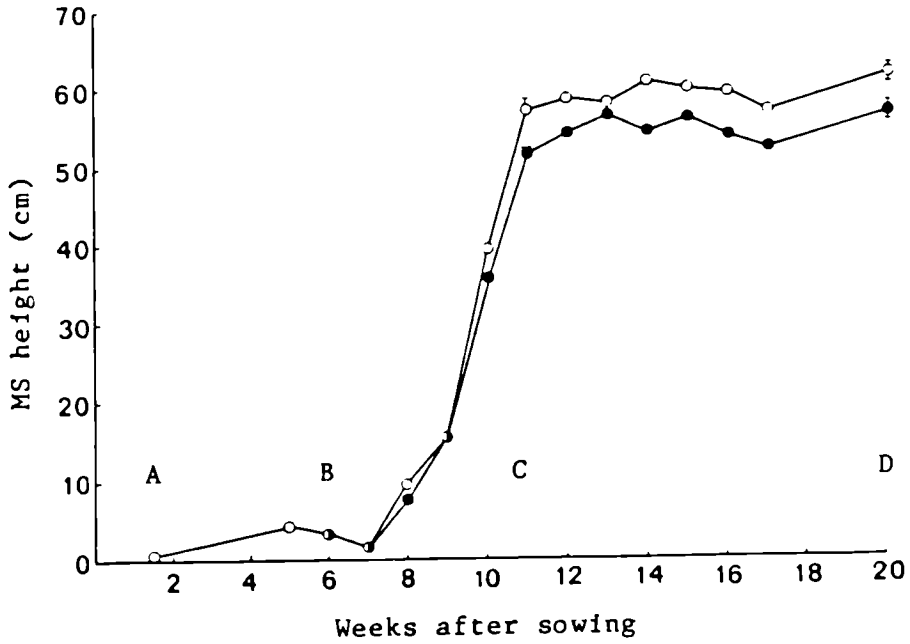

70
60
50
40
30
20
10
0
MS height (cm)
A
B
C
D
2
4
6
8
10
12
14
16
18
20
Weeks after sowing

Fig. 2.5

Effect of Terpal on the mean height of the MS and individual tillers with time.

Control plants

Terpal treated plants

(a) 9 weeks after sowing

(b) 11 " "

(c) 13 " "

(d) 15 " "

(e) 20 " "

Identity of each block as in (e).

Vertical bars represent ±SE.

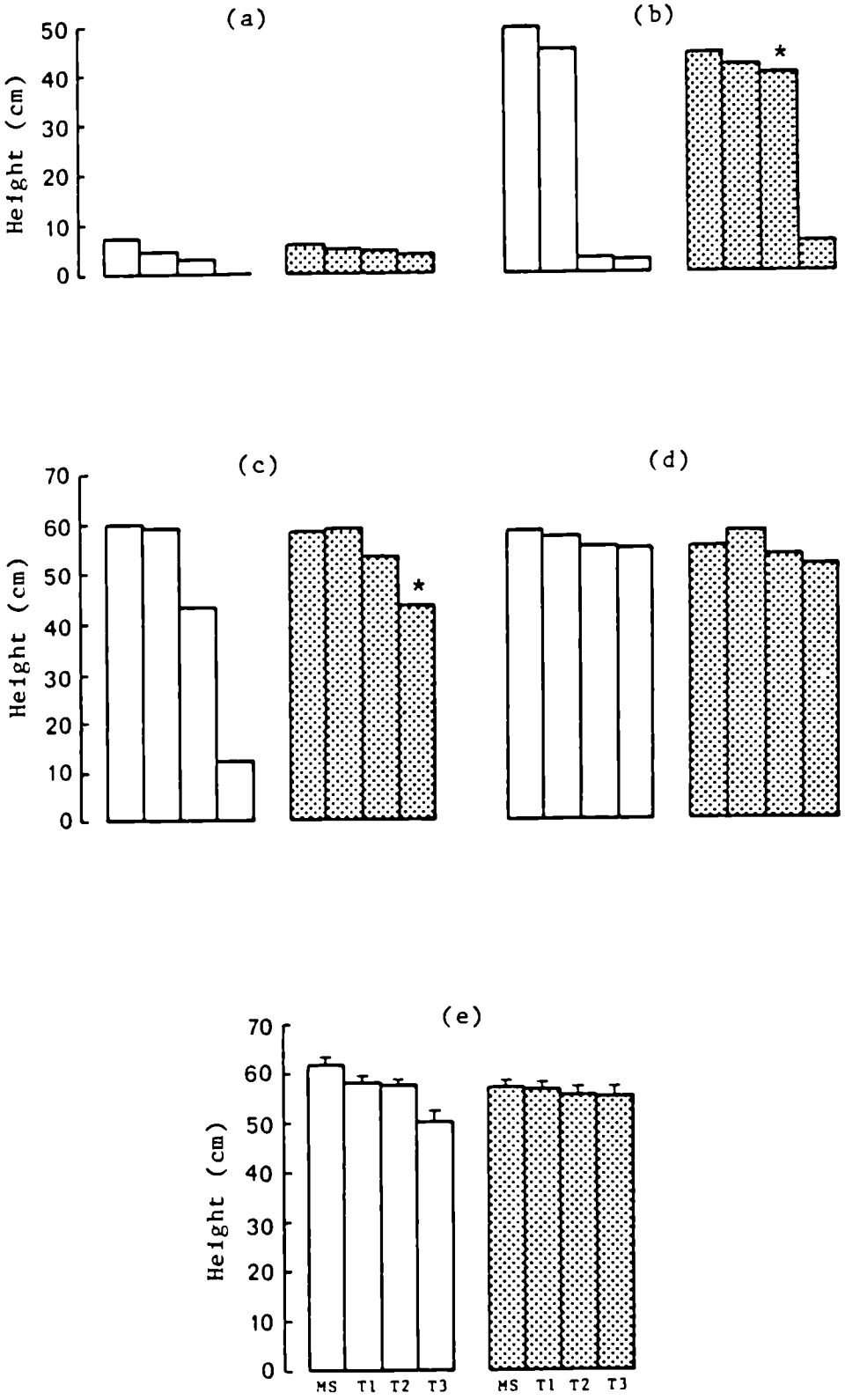

(a)
(b)
(c)
(d)
(e)
Height (cm)
0
10
20
30
40
50
60
70
*
MS
T1
T2
T3

Table 2.6 Mean length (mm) of MS, T1, T2 and T3 inflorescence with time ±SE.

Weeks after sowing	Tiller			
	MS	T1	T2	T3
9	11.1±0.5	7.5±0.6	5.1±0.7	<2.0
10	72.2±6.3	62.4±5.6	42.4±7.7	7.9±3.1
11	85.0±2.6	78.1±3.9	73.3±3.4	67.0±7.6

Table 2.7 Effect of Terpal on mean total shoot dry weight (g) per plant with time ±SE.

Weeks after sowing	Control	Terpal
9	0.845±0.15	1.031±0.11
11	2.939±0.48	3.085±0.27
13	3.555±0.50	4.482±0.48
15	4.484±0.33	5.340±0.96
17	6.612±0.72	5.510±0.61
20	7.464±0.72	7.712±0.87

individual plants, related as before, to the order of tiller emergence (Fig. 2.6). Terpal reduced this pattern by increasing the weight of T2 and T3, although overall this effect was not statistically significant. The dry weight of the MS remained little affected until final harvest when it was significantly ($p<0.05$) reduced by Terpal treatment compared with control plants (Fig. 2.6). Terpal treatment did not significantly modify the total dry weight of the MS and tillers per plant (Table 2.7).

At the final harvest it was evident that the hierarchical distribution of dry weight was altered by the Terpal treatment. The weights of MS, T1 and T2 were reduced whilst that of T3 and T1P were increased (Fig. 2.6e and 2.7). This was particularly evident for the weight of the ear although only the effects of Terpal on MS and T3 were significant ($p<0.01$ and $p<0.05$ respectively). Overall there was a more even distribution of dry matter between the ear-bearing tillers of the plant and this was reflected also by the percentage contribution to final dry matter yield of the various tillers (Table 2.8). Terpal also significantly ($p<0.01$) reduced the grain weight per ear of the MS and significantly ($p<0.05$) increased that of T3 (Table 2.9). The weight of grain represented almost 90% (89.4 $\pm$ 0.5%) of the total ear weight and this was constant between the tillers and the treatments. Despite the above changes there was no significant effect of Terpal on the number of grains per ear (Table 2.9).

The total dry weight of the ears, straw and whole plant and the harvest index were not modified by treatment with Terpal (Table 2.10). Similarly the total grain yield per plot obtained by combine harvester was not significantly different between the control and Terpal treated plots (mean value = 713 $\pm$ 22.9 g m^{-2}).

Fig. 2.6

Effect of Terpal on the mean dry weight of the MS and individual tillers with time.


Control plants


Terpal treated plants

(a) 9 weeks after sowing

(b) 11 " "

(c) 13 " "

(d) 15 " "

(e) 20 " "

Identity of each block as in (e).

Vertical bars represent ±SE.

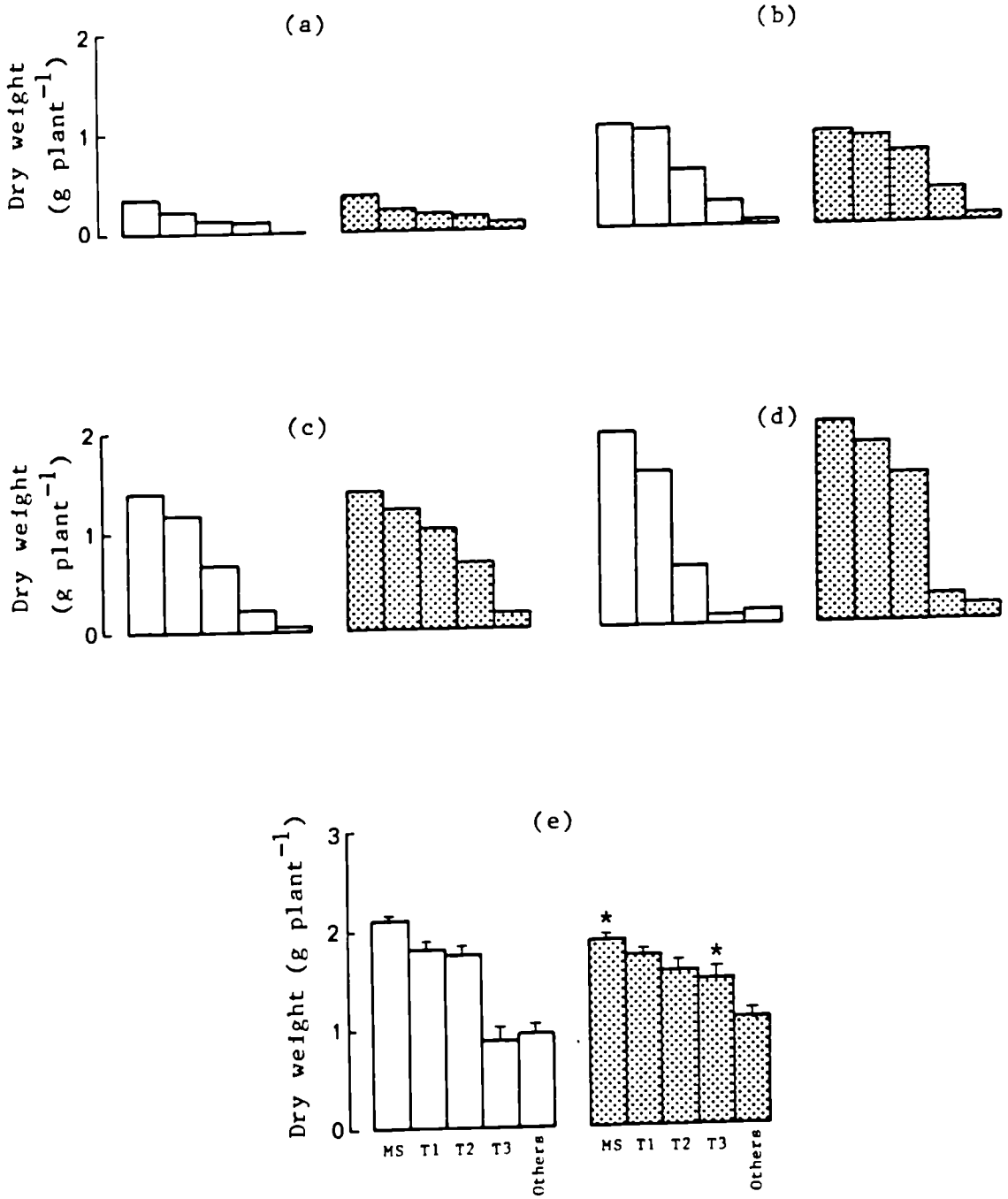

(a)
(b)
(c)
(d)
(e)
Dry weight (g plant^{-1})
0
1
2
3
MS
T1
T2
T3
Others
*
*

Fig. 2.7

Effect of Terpal on the dry weight distribution between the MS and tillers at final grain harvest.

Control plants

Terpal treated plants

(a) Ear dry weight.

(b) Straw, and intertile tiller dry weight.

Vertical bars represent ±SE.

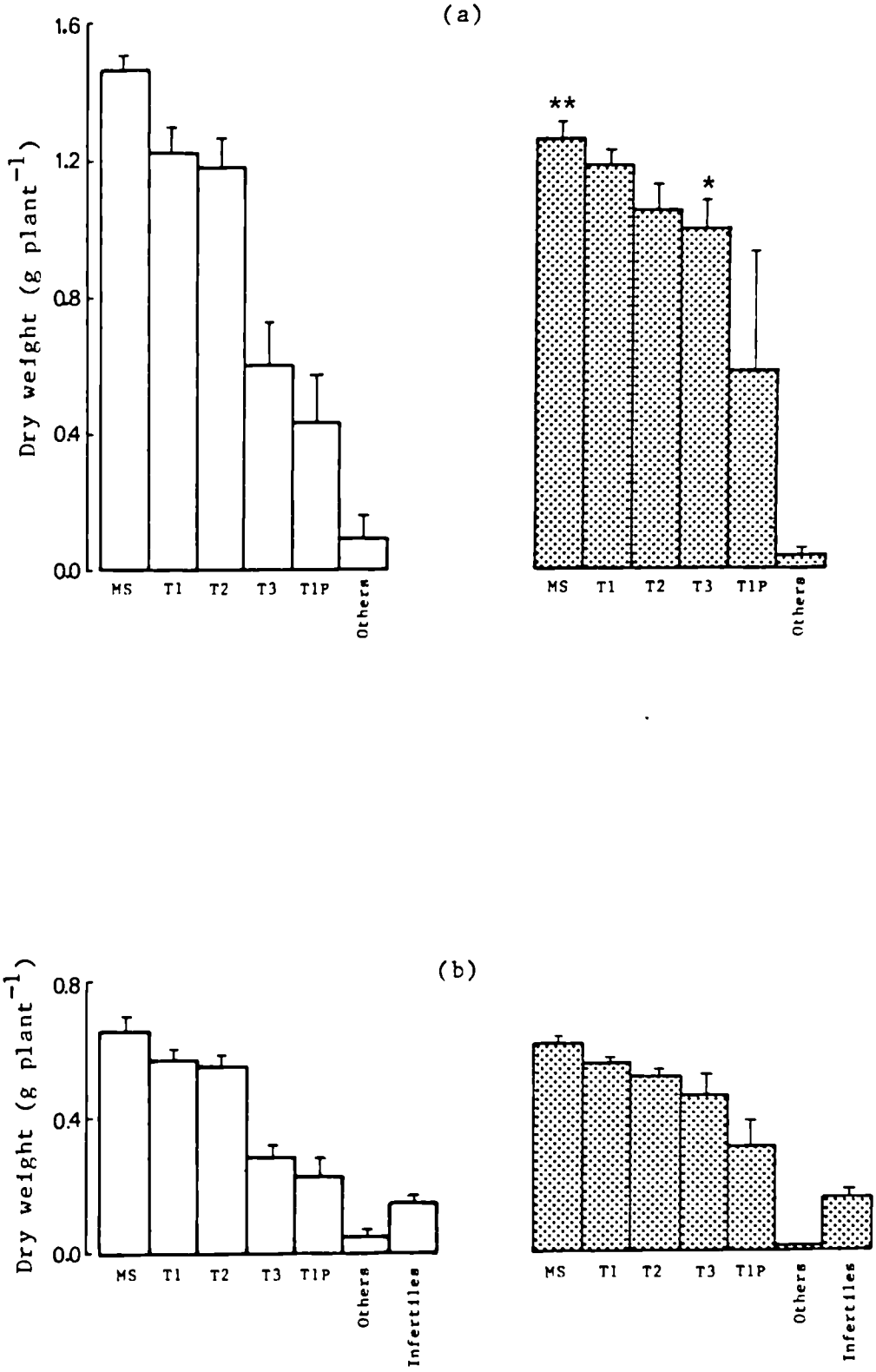

(a)
Dry weight (g plant^{-1})
1.6
1.2
0.8
0.4
0.0
MS
T1
T2
T3
T1P
Others
**
*
(b)
Dry weight (g plant^{-1})
0.8
0.4
0.0
MS
T1
T2
T3
T1P
Others
Infertiles

Table 2.8 Effect of Terpal on the mean percentage contribution of component tillers to final dry matter yield.

Tiller	Control	Terpal
MS	28.3	24.2
T1	24.0	22.4
T2	23.2	20.2
T3	11.8	19.1
T1P	8.7	11.5
Others	1.9	0.6
Infertile	2.1	2.0

Table 2.9 Effect of Terpal on mean total grain weight (g) per ear and number of grains per ear of the MS and individual tillers ±SE.

Tiller	Grain weight		Number of grains	
	Control	Terpal	Control	Terpal
MS	1.31±0.03	1.13±0.04**	25.7±0.3	24.6±0.5
T1	1.10±0.06	1.05±0.03	22.6±0.7	23.1±0.6
T2	1.04±0.09	0.95±0.05	22.0±1.0	20.8±1.1
T3	0.45±0.14	0.97±0.10*	14.3±2.1	16.5±3.3
T1P	0.39±0.16	0.61±0.26	10.2±2.8	12.8±4.0

Table 2.10 Effect of Terpal on the mean total dry weight (g) of ears, straw and whole plant, and on harvest index per individual plant at final harvest ±SE.

	Ear weight	Straw weight	Total weight	Harvest index
Control	4.981±0.41	2.483±0.28	7.464±0.72	0.56
Terpal	5.089±0.57	2.623±0.33	7.712±0.87	0.55

Experiment 2.2

MATERIALS AND METHODS

This experiment was essentially a repetition of Experiment 2.1. It was conducted at the same site and was managed in a similar way. Four 10m x 1.2m plots of spring barley, cv. Triumph, were sown on 18 April, 1983. On emergence (3 May, 1983) the plant population was 200 plants m^{-2}, this was somewhat lower than in the previous experiment. Terpal was applied using a calibrated knapsack sprayer at the recommended rate of 2.5 dm^3 ha^{-1} on 10 June, 1983 at GS 15. Terpal was applied later in this experiment than in the previous experiment due to the adverse weather conditions in the early summer. Fertilizer, consisting of 150 kg N ha^{-1} and 80 kg of P and K ha^{-1}, was applied after emergence. Fisons "Springclene" herbicide was applied on 25 May, 1983 at GS 13 and Bayer "Bayleton" fungicide on 13 July, 1983 at GS 59.

As in 1982, six plants from one half of each plot were continuously recorded and weekly measurements were taken of the appearance and identity of tillers, and their survival. Plants were also sampled weekly from the remaining half of each plot (6 per plot). The heights and dry weights of the MS and all tillers of these plants were recorded. At the final harvest three 0.1 m^2 samples of ears per plot were taken by hand for grain yield analysis. Grain yield per plot was obtained by combine harvester.

A detailed record of temperature and rainfall was obtained throughout the duration of the experiment from the UCNW farm weather station and this is included in the Appendix.

RESULTS

There was much more evidence from the results obtained in this experiment that the pattern of tillering and final yield had been modified by the use of the growth regulator, Terpal. Correspondingly the results presented here illustrate this modification to growth; the dynamics of the tiller population are not considered in detail as they were essentially the same as in the previous experiment.

Tillering pattern.

The overall pattern of tillering was the same as in the previous experiment with tiller production beginning at GS 13, when the MS had 3 fully expanded leaves, ceasing around the final stages of MS elongation and then continuing after anthesis (Fig. 2.8). The latter phase was less marked than that observed in the previous year (Fig. 2.1). However, in this experiment tillering increased rapidly immediately after the application of Terpal (week 8) and a significantly ($p<0.01$) higher number of tillers was maintained until final harvest when Terpal treated plants had a mean of 1.6 more tillers than control plants (Fig. 2.8). This increase was due to the emergence of a higher number of T3 and secondary tillers (Fig. 2.9). In contrast to the previous year no T4 tillers emerged in this experiment. The order of appearance and subsequent death of tillers was essentially the same as in the previous experiment. The onset of death of non-flowering tillers was one week earlier in control plants compared to Terpal treated plants (Fig. 2.8). By final harvest it was clear that Terpal had significantly ($p<0.01$) increased tiller survival, in the Terpal treated plants 76% of tillers survived to produce ears compared to 63% in control plants (Table 2.11). The additional tillers that survived to produce ears were T3 and secondary tillers, particularly T1P and T2P (Fig. 2.9). These tillers had a longer lifespan in the Terpal treated plants (Table 2.12) since they emerged earlier. Generally tillers with lifespans of four or less

Fig. 2.8

Effect of Terpal on the mean total tiller number per plant and the mean number of dead tillers per plant with time (excluding MS).

○ ● Total tiller number.

△ ▲ Dead " "

Open symbols represent control plants.

Solid symbols represent Terpal treated plants.

A : Emergence

B : Terpal application

C : MS anthesis

D : Final harvest

Vertical bars represent ±SE.

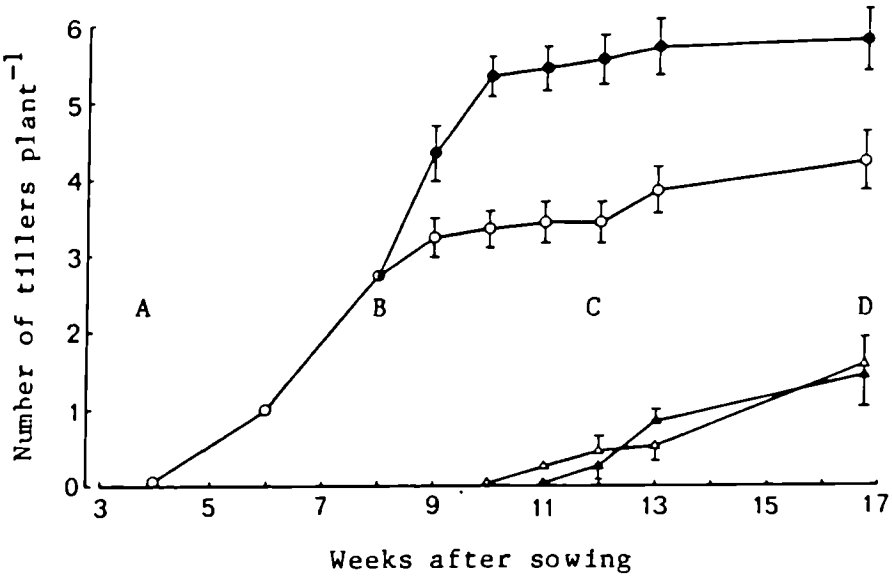
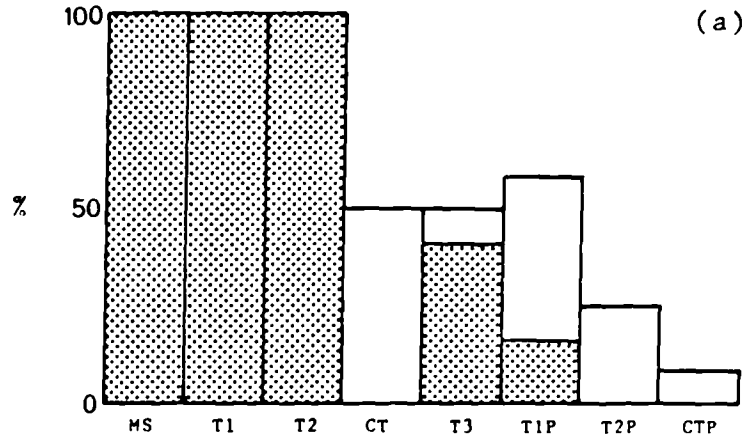

Number of tillers plant^{-1}
0
1
2
3
4
5
6
A
B
C
D
3
5
7
9
11
13
15
17
Weeks after sowing

Fig. 2.9

Effect of Terpal on the percentage representation of shoots in a population of plants (n=12) in order of appearance. Shading represents the percentage of tillers that produced ears at final harvest.

(a) Control plants.

(b) Terpal treated plants.


(a)
100
%
50
0
MS
T1
T2
CT
T3
T1P
T2P
CTP

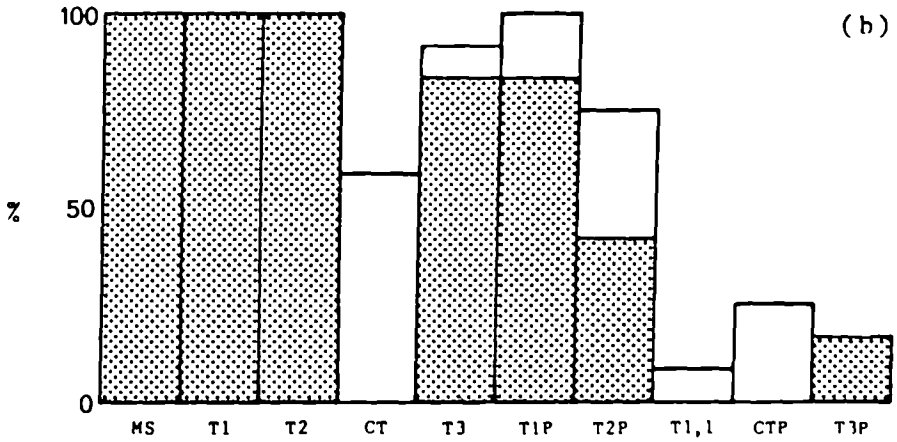

(b)
100
%
50
0
MS
T1
T2
CT
T3
T1P
T2P
T1,1
CTP
T3P

Table 2.11 Effect of Terpal on the mean number of ear-bearing and infertile tillers per plant (excluding MS) at final grain harvest ±SE.

Tillers	Control	Terpal	
Ear-bearing	2.67±0.19	4.42±0.26	**
Infertile	1.58±0.36	1.42±0.36	
Total	4.25±0.39	5.84±0.39	*

Table 2.12 Effect of Terpal on the mean lifespan of individual tiller ±SE.

	Lifespan (weeks)		
Tillers	Control	Terpal	
MS	14.0±0.00	14.0±0.00	
T1	9.4±0.52	10.0±0.00	
CT	6.7±0.80	4.1±0.75	*
T2	9.0±0.00	9.0±0.00	
T3	6.0±0.66	6.8±0.27	
T1P	5.1±0.51	6.5±0.17	*
T2P	1.5±0.50	5.5±0.44	**
T1,1		3.5±1.04	
CTP		2.0±0.42	
T3P		2.0±0.58	

weeks failed to survive to ear production (Table 2.12).

Stem growth.

Maximum MS height was attained by week 13, one week after anthesis. Terpal significantly ($p<0.05$) reduced the height of the MS by week 10 (Fig. 2.10a). By week 13 Terpal had also modified the hierarchical pattern of shoot growth by significantly ($p<0.05$) decreasing the heights of MS and T1 and by increasing the heights of T3 and T1P; this latter effect was not statistically significant (Fig. 2.10b).

Dry weight and final yield.

One week after anthesis the dry weights of MS, T1 and T2 were little affected by Terpal but the weights of T3, T1P and of the remaining secondary tillers collectively were increased resulting in a more even distribution of dry weight between the various shoots (Fig. 2.11a). Only the effects of Terpal on T3 and the secondary tiller group were significant ($p<0.01$). Total plant dry weight was significantly ($p<0.01$) greater in the Terpal treated plants due to the higher number of tillers produced (Fig. 2.11b).

At the final harvest it was again evident that the Terpal treatment had caused a more even distribution of dry weight between the ear-bearing tillers (Fig. 2.12). The ear and straw weights of MS, T1 and T2 were little affected, but the ear and straw weights of T3, T1P and other tillers were markedly increased (Fig. 2.12). Despite these changes there was little effect of Terpal on grain number per ear except for T1P where grain number was significantly ($p<0.05$) increased by the Terpal treatment (Table 2.13). In contrast to the previous year the total dry weight of ears and straw per plant was significantly increased by Terpal treatment, although the harvest index was not affected (Table 2.14).

Fig. 2.10

Effect of Terpal on the mean height of:

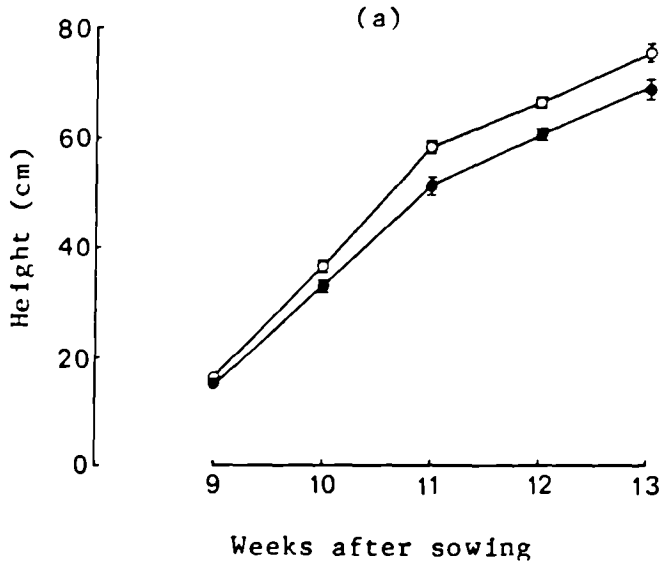
(a) MS with time.

○ Control plants.

● Terpal treated plants.

(b) MS and individual tillers at 13 weeks after sowing (start of grain filling).

Vertical bars represent ±SE.


(a)
80
60
40
20
0
Height (cm)
9
10
11
12
13
Weeks after sowing

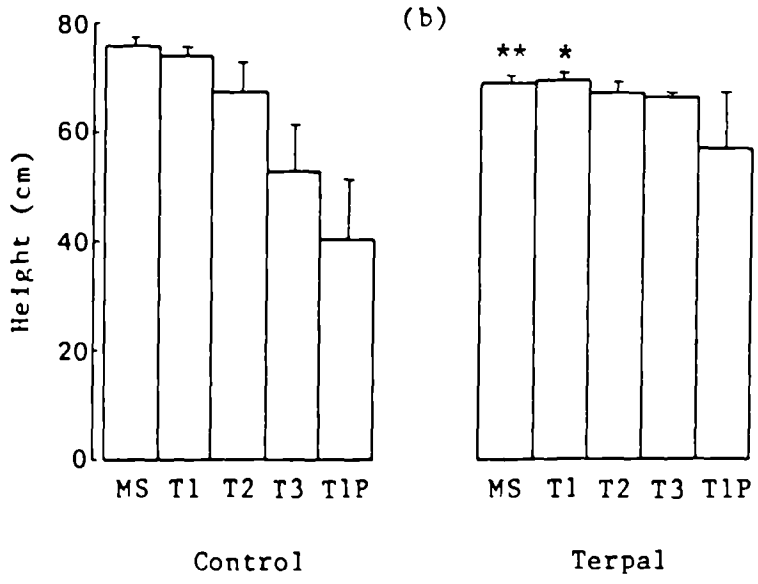

(b)
80
60
40
20
0
Height (cm)
**
*
MS T1 T2 T3 T1P
MS T1 T2 T3 T1P
Control
Terpal

Fig. 2.11

Effect of Terpal on the mean dry weight of:

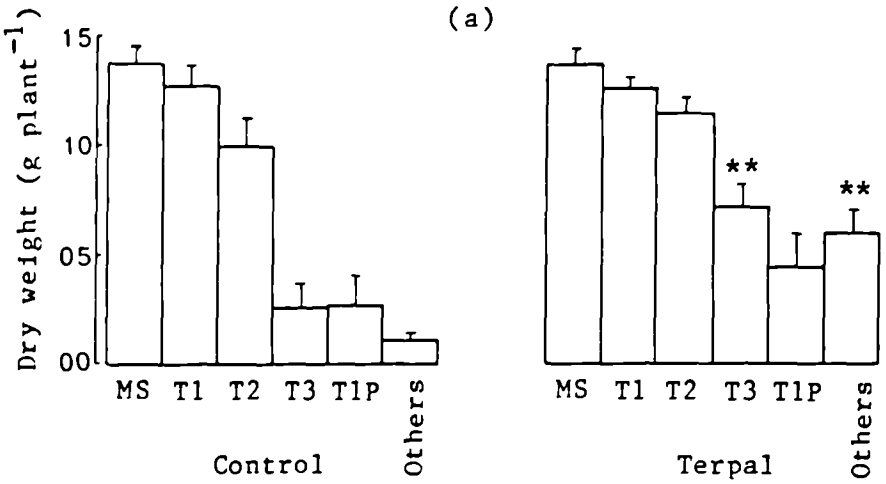
(a) MS and individual tillers at 13 weeks after sowing (start of grain filling).

(b) Total plant.

○ Control plants.

● Terpal treated plants.

Vertical bars represent ±SE.


(a)
Dry weight (g plant^{-1})
15
10
05
00
MS T1 T2 T3 T1P Others
Control
**
**
MS T1 T2 T3 T1P Others
Terpal

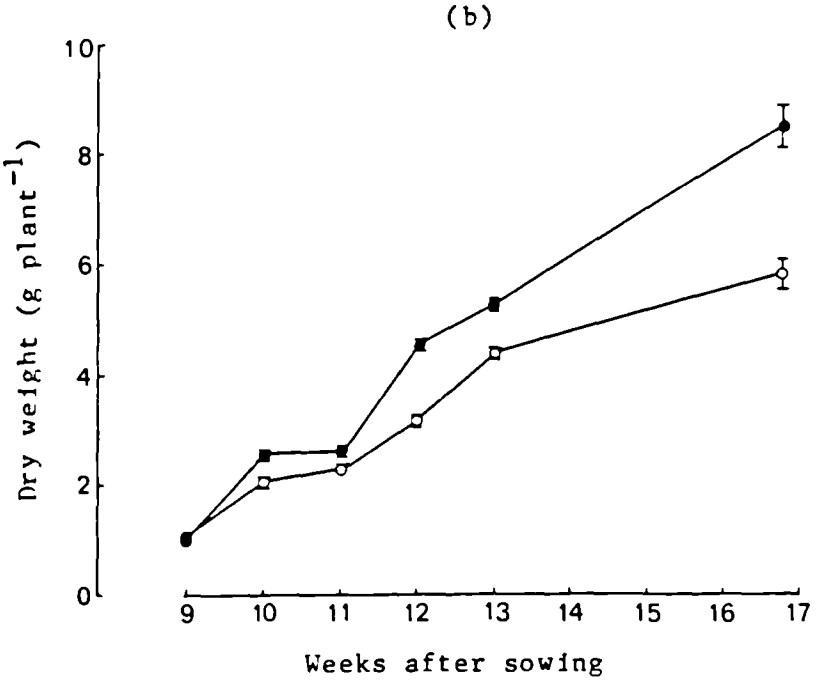

(b)
Dry weight (g plant^{-1})
10
8
6
4
2
0
9 10 11 12 13 14 15 16 17
Weeks after sowing

Fig. 2.12

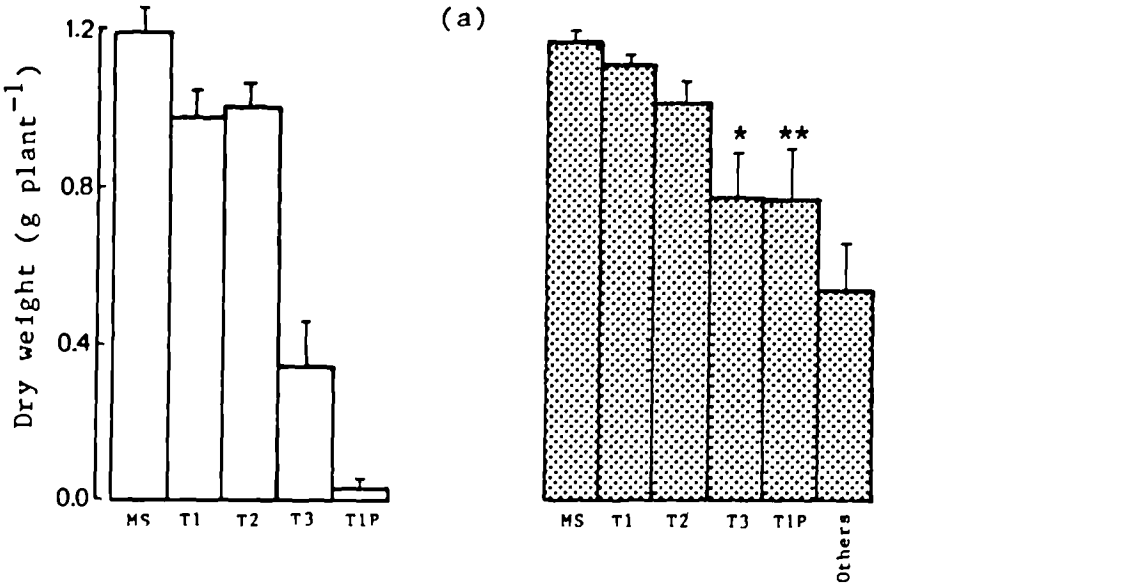
Effect of Terpal on the dry weight distribution between the MS and tillers at final grain harvest.

(a) Mean ear dry weight.

(b) Mean straw dry weight.

(c) Mean infertile tiller dry weight.

Vertical bars represent ±SE.


(a)
Dry weight (g plant^{-1})
1.2
0.8
0.4
0.0
MS
T1
T2
T3
T1P
*
**
Others

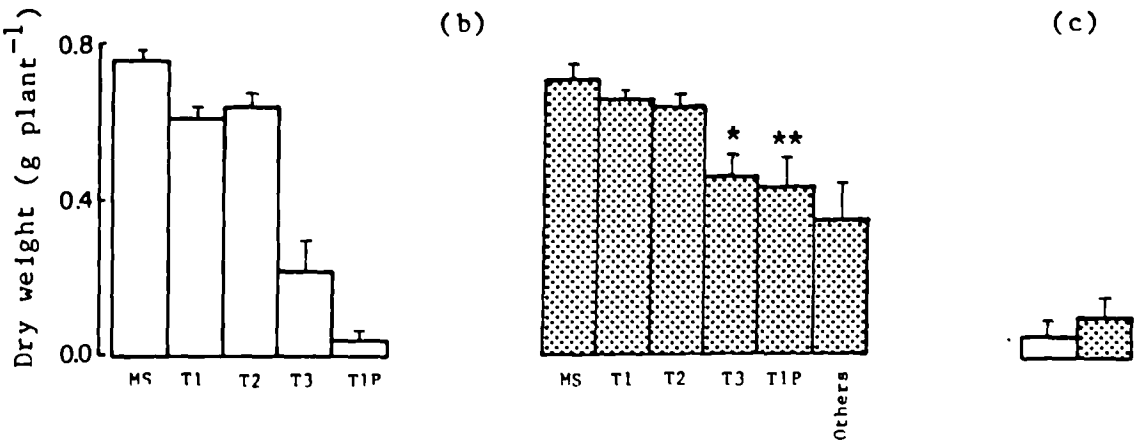

(b)
(c)
Dry weight (g plant^{-1})
0.8
0.4
0.0
MS
T1
T2
T3
T1P
*
**
Others

Table 2.13 Effect of Terpal on mean grain number per ear of the MS and individual tillers ±SE.

	Number of grains per ear	
Tillers	Control	Terpal
MS	25.4±0.9	24.4±0.7
T1	21.8±0.9	23.2±0.7
T2	21.8±0.8	22.0±0.7
T3	19.8±2.3	17.1±2.5
T1P	7.5±3.5	15.6±2.6 *
T2P	0	7.2±2.8
T3P	0	4.3±2.3

Table 2.14 Effect of Terpal on the mean dry weight of component parts per plant (g) and harvest index at final grain harvest ±SE.

Treatment	Ear weight	Straw weight	Total weight	Harvest index
Control	3.54±0.19	2.33±0.13	5.87±0.31	0.52
Terpal	5.33±0.34	3.33±0.20	8.66±0.48	0.54
	**	**	**	

From the 0.1 m^2 samples of ears harvested by hand it was calculated that the Terpal treated plots yielded a greater weight of grain per m^2, that is, 842.3 $\pm$ 57.8g compared to a yield of 688.4 $\pm$ 42.6g from control plots. However, this difference in grain weight was not statistically significant. Also there was no significant difference in the yield of grain obtained by combine harvester from the Terpal treated and control plots, that is, 673.9 $\pm$ 57.2g m^{-2} and 639.5 $\pm$ 39.6g m^{-2} respectively.

Climatic data for 1983 are included in the Appendix, there was high rainfall during the vegetative stage of growth and no unusually cold or hot periods.

DISCUSSION

The pattern of tillering in both years was generally similar to that previously described for field grown barley (Kirby, 1967; Cannell, 1969a) and for glasshouse grown barley (Aspinall, 1961; Laude et al., 1967). Three phases in this pattern were identified; an early phase of rapid tillering, a phase prior to ear emergence when tiller production declined and halted temporarily and during which tiller death commenced, and a third phase where tillering resumed after anthesis. This latter phase, which was well marked in Experiment 2.1, was not observed in the field studies of Darwinkel (1978), Fraser et al. (1982) and Garcia del Moral et al. (1984), but has been reported in pot experiments (Aspinall, 1961; Jewiss, 1972).

The first tiller appeared when the MS had three fully expanded leaves with the fourth unfolding; the MS apex was becoming reproductive at this time. Early rapid tillering (approximately one tiller per week in Experiment 2.1 and 2.2) is related to the high soil fertility and to the full illumination of all leaves. As the canopy closes and leaves become partially shaded tillering tends to decline. The phase of early tillering is especially important since it establishes leaf area and maximises light interception early in the life of the crop (Jewiss, 1972). When Terpal was applied during this period, in Experiment 2.2, the production of tillers was increased by one week after application. Similarly CCC has been shown to increase tiller production in field grown spring barley when applied early, at GS 13 (Koranteng, 1981) and also Cerone when applied at GS 37 and 41 to winter wheat (Hill et al., 1982).

The production of tillers continued until just before ear emergence when it declined and stopped. Aspinall (1961) also describes a period

of slow tiller production prior to ear emergence in glasshouse grown barley, and similarly in wheat Jewiss (1972) found that tillering was temporarily halted at this time. Tiller mortality also began at this time. An increased amount of tiller mortality during the final stages of MS stem elongation prior to ear emergence has been reported previously (Thorne, 1962; Langer et al., 1964; Laude et al., 1967). In the Terpal treated plants in Experiment 2.2 the decline in tiller production and the onset of tiller death were delayed by one week.

It seems likely that the sudden decline in tillering described above is influenced by the processes that are coincident with it, namely the rapid elongation of the apices and internodes of the MS, T1 and T2. It is considered that the controlling mechanisms at work here fall into two categories which are not, however, mutually exclusive. On the one hand the decline of tiller production may be related to increased competition between MS and tiller buds for a diminishing supply of carbohydrate or mineral nutrients. Lower leaves will be aging and shaded so their photosynthetic activity will be reduced; nutrient uptake by crops is rapid so the soil can soon become depleted (Kirby and Appleyard, 1984b). The developing inflorescences and elongating stems of the MS, T1 and T2 represent sinks with high demands for nutrients and assimilates which compete successfully with the smaller, most recently produced tillers and tiller buds causing their growth and development to be arrested. This decline in tillering has been shown to be less pronounced with greater nutrient supply, particularly N (Aspinall, 1961; Thorne, 1962). The direct effects of N on tillering are discussed in Chapter 1 and Chapter 4. On the other hand, tillering may be primarily regulated during this period by the action of growth substances, in a manner analagous to apical dominance. Such substances, for example, auxin from the MS apex and young leaves and gibberellins from elongating internodes may indirectly inhibit tiller buds by

influencing their sink activity, and correspondingly their supply of nutrients and assimilates (Aspinall, 1961; Johnston and Jeffcoat, 1977). It can therefore be suggested that apical dominance becomes stronger during the phase of increased reproductive activity (Jewiss, 1972).

There is evidence from the present study (Experiment 2.2) that Terpal can diminish and perhaps delay the influence of apical dominance since early tillering was promoted and tiller production declined later than in control plants. This supports the view that hormonal factors play a part in regulating tiller growth and development at this stage of development, as concluded by Jewiss (1972); but alternatively Terpal may act by modifying the source-sink balance. Hence Terpal may reduce apical dominance by retarding MS stem extension thereby increasing the availabilty of resources for tillering.

Tillering resumed around anthesis and continued until grain filling, but this was not well pronounced in Experiment 2.2. Langer et al. (1973) suggest that this renewed tiller production is because of weakened apical dominance. This may be due to a reduced demand for resources as stem elongation is completed or due to a modified hormonal balance. Coincident with this renewal of tillering at anthesis was a period of about one week when MS leaf senescence and tiller death stopped. However, when leaf and tiller senescence began again during grain filling some new tillers were still produced, the death of elongating buds was also observed at this time. Thus some tiller buds were favoured more than others; the dying buds were the latest commencing growth. The ability to produce late tillers is an important feature of the reproductive biology of the Gramineae since if the MS and other inflorescences are lost there are new shoots ready to begin reproductive growth.

A distinct hierarchical pattern of shoot development occurred. The position of a shoot in the hierarchy was dependent upon its time of appearance relative to the other shoots; appearance being dependent upon the position and age of tiller apices on the plant. The tillers emerged in an order related to the sequence of MS leaf appearance with the tillers in the axil of L1 emerging slightly before the corresponding tillers in the axil of L2 and so on. The position of a tiller within this hierarchy governed its size, with the earliest formed shoots having a greater leaf number, height and dry weight than the later formed shoots. Tillers produced successively fewer leaves; this tends to synchronise their development so that ear emergence, anthesis and grain ripening take place almost simultaneously in all shoots on the plant (Fletcher and Dale, 1977; Kirby and Appleyard, 1984a). However, the later a tiller emerged the less time it had for growth and development before crop maturity and subsequently its ear size was diminished. The general pattern of emergence and subsequent size hierarchy was therefore, MS, T1, T2, T3, T1P, T2P, T1P,1, T4, T3P, T2P,1. Thorne (1962) and Cannell (1969a) described a similar pattern of tiller production for barley and also Rawson (1971) for wheat. There is evidence from both Experiment 2.1 and 2.2 that Terpal modified the size hierarchy so that there was less difference between the tillers, later produced tillers were larger, for example, T2P and T3P. The earlier emergence of tillers in the Terpal treated plants resulted in longer lifespans and thus the time to attain a greater size, for example, T2P in Terpal treated plants survived for 5.5 weeks compared with only 1.5 weeks in the non-treated plants in Experiment 2.2. The onset of tiller death was delayed by one week in Experiment 2.2 in the Terpal treated plants thereby further increasing the lifespan of some tillers. The number of tillers represented in the population was also related to the hierarchy, the later produced tillers being less represented. This

observation was also made in field-grown wheat by Fraser et al. (1982). In Experiment 2.2 Terpal increased the number of later produced tillers represented in the population; in control plants these remained as buds. Cannell (1969a) found that the number and position of axillary buds which developed and the extent of development varied, which was a reflection of the degree of apical dominance. The ability of a grass to tiller from every leaf axil position during establishment ultimately depends on seed size, depth of sowing and environmental conditions, particularly temperature and N supply (Ryle, 1964; Jewiss, 1972).

The later produced tillers were generally the first to die, this is comparable with the findings of Thorne (1962) with barley and of Darwinkel (1978) and Power and Alessi (1978) with winter and spring wheat respectively. As previously stated tiller death began during the phase of MS ear development and rapid stem elongation and continued throughout grain filling. The onset of death coincided with the phase of tiller bud inhibition described earlier and as such it is suggested that both are caused by similar processes, that is, by direct competition for assimilates and nutrients and this may also be associated with increased apical dominance. This will be especially acute in the young, late emerging tillers as they will become increasingly shaded with time and this may be an important contributing factor in their overall carbon balance. Thus their photosynthetic capacity will be greatly restricted and they must die if not supported by assimilate transported from other parts. Thus tiller death may be initiated by shading (Bean, 1964; Ong, 1978; Ong et al., 1978). Reductions in irradiance are associated with low carbohydrate levels in the affected plant parts (Jewiss, 1972; Darwinkel, 1978) and thus this together with internal competition with ear and stem sinks must accelerate tiller mortality. In the present study it is interesting to note that the onset of tiller bud death was not observed until 3 weeks

after the onset of tiller death, thus small sinks with relatively small demands appear to be able to be sustained for a longer period than the larger sinks of the newly emerged tillers.

Factors other than those outlined above may also have a significant influence on the survival of very late tillers, that is, those tillers which emerged in the second phase of tillering after anthesis. The distance of these tillers from the main vascular strands of the MS may influence their survival; the distance for assimilates and growth substances to travel is greater than for the earlier emerged primary tillers (Fletcher and Dale, 1974). Furthermore late tillers have only a short time for development before the rest of the plant reaches maturity and as such their maximum leaf area and dry weight is very small. They also produce very few adventitious roots compared with the MS and first emerging primary tillers and many are unrooted (Anderson-Taylor and Marshall, 1983). Thus in comparison with early emerging tillers, late tillers may be far more dependent on their parental tiller for supplies of water and minerals. The late tillers do, however, develop more rapidly, but this restricts their apical development and so the later the tiller emerges, the smaller are its chances of producing a fertile ear (Darwinkel, 1978). In the present study none of the T4 tillers and very few secondary tillers survived to produce grain-bearing ears. From the results of Experiment 2.1 there is some evidence that there may be a critical size that a tiller must attain in order to survive. All of the tillers that died had 2 or less leaves, T3 and T1P had 2.8 and 2.1 leaves respectively and their survival rate was low, whereas most tillers that survived had 6 or more leaves. It is possible that a tiller with more than 6 leaves had become independent of its parent MS and was in a stronger position to compete for nutrients and light. This idea of a critical size for tiller survival has been postulated before by Garcia del Moral et al. (1984).

They suggested that tillers less than one third the height of the MS at the end of MS elongation would fail to produce ears. In the present study the dry weight accumulated by these non-productive tillers was negligible (1 or 2% of total plant dry weight) at final harvest. The effect on yield of these later produced and generally unproductive tillers is debatable. Lupton and Pinthus (1969) and Russelle et al. (1984) showed that $^{14}CO_2$ in wheat and ^{32}P in maize was translocated from infertile tillers to ear-bearing tillers and as such suggested that infertile tillers contribute to grain yield. On the other hand, Gallagher and Biscoe (1978) state that late tillers make no sensible contribution to yield and may delay crop harvest if they remain green after the rest of the crop is ripe. Rawson and Donald (1969) considered that the amount of labelled N remobilized from dying tertiary tillers was not enough to have any effect on increasing yield potential. It is thought that these late tillers may be wasteful of the plant's resources; the selection of a uniculm (Donald, 1979) or low tillering variety instead of a freely tillering variety may increase potential grain yield. In this respect it would be useful to have a PGR that could inhibit tillering from MS emergence onwards.

Similar grain yields were obtained in both years of around 700 g m^{-2} (equivalent to 7.0 t ha^{-1}) which is comparable to yields of 6.68 t ha^{-1} previously obtained from Triumph (Riggs et al., 1981). In Experiment 2.2, Terpal increased grain yield by between 5 and 22% but this effect was not statistically significant even though ear number per plant was significantly increased. Terpal has, however, been previously reported to significantly increase yield in spring barley by increasing the number of ears m^{-2} (Scheffer et al., 1983). CCC has also been shown to increase ear number thus enhancing grain yield (Humphries et al., 1965; Koranteng, 1981).

In both experiments the MS made the most important contribution to yield; about 30% of the total plant ear weight. High survival rates and grain weights also came from the earliest produced tillers, especially T1 and T2, the later emerged tillers were less productive. Krishnamurphy (1963, in Bunting and Drennan, 1966) reported higher survival rates in earlier appearing tillers of wheat which also had larger ears. Rawson (1971) and Darwinkel (1978) also found later appearing tillers to be less productive. In the Terpal treated plants the contribution to yield of the MS was reduced to around 23% in both experiments and that of T1P and T3 increased from about 4.6 to 13.1% and from 10.4 to 16.8% respectively. In Experiment 2.2 Terpal also increased the number of late tillers surviving to grain production so that they represented 10% of the total grain weight compared to 0% in control plants. Rawson (1971) found that given better fertility and wider spacing the relative contribution of the MS declines due to a greater production and survival of tillers.

Differences in vigour between the coleoptile tiller and other tillers have been observed previously (Jewiss, 1972; Kirby and Faris, 1972). In Experiment 2.1 only 5% of the plants had CT tillers whereas in Experiment 2.2 approximately 50% had a tiller at the coleoptile node, none of these survived to final harvest. Since the coleoptile tiller bud is positioned at the depth of the seed, Fraser (1978, in Fraser et al., 1982) suggests that its limited productivity and poor survival may be attributable to its burial deeper in the soil than other tiller buds emerging from leaf axils. Deep sowing which delays emergence and expansion of the first leaf often results in failure of the coleoptile tiller to emerge (Gallagher and Biscoe, 1978). Other factors influencing its outgrowth are seed size, seed bed conditions, temperature, irradiance, daylength and cultivar (Cannell, 1969b; Peterson et al., 1982). Rawson (1971) found that CT did not yield as

well as true-leaf tillers and suggested that this was because the CT bud was less well positioned on the plant to receive assimilates.

Until the present study little was known of the effects of Terpal on tillering in spring barley. Modification of growth by this PGR was particularly marked in Experiment 2.2 where tiller production and survival were significantly increased. It was thought that certain weather conditions during the day of Terpal application could have hindered uptake in Experiment 2.1 resulting in a less marked response. Although variability in field conditions from year to year could also result in differences of response. Apart from these explanations, it must be remembered that Terpal was applied later in Experiment 2.2, that is, at GS 15 compared to GS 13 in Experiment 2.1 and this could be the reason for the difference in response. A further factor may have been the differences in plant density, as density is known to influence tillering (Darwinkel, 1978). Plant density was higher in Experiment 2.1 than in Experiment 2.2; this may have diminished tillering capacity in Experiment 2.1 thereby reducing the potential for increased tiller production by Terpal treatment. Besides enhancing the growth of lateral buds (tillers), Terpal also significantly reduced MS height and dry weight (by between 2 and 14%) and reduced the hierarchical pattern of shoot development resulting in a more even crop of tillers. The size of T1 and T2 was little affected whereas the size of the later emerged tillers was increased by up to 60% resulting in a more even balance of growth between the tillers. Koranteng and Matthews (1982) demonstrated the ability of CCC to reduce the apical dominance of the MS which resulted in a more even tiller size. All of the modifications to growth found in the present study suggest that Terpal had been successful in reducing the effect of apical dominance. However, a straight forward redistribution of resources from the retarded MS to the tiller buds could have been initiated by Terpal application.

CHAPTER 3

TILLER BUD OUTGROWTH

INTRODUCTION

Since tiller buds arise in leaf and prophyll axils, the maximum potential tiller number is determined by the number of these sites produced by an individual plant. However, it has already been seen (Chapter 2) that buds may not grow out from every leaf or prophyll axil even though they are formed. The degree of bud outgrowth is a reflection of the strength of apical dominance. It is well known that lateral bud development and outgrowth is under the control of the MS apex (Ali and Fletcher, 1970; Phillips, 1975; Clifford, 1977; Harrison and Kaufman, 1982) since the removal of the latter promotes lateral bud growth (Leopold, 1949; Laidlaw and Berrie, 1974). The way in which the apex exerts its inhibitory influence on lateral buds is not fully understood. There is support for hypotheses in which growth substances, especially auxin, are centrally involved (Phillips, 1975) and also for a nutritive hypothesis based on competition within the plant for a limited supply of nutrients that are utilized in growth (McIntyre, 1977). Such hypotheses were discussed in Chapter 1. To examine these hypotheses further the influence of applied PGRs and nutrient supply on tiller bud outgrowth was investigated. Young barley seedlings were used (GS 11) in order to modify bud growth at an early stage of development.

EXPERIMENTAL

Experiment 3.1 The effect of PGRs and nutrient supply on tiller bud outgrowth.

MATERIALS AND METHODS

Germination.

Seeds of spring barley, cv. Triumph, were soaked in aerated, distilled water for 12 hours to facilitate uniform germination. The imbibed seeds were then allowed to germinate on moist tissue paper in a propagator at 20°C under fluorescent lighting. After 3 days, when the first seminal root and the coleoptile were about 15 and 10 mm long respectively, the seedlings were transferred to pots containing nutrient solution.

Culture.

From preliminary experiments (not reported here) using various culture solutions it was found that the plants grew best in a modified Hoagland's solution (Table 3.1). This solution is described in full by Epstein (1972), and some additional modifications are shown in Table 3.1. The nutrient solution was contained in plastic pots, each with a capacity of 333 cm^3, which had tightly fitting lids. Both the pots and the lids were painted black to eliminate light and reduce algal growth and were thoroughly cleaned before use. The seedlings were supported with their roots submerged in the nutrient solution by means of two plastic tubes, with nylon gauze inserts, which fitted exactly into the holes in the pot lids (Fig. 3.1). On potting up, the first seminal root of each seedling was carefully pushed through a hole in the gauze. Later emerged roots grew through the gauze mesh to the nutrient solution. As the seedlings developed they obtained adequate support from the gauze and tube and thus tiller buds were able to develop without any mechanical constraint from the tube culture system. Four

Table 3.1 Hoagland's nutrient solution (after Epstein, 1972).

Compound	Molecular weight	Concentration of stock solution g dm^{-3}	Volume of stock cm^3 dm^{-3} of final solution	Element	Final concentration of element μM
				N	16,000
KNO_3	101.10	101.10	6.0	K	6,000
$Ca(NO_3)_2 \cdot 4H_2O$	236.16	236.16	4.0	Ca	4,000
$NH_4H_2PO_4$	115.08	115.08	2.0	P	2,000
$MgSO_4 \cdot 7H_2O$	246.49	246.49	1.0	Mg	1,000
				S	1,000
KCl	74.55	3.73		Cl	50.0
H_3BO_3	61.84	1.55		B	25.0
$MnSO_4 \cdot H_2O$	169.01	0.34		Mn	2.0
$ZnSO_4 \cdot 7H_2O$	287.55	0.57	1.0	Zn	2.0
$CuSO_4 \cdot 5H_2O$	249.71	0.12		Cu	0.5
H_2MoO_4	161.97	0.08		Mo	0.5
Fe-EDTA	346.08	6.92	1.0	Fe	20.0

AMMENDMENTS

a) Sodium metasilicate ($NaSiO_3 \cdot 5H_2O$) was also included, 10 mg dm^{-3} of final solution, as this prevented chlorosis.

b) Only 50% of the ammonium dihydrogen orthophosphate ($NH_4H_2PO_4$) was added for the first 3 days after potting up, as this was found to improve seedling establishment.

c) The whole solution was diluted to 50% strength for the first 5 days after potting up, this was also found to improve seedling establishment. This reduced the concentration of $NH_4H_2PO_4$ to 25% for the first 3 days.

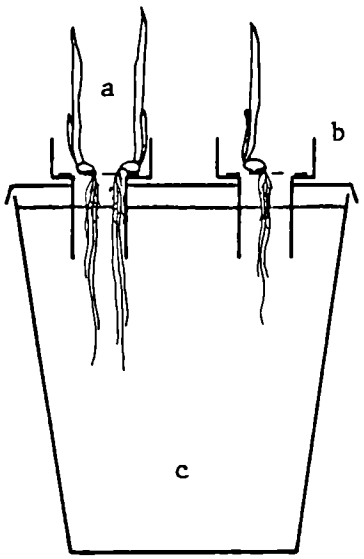


Fig. 3.1 Cross-sectional diagram of pot culture system.

(a) Seedlings supported on gauze disc.

(b) Tube slotted into lid.

(c) Nutrient solution.

seedlings, selected for uniformity, were placed in each pot, 2 in each of 2 tubes. After 3 days the smallest seedling was discarded leaving 3 plants per pot. The pots were placed randomly, in 6 blocks, in a Fisons controlled environment cabinet. Plants were illuminated by fluorescent lighting for a 16 hour photoperiod at an irradiance of 320 $\mu E\ m^{-2}\ s^{-1}$. Day and night temperatures were maintained at 21 and 18°C respectively.

Experimental treatments.

Several preliminary experiments were conducted to determine appropriate nutrient and PGR concentrations, these are not presented.

a) Nutrient regimes.

After 5 days in 50% nutrient solution half of the plants were transferred to full strength nutrient solution and half to a 20% solution. The plants were grown from then onwards at these 2 nutrient supply levels. The solutions were renewed twice weekly.

b) PGRs.

A range of PGRs were applied by foliar spray, until runoff, using a laboratory spray gun. The plants were treated and left to dry for 4 hours outside the growth cabinet to prevent cross-contamination of the treatments. Terpal, Cerone, TIBA, GA_3, and the synthetic cytokinin, BAP (benzylamino purine) were applied to 6 pots 7 days after potting up, that is, 2 days after exposure to the 2 nutrient levels at GS 11. The concentrations of Terpal and Cerone used were equivalent to the recommended agricultural rates of application, that is, 2.5 $dm^3\ ha^{-1}$ in 220 $dm^3\ H_2O\ ha^{-1}$ and 1 $dm^3\ ha^{-1}$ in 300 $dm^3\ H_2O\ ha^{-1}$ respectively. TIBA, GA_3 and BAP were applied at a concentration of 10^{-4}M. These compounds were first dissolved in 100% ethanol before adding to warm distilled water giving a final concentration of ethanol of 0.05% v/v. A surfactant, Tween 20, was added at 0.05% v/v. Control treatments consisted of distilled water + 0.05% v/v ethanol + 0.05% v/v Tween 20.

An experiment incorporating all the above treatments was conducted, but had to be undertaken in 2 stages because of lack of space in the growth cabinet. In the first stage the effects of low and high nutrient regimes on the response to Terpal and TIBA were examined, and in the second stage the effects of nutrient regime on Cerone, GA_3 and BAP were followed. Control plants were monitored in both stages. There were 6 replicate pots of each treatment.

Plants were harvested 5, 10 and 15 days after PGR application. At the first harvest one plant was removed from the tube containing 2 plants so that one plant per tube (2 plants per pot) remained until the later harvests. At each harvest tiller buds visible to the naked eye were identified according to their origin and their length and dry weight recorded. The growth and development of the MS and root system was also recorded, and dry weights were determined after oven drying at 70°C for 4 days.

RESULTS

Results of control plants from both parts of the experiment were pooled for presentation and analysis.

Tiller bud sites.

As tiller buds originate in the axils of MS and tiller leaves and prophylls, the effects of the treatments on these bud sites are described first. The rate of MS leaf production was not significantly affected by the PGR treatments or nutrient supply; most plants had 5 fully expanded MS leaves at 15 days after PGR application (GS 15) (Fig. 3.2). On the other hand, the number of tiller leaves per plant was modified by the treatments. At 10 days after PGR treatment, both Terpal

Fig. 3.2

Effect of PGR and nutrient treatments on the number of bud sites with time (days after treatment application).

Bud sites:

Fully expanded MS leaves.

" " tiller leaves.

Prophylls of emerged tillers (including the MS).

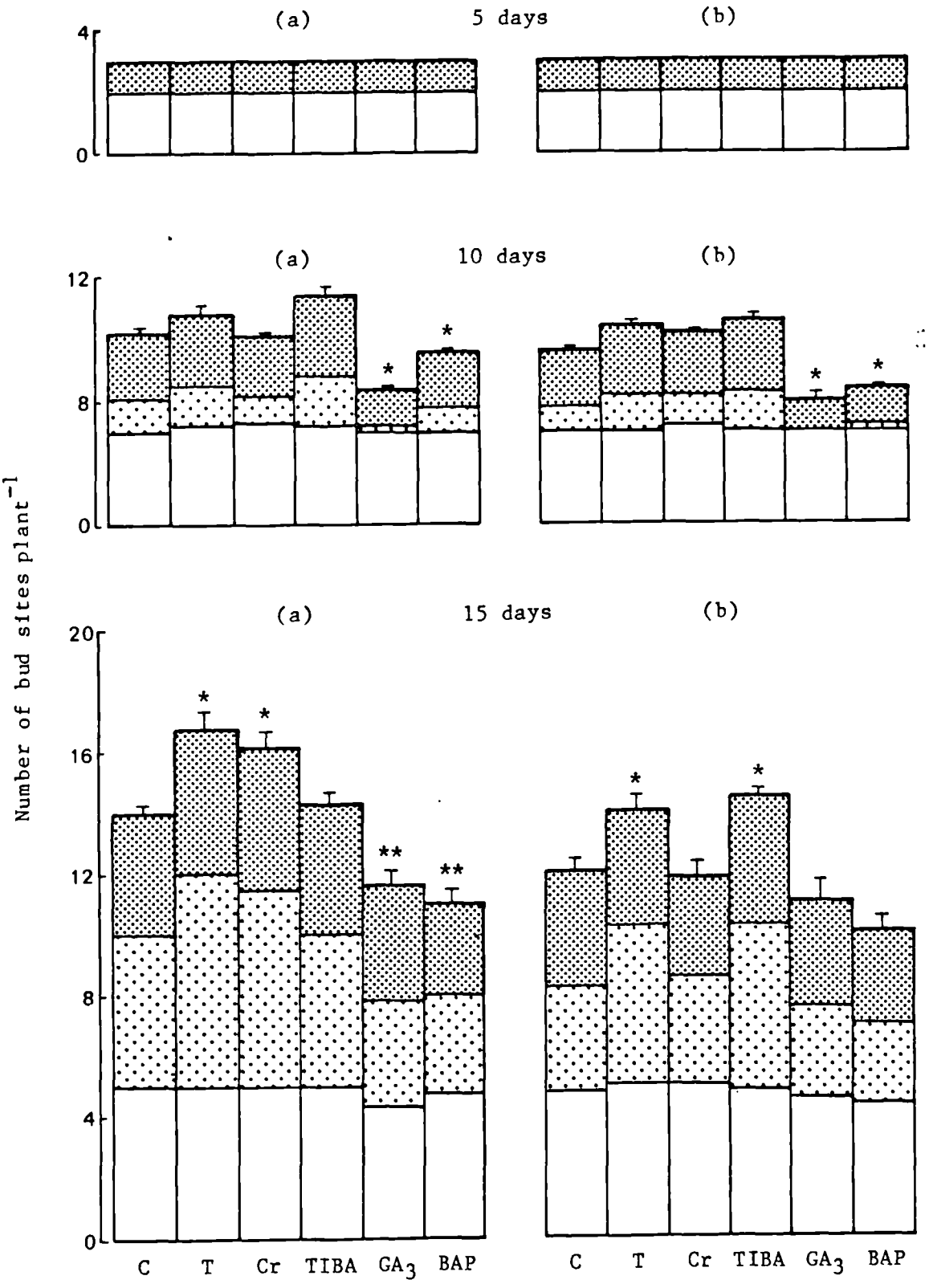
PGR treatments:

Control (C), Terpal (T), Cerone (Cr), TIBA, GA_3, and BAP.

Nutrient supply level:

(a) 100% (b) 20%

Vertical bars represent $\pm$SE.


(a)
5 days
(b)
4
0
(a)
10 days
(b)
12
8
0
*
(a)
15 days
(b)
20
16
12
8
4
0
*
**
C
T
Cr
TIBA
GA3
BAP
Number of bud sites plant-1

and TIBA increased the number of tiller leaves, although this was not statistically significant, whereas Cerone had little effect and GA_3 and BAP reduced ($p<0.05$) the number of tiller leaves. There was no effect of nutrient supply level at this time (Fig. 3.2). Later, at 15 days after PGR application Terpal and Cerone increased ($p<0.05$), TIBA had no effect and both GA_3 and BAP reduced ($p<0.01$) the number of tiller leaves at the high nutrient level. At the low nutrient level only Terpal and TIBA increased ($p<0.05$) the number of tiller leaves, the other PGR treatments had no effect. The number of tiller leaves was less in control and Terpal and Cerone treated plants at the low nutrient level, whereas there was little effect of nutrient supply level in TIBA, GA_3 and BAP treated plants (Fig. 3.2). The production of prophylls (one per shoot) was only slightly modified by the PGR treatments (Fig. 3.2) reflecting the effects of the PGRs on tiller production which are described later (Table 3.3). Therefore, the treatment effects on the total number of bud sites were mainly due to effects on tiller leaf number (Fig. 3.2).

As expected bud number and the order of bud appearance were related to the number and order of appearance of MS and tiller leaves and prophylls. For example, at GS 12 (5 days after treatment application) 2 to 3 buds were visible in control plants. These were T1 and T2 found in the axils of L1 and L2 respectively and in some plants the CT bud was also present within the prophyll (coleoptilar sheath) of the MS. At 10 and 15 days after PGR application the number of elongating buds was closely related to the number of bud sites (MS and tiller leaves and prophylls). Of all the sites, 61% (mean value from all treatments) possessed an elongating bud (Fig. 3.2 and Fig. 3.3) and 18% had visible non-growing buds. Buds in the remaining 21% of sites were not recorded as they were not observed by eye. No bud mortality was observed in this experiment.

Tiller bud outgrowth.

a) Control

Not all buds revealed by dissection commenced elongation. In control plants around 77% of all visible buds had begun growth by GS 15 (Fig. 3.3). At the high and low nutrient levels respectively, 43 and 52% of buds produced by control plants were primary tiller buds; all plants had T1, T2, T3 and T4 buds and all of these commmenced elongation (Table 3.2). Fifty three and 46% of buds from plants grown at high and low nutrient levels respectively, were secondary tiller buds. Of these, T1P, T1,1, T1,2, T2P and T2,1 were most frequently produced, particularly at the high nutrient supply level. Not all these buds commenced elongation. The control plants produced only one tertiary tiller bud, that is, T1P,1 (Table 3.2). By GS 15 about 33% of all visible buds, mainly T1, T2 and T3, had emerged as tillers (Table 3.3).

b) Terpal

Terpal had no significant effect on bud production until GS 15, when it was increased ($p<0.05$) by around 17%. Bud elongation was stimulated ($p<0.01$) earlier at GS 12, that is, 5 days after application (Fig. 3.3). These effects were mainly due to the earlier and increased production and growth of secondary and tertiary tiller buds due to the greater number of tiller leaves; the appearance and growth of T3P and T1P,1 were particularly enhanced (Table 3.2). Terpal significantly ($p<0.01$) increased the rate of tiller emergence, but only at the high nutrient level, this was due to more CT and T1P buds growing into tillers and therefore providing more sites for buds in tiller leaf axils (Table 3.3). At 5 and 10 days after application Terpal reduced the length of T1, except at the low nutrient level at the 1st harvest when it was increased; Terpal also increased the length of T2 although these results were generally not significant (Tables 3.4 and 3.5). By

Fig. 3.3

Effect of PGR and nutrient treatments on tiller bud production (non-elongating buds and elongating buds) with time (days after treatment application).

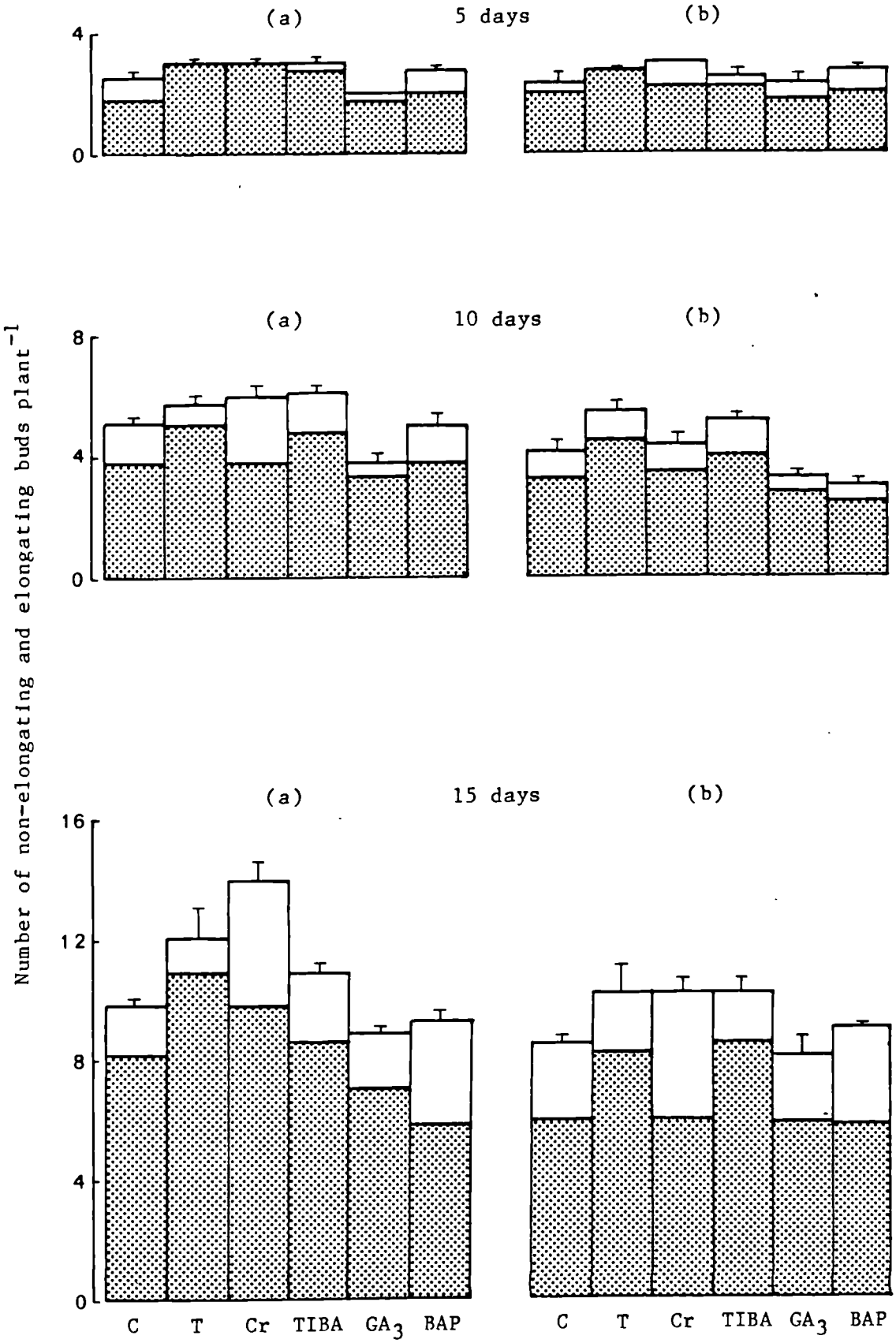
Non-elongating buds.

Elongating buds.

Nutrient supply level:

(a) 100% (b) 20%

Vertical bars represent ±SE.


(a)
5 days
(b)
4
0
(a)
10 days
(b)
8
4
0
(a)
15 days
(b)
16
12
8
4
0
Number of non-elongating and elongating buds plant^{-1}
C
T
Cr
TIBA
GA_3
BAP
C
T
Cr
TIBA
GA_3
BAP

15 days after application the combined lengths of all primary tiller buds and tillers were significantly reduced by Terpal at both nutrient supply levels, this was due particularly to the reduced lengths of T1 and T2 (Fig. 3.4). The combined length of all secondary tiller buds was not significantly affected by Terpal although the lengths of T1P, T1,1 and T2P were increased at the high nutrient level (Fig. 3.5). The distribution of dry weight to primary tiller buds was little affected whereas that to secondary and tertiary tiller buds was greatly increased by up to 5.4 times and 35 times at the high and low nutrient levels respectively (Table 3.6).

c) Cerone

Cerone increased bud number but this was not statistically significant at either nutrient level until 15 days after application when increases of 40 and 20% were seen at the high and low nutrient level respectively (Fig. 3.3). Besides increasing tiller leaf number, at the high nutrient level only, Cerone increased the proportion of bud sites possessing a visible bud from 70.5% in control plants to 86.0% (Fig. 3.2 and Fig. 3.3). Overall, Cerone had little influence on the number of elongating buds, although there were significant increases at the high nutrient level only, at 5 and 15 days after application (Fig. 3.3). Cerone greatly increased the number of quiescent and growing primary tiller buds, the occurrence and outgrowth of T5 was increased by 4 to 5 times and that of CT, 2 to 4 times (Table 3.2). Although the occurrence of secondary and tertiary buds, was significantly increased, particularly CT secondaries and T3P at the high nutrient level, the proportion commencing elongation was decreased. For example, at the low nutrient level only about 25% of buds produced began elongation compared to about 50% in control plants (Fig. 3.3). Cerone increased ($p<0.01$) tiller production at the 100% nutrient level, because more CT tillers emerged. Tiller production was slightly reduced at the lower nutrient

Table 3.2 Effect of PGR and nutrient treatments on the number of 6 replicate plants with component buds (elongating buds in parentheses) 15 days after treatment application (GS 15).

	Number of plants with bud (elongating bud)											
	Nutrient supply level											
	100%						20%					
	PGR treatments						PGR treatments					
	C	T	Cr	TIBA	GA_3	BAP	C	T	Cr	TIBA	GA_3	BAP
(a) Primary tiller buds												
CT	0	2(2)	4(4)	4(4)	3(3)	1(1)	0	1(1)	2(2)	1(1)	0	3(3)
T1	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)
T2	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)
T3	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)	5(5)	6(6)	6(6)	6(6)	6(6)
T4	6(6)	6(6)	6(6)	5(5)	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)	6(6)
T5	1(0)	0	6(5)	0	2(1)	1(0)	0	0	5(4)	0	1(0)	0
Total	25	26	34	27	29	26	24	24	31	25	25	27
	(24)	(26)	(33)	(27)	(28)	(25)	(24)	(24)	(30)	(25)	(24)	(27)
(b) Secondary tiller buds												
CTP	0	0	2(0)	1(0)	0	0	0	1(0)	0	0	0	0
CT,1	0	1(1)	3(0)	1(0)	0	0	0	1(0)	0	0	0	0
CT,2	0	1(1)	2(0)	0	0	0	0	1(0)	0	0	0	0
T1P	6(4)	6(6)	6(5)	6(5)	6(3)	6(2)	6(3)	6(4)	6(2)	6(6)	5(2)	6(4)
T1,1	6(6)	5(5)	6(6)	6(6)	5(2)	6(3)	6(4)	6(6)	6(2)	6(6)	2(1)	6(2)
T1,2	4(4)	5(5)	6(6)	5(2)	1(0)	4(2)	3(2)	5(4)	0	5(2)	1(1)	2(0)
T1,3	0	1(1)	1(0)	0	0	0	0	0	0	0	0	0
T2P	6(5)	6(6)	6(4)	6(6)	3(3)	6(2)	4(2)	4(3)	6(0)	6(5)	6(5)	6(0)
T2,1	6(5)	6(5)	6(4)	6(4)	0	4(2)	0	1(0)	3(1)	5(3)	5(1)	5(0)
T2,2	0	1(0)	2(0)	0	1(0)	1(0)	1(0)	0	0	0	0	0
T3P	3(2)	6(3)	6(1)	4(3)	0	1(0)	1(0)	1(1)	3(0)	2(1)	2(0)	1(1)
T3,1	0	0	1(0)	0	0	0	0	0	0	0	0	0
Total	31	38	47	35	16	28	21	26	24	30	21	26
	(26)	(33)	(26)	(26)	(8)	(11)	(11)	(18)	(5)	(23)	(10)	(7)
(c) Tertiary tiller buds												
T1P,1	2(1)	4(4)	1(0)	1(0)	0	0	1(0)	2(2)	0	3(3)	1(0)	0
T1P,2	0	1(1)	1(0)	0	0	0	0	1(0)	0	1(0)	0	0
T1P,3	0	0	0	0	0	0	0	1(1)	0	0	0	0
T1P,4	0	0	0	0	0	0	0	1(1)	0	0	0	0
T1,1P	0	1(1)	1(0)	0	0	0	0	0	0	1(0)	0	0
T2P,1	0	0	1(0)	1(0)	0	0	0	0	0	1(0)	0	0
Total	2	6	4	2	0	0	1	5	0	6	1	0
	(1)	(6)	(0)	(0)	(0)	(0)	(0)	(4)	(0)	(3)	(0)	(0)

level (Table 3.3). Cerone significantly reduced the lengths of T1 at 5 and 10 days after application and T2 at 5 days after application at the 100% nutrient level. These were the only significant effects of Cerone on bud length at the first two harvests although reductions in the length of T1 were also observed at the lower nutrient level (Table 3.4 and 3.5). At 15 days after application there was no significant effect of Cerone on the combined lengths of primary tiller buds although the length of T2 was reduced slightly (Fig. 3.4). Cerone reduced the combined length of all secondary tiller buds but this was only significant at the lower nutrient level where the combined length of buds was reduced by about 85%. At the high nutrient level the length of T2P was significantly ($p<0.01$) reduced (Fig. 3.5). There was no effect of Cerone on the distribution of dry weight to the tiller buds collectively at the high nutrient level, but T3, T4 and T5 were increased ($p<0.05$) in weight and T2, T1P and T2P were smaller ($p<0.05$) (Table 3.6). At the lower nutrient level Cerone reduced ($p<0.05$) the allocation of dry weight to all the tiller buds collectively and this was characterised by the smaller dry weight of T1 ($p<0.05$), T2(NS) and secondary (not T1P and T2P) and tertiary tiller buds ($p<0.05$) (Table 3.6).

d) TIBA

TIBA increased bud production at both nutrient levels at all harvests, but this effect was not statistically significant until 15 days after application (Fig. 3.3). There was also a promotory effect on the number of elongating buds, which was statistically significant at the high nutrient level at 5 and 10 days after application and at the lower nutrient level at 10 and 15 days after application, this effect was mainly due to the increased production of tiller leaves (Fig. 3.2 and Fig. 3.3). TIBA had little effect on the production and growth of primary tiller buds except to increase the occurrence of CT

Table 3.3 Effect of PGR and nutrient treatments on the percentage of visible buds that emerged as tillers by 15 days after treatment application and on the mean tiller number per plant ±SE.

Tiller identity	Nutrient level	PGR treatment					
		C	T	Cr	TIBA	GA_3	BAP
CT	100%	0	100	75	75	67	0
T1	"	100	100	100	100	100	100
T2	"	100	100	100	100	100	83
T3	"	100	83	100	50	50	17
T1P	"	0	67	17	33	0	0
Tillers $plant^{-1}$	"	3.0±0.0	3.8±0.2 **	3.7±0.2 **	3.3±0.3	2.8±0.2	2.0±0.3 **
CT	20%	0	100	0	100	0	0
T1	"	100	100	100	100	83	100
T2	"	100	100	100	100	100	100
T3	"	67	40	33	67	50	0
T1P	"	17	33	0	67	20	0
Tillers $plant^{-1}$	"	2.8±0.2	2.8±0.2	2.3±0.2	3.3±0.3	2.5±0.2	2.0±0.0 **

particularly at the high nutrient level (Table 3.2). TIBA had a very small effect on the production and growth of secondary and tertiary tiller buds at the high nutrient level. In contrast, the number of quiescent and growing secondary (particularly T2P and T2,1) and tertiary tiller buds was greatly enhanced at the lower nutrient level (Table 3.2). TIBA increased the proportion of emerging tillers slightly at both nutrient levels, but this was not statistically significant (Table 3.3). At 5 days after application bud length was unaffected with the exception of T1 at the 20% nutrient level which was increased (Table 3.4). By 10 days after application both the lengths of T1 and T2 were increased at the low nutrient level but this was not statistically significant. The length of T2 at the higher nutrient level was also increased ($p<0.05$) (Table 3.5). By 15 days after application the lengths of all primary tiller buds were reduced at the high nutrient level whereas there was no effect of TIBA on primary tiller bud length at the low nutrient level (Fig. 3.4). There was no significant effect on the combined lengths of secondary tiller buds at the 100% nutrient level, although the length of T1,1 was reduced significantly ($p<0.05$). In contrast, TIBA increased ($p<0.05$) the combined length of secondary tiller buds at the 20% nutrient level. This was mainly due to an increase of 188% in the length of T1P (Fig. 3.5). At the high nutrient level TIBA reduced the distribution of dry weight to all tiller buds and this primarily reflected the reduced growth of T3, T4, T1P and other secondary and tertiary tiller buds (Table 3.6). In contrast, the distribution of dry weight to tiller buds at the lower nutrient supply level was significantly ($p<0.05$) increased. This was mainly due to the increased growth of secondary and tertiary tiller buds (Table 3.6).

Table 3.4 Effects of PGR and nutrient treatments on the lengths (mm) of T1 and T2, 5 days after application ±SE.

Tiller	Nutrient level	PGR treatment					
		C	T	Cr	TIBA	GA_3	BAP
T1	100%	28.2±6.1	17.8±2.8	6.0±1.4 **	27.9±5.6	4.7±1.4 **	8.3±2.3 *
T2	100%	2.9±0.2	3.5±0.4	2.3±0.2 *	2.8±0.8	1.7±0.3 **	2.1±0.3 *
T1	20%	12.0±3.7	20.7±4.1	5.1±1.3	24.3±3.1 *	3.0±0.3 *	5.0±0.6
T2	20%	1.6±0.3	3.1±0.4 *	2.3±0.7	1.7±0.5	1.7±0.3	1.5±0.2

Table 3.5 Effects of PGR and nutrient treatments on the lengths (mm) of T1 and T2, 10 days after application ±SE.

Tiller	Nutrient level	PGR treatment					
		C	T	Cr	TIBA	GA_3	BAP
T1	100%	136.0±11.2	98.0± 5.6 *	90.0±11.7 **	124.8± 8.4	74.0±28.5 *	95.2±12.7 *
T2	100%	43.6± 3.9	46.8± 3.2	50.8±10.5	76.0±12.1 *	25.9± 4.9 *	28.7±11.9
T1	20%	97.2± 9.0	80.5± 6.8	77.7±12.8	116.3± 8.2	70.2±29.7	34.0±10.6 **
T2	20%	31.0± 5.2	36.3± 8.7	39.7±13.1	39.2± 8.5	24.2± 5.8	11.1± 3.3 *

e) Gibberellic acid

At the high nutrient level GA_3 reduced ($p<0.05$) the total production of buds at all harvests but at the lower nutrient level bud production was only significantly reduced at the 2nd harvest (Fig. 3.3). The number of elongating buds was not affected by GA_3 at either nutrient level at any harvest except at the high nutrient level 15 days after application when it was reduced slightly (Fig. 3.3). At the high nutrient level GA_3 increased the number of primary tiller buds both produced and growing out but this was accompanied by a large reduction in the numbers of secondary and tertiary tiller buds produced and growing out. This was because the number of sites for secondary tiller buds (tiller leaves and prophylls) were reduced by the GA_3 treatment whereas the sites for primary tiller buds (MS leaves) were little affected (Fig. 3.2). The numbers of quiescent and later produced tiller buds that elongated, for example T2P, T2,1, T2,2 and T3P, were particularly inhibited (Table 3.2). GA_3 had no effect on the production and outgrowth of any tiller bud at the lower nutrient level. Tiller emergence was reduced slightly but this was not statistically significant at 15 days after application (Table 3.3). Generally GA_3 reduced the lengths of T1 and T2 at 5 and 10 days after application although this effect was not statistically significant in all cases (Tables 3.4 and 3.5). At 15 days after application the lengths of all primary and secondary tiller buds were significantly reduced at the high nutrient level (Fig. 3.4 and 3.5). There was little effect of GA_3 on the combined lengths of primary and secondary tiller buds at the lower nutrient level although the lengths of T1,1 and T2P were significantly reduced (Fig. 3.5). The distribution of dry weight to all tiller buds was greatly reduced ($p<0.05$) at both nutrient levels (Table 3.6).

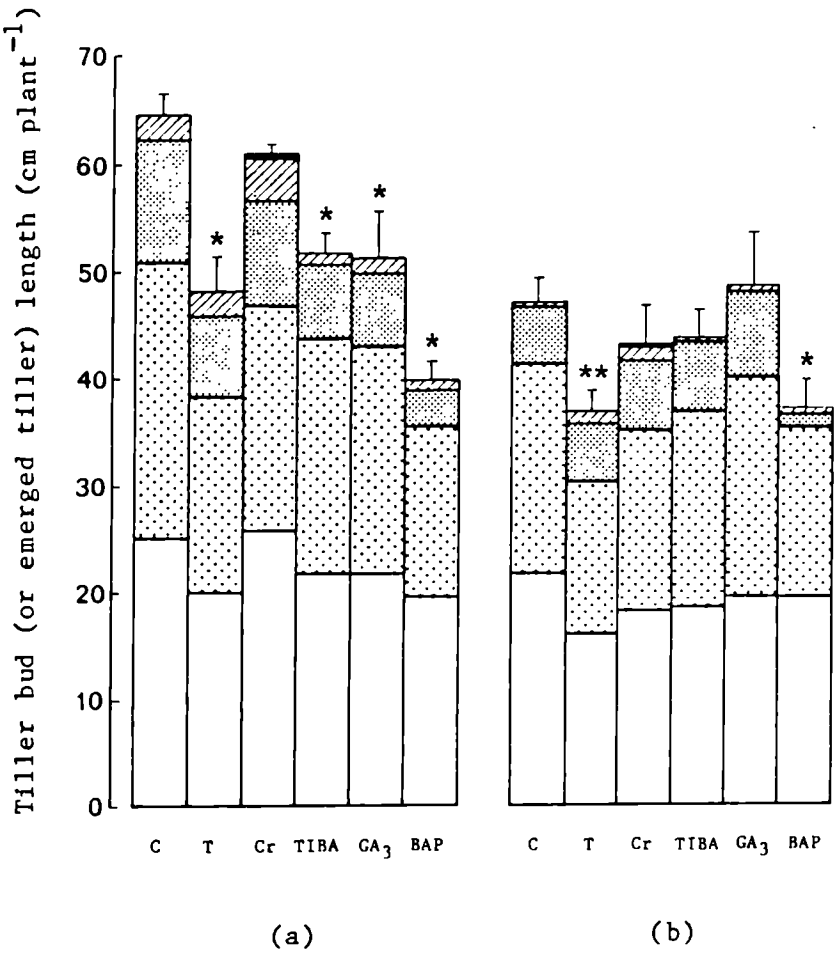
Fig. 3.4

Effect of PGR and nutrient treatments on primary tiller bud (or emerged tiller) length 15 days after treatment application.

Nutrient supply level:

(a) 100% (b) 20%

Vertical bars represent ±SE.


Tiller bud (or emerged tiller) length (cm plant^{-1})
70
60
50
40
30
20
10
0
C
T
Cr
TIBA
GA$_3$
BAP
*
**
(a)
(b)

e) BAP

Generally BAP had no effect on the number of quiescent and elongating buds. However, the number of both these were reduced ($p<0.05$) at the low nutrient level at 10 days after application and the number of elongating buds reduced at the high nutrient level 15 days after application (Fig. 3.3). Primary tiller bud production and growth was little affected apart from the increased production and elongation of CT buds at the lower nutrient level only (Table 3.2). The production of secondary tiller buds was also little affected but the number commencing elongation was reduced by 60 and 36% at the high and low nutrient levels respectively. No tertiary tiller buds were produced at either nutrient level (Table 3.2). The number of secondary and tertiary tiller bud sites were reduced by BAP at 10 and 15 days after application (Fig. 3.2). Tiller number was significantly ($p<0.01$) reduced at both levels of nutrients (Table 3.3). BAP reduced the lengths of all tiller buds at both nutrient levels at all harvests (Table 3.4 and 3.5; Fig. 3.4 and 3.5). This effect was statistically significant for all tiller buds at 15 days after application (Fig. 3.4 and 3.5). At the high nutrient level BAP significantly reduced the distribution of dry weight to all tiller buds except T1 (Table 3.6). At the low nutrient level BAP had little influence on the dry weight distribution to tiller buds (Table 3.6).

f) Nutrient supply

By the second harvest, bud number and the number of buds beginning to elongate were significantly less at the 20% nutrient level in control plants as was the number of bud sites (Fig. 3.2 and Fig. 3.3). The total number of tiller buds was reduced to a similar extent at both the 2nd and 3rd harvests but the number of elongating buds was reduced more at the later harvest. That is, at the 3rd harvest the number of elongating buds was reduced by 25% at the lower nutrient level compared

Fig. 3.5

Effect of PGR and nutrient treatments on secondary tiller bud (or emerged tiller) length at 15 days after treatment application.

Tiller identities indicated by numbers in the first block:

1 T1P

2 T1,1

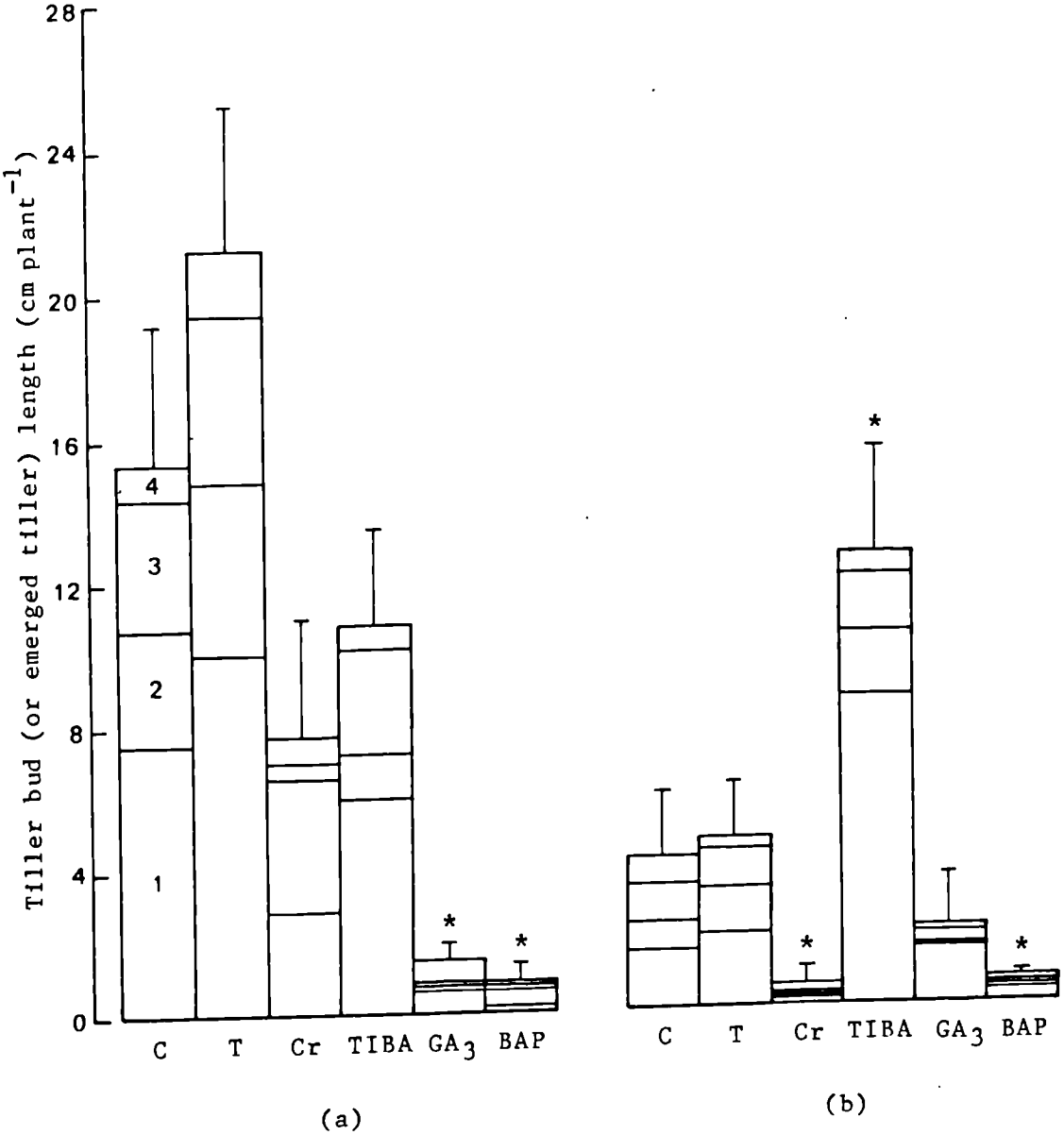
3 T2P

4 Others (including T1P,1, T1,2, T2,2, T2,1, T3P)

Nutrient supply level:

(a) 100% (b) 20%

Vertical lines represent ±SE.


Tiller bud (or emerged tiller) length (cm plant^{-1})
28
24
20
16
12
8
4
0
4
3
2
1
*
C
T
Cr
TIBA
GA$_3$
BAP
(a)
(b)

to a reduction of only 15% at the 2nd harvest. At 15 days after application, only Terpal and Cerone treated plants responded to nutrient supply level and this was in the same way as control plants; there was no significant effect of nutrient level on bud numbers in plants treated with TIBA, BAP and GA_3 (Fig. 3.3). At the 20% nutrient level, Terpal, Cerone and TIBA all produced identical numbers of buds, that is, 10.2 per plant which was more than the other treatments. At the 100% nutrient level the number of buds produced was variable within these treatments reaching a maximum of 13.9 per plant. It is possible that the plants treated with these PGRs may have produced their maximum yield of buds at the 20% nutrient level since these plants may have become nutrient deficient by 15 days after treatment application. Overall, there were no significant effects of nutrient level on primary and tertiary tiller bud number or on the proportion commencing outgrowth although tertiary tiller bud number was increased in TIBA treated plants at the low nutrient level (Table 3.2). Secondary tiller buds were affected by nutrient level. In control plants the number of quiescent and elongating secondary tiller buds were reduced by 32 and 61% respectively at the lower nutrient level. There were less sites for secondary and tertiary tiller bud production at the lower nutrient level (Fig. 3.2). Terpal, Cerone and TIBA also produced less secondary tiller buds at the lower nutrient level. There was no effect of nutrient level in GA_3 and BAP treated plants (Table 3.2). Tiller emergence was little effected by nutrient level with the exceptions of Terpal and Cerone treated plants where it was significantly reduced at the lower nutrient level (Table 3.3). Lengths of T1 and T2 were reduced by about 50% in control plants at the low nutrient level at the first harvest. In contrast there was no effect of nutrients on T1 and T2 length in any of the PGR treated plants (Table 3.4). However, by the second harvest T1 and T2 buds in all plants were shorter at the lower nutrient level (Table 3.5). At the third harvest, the lengths of both

Table 3.6 Effect of PGR and nutrient treatments on the percentage distribution of dry weight to all tiller buds collectively and individually at 15 days after application.

	C	T	Cr	TIBA	GA_3	BAP
			(a) 100% nutrient level			
Total	36.7	39.6	35.4	31.7	26.9*	27.9*
T1	16.0	16.2	18.0	18.0	13.0*	16.0
T2	13.4	10.0*	9.4*	11.8	11.0*	9.7*
T3	2.6	2.4	3.9*	0.9*	2.3	1.8*
T4	0.4	0.3	1.4*	0.1*	0.1*	0.3*
T5			<0.1			
CT			2.4	0.6	0.3	
T1P	3.3	7.1*	<0.1*	<0.1*	<0.1*	<0.1*
T2P	0.5	0.8*	<0.1*	0.3	<0.1*	<0.1*
Others	0.5	2.7*	0.2	0.1*	<0.1*	0.1*
			(b) 20% nutrient level			
Total	27.3	33.4*	21.6*	33.5*	18.7*	28.4
T1	15.1	16.1	10.3*	16.3	7.0*	18.4
T2	10.0	9.9	8.1	9.5	9.1	9.7
T3	1.9	0.9	3.0	2.7	2.5	0.1*
T4	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
T5			<0.1			
CT			<0.1			
T1P	0.1	3.5*	<0.1	3.2*	<0.1	<0.1
T2P	<0.1	0.2*	<0.1	0.1	<0.1	<0.1
Others	0.2	2.7*	0.1*	1.7*	<0.1*	0.1

primary and secondary tiller buds were significantly reduced at the 20% nutrient level in control, Terpal and Cerone treated plants. The effects of TIBA, GA_3 and BAP on bud length were not influenced by nutrient level (Fig. 3.4 and 3.5).

There was a significant effect of nutrient supply on dry weight distribution to tiller buds (Table 3.6). In control plants the allocation of dry weight to buds was reduced by 26% at the low level of nutrients. Similarly the allocation of dry weight to buds in Terpal, Cerone and GA_3 treated plants was also reduced at the low nutrient level (by 16, 39 and 31% respectively). There was no effect of nutrients on the dry weight distribution to buds in those plants treated with TIBA or BAP (Table 3.6).

Main shoot and root growth.

Besides influencing bud production and growth, the treatments also modified the growth of other parts of the plant. At the 100% nutrient level all treatments caused some reduction in MS height (as measured from the base of the plant to the newest leaf ligule) with the exception of GA_3 (Fig. 3.6A). Terpal, Cerone and BAP all reduced MS height only 5 days after application, TIBA did not reduce MS height until 10 days after application. The effects of Terpal, TIBA and BAP were significant ($p<0.01$) by 15 days after application, Terpal having the greatest effect, reducing MS height by 13%. In contrast, GA_3 increased MS height by 18% after only 5 days after application and maintained this increase thereafter (Fig. 3.6A). At the lower nutrient level, Terpal, Cerone and BAP had all reduced MS height only 5 days after application by between 15 and 26%. As time went on the treatments had less effect so that by 15 days after application none of the treatments, with the excepton of GA_3, significantly modified MS height. Again GA_3 increased MS height at 5 days after application, by about 26%

Fig. 3.6

Effect of PGR and nutrient treatments on:

(A) MS height with time.

PGR treatments:

○ Control	▲ TIBA
● Terpal	□ GA_3
△ Cerone	■ BAP

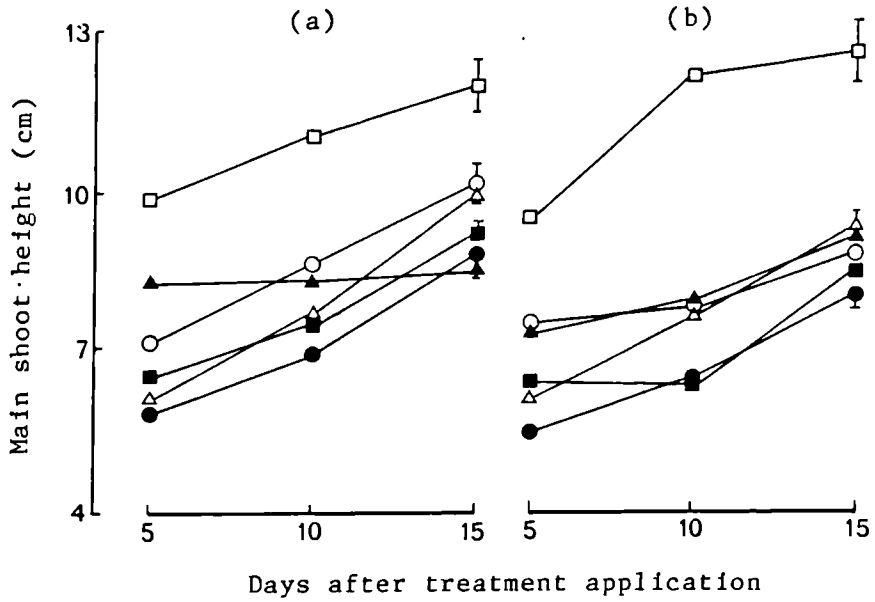
(B) Length of the root system at 15 days after treatment application.

Nutrient supply level:

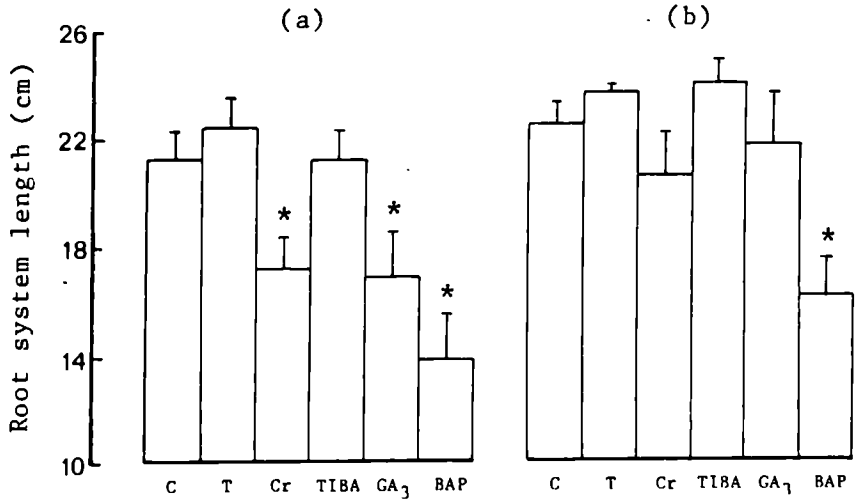
(a) 100% (b) 20%

Vertical lines represent $\pm$SE.

A


(a)
(b)
Main shoot height (cm)
13
10
7
4
5
10
15
Days after treatment application

B


(a)
(b)
Root system length (cm)
26
22
18
14
10
C
T
Cr
TIBA
GA3
GA7
BAP
*

and maintained this increase thereafter (Fig. 3.6A). The MS height of GA_3 treated plants was similar at both nutrient levels whereas MS height was less at the 20% nutrient level in control plants and other PGR treated plants (Fig. 3.6A).

At 15 days after treatment application Cerone, GA_3 and BAP reduced the depth of rooting (length of the longest root) by about 25% at the high nutrient level (Fig. 3.6B) whereas Terpal and TIBA had no effect. At the lower nutrient level BAP significantly reduced the length of the root system (by 29%) but all other PGR treatments had no effect on depth of rooting. Roots were longer in control plants and in all PGR treated plants at the lower nutrient level (Fig. 3.6B).

At GS 15, 15 days after application, Terpal had no significant effect on total plant dry weight at either nutrient level although at the high nutrient level the dry weight of the MS was reduced and that of the tiller buds increased slightly (Fig. 3.7). Cerone significantly ($p<0.05$) reduced total plant dry weight at both nutrient levels, and this was mainly due to a reduction in the dry weight of roots and tillers. TIBA reduced ($p<0.05$) total plant dry weight at the 100% nutrient level and increased ($p<0.05$) it at the low level of nutrients, this was due to the reduction and increase respectively, in dry weight of tiller buds. GA_3 also reduced ($p<0.01$) total plant dry weight at the higher nutrient level, since the dry weight of roots and tiller buds was decreased. At the lower nutrient level GA_3 had no effect on total plant dry weight, but that of the MS was increased and that of the tiller buds reduced. BAP reduced ($p<0.01$) total plant dry weight at both nutrient levels by decreasing the dry weight of all fractions. Total plant dry weight in control and Terpal and Cerone treated plants was less at the low nutrient level whereas there was little effect of nutrient level on the total dry weight of TIBA, GA_3 and BAP treated

Fig. 3.7

Effect of PGR and nutrient treatments on the distribution of dry weight between roots, MS and tiller buds (and emerged tillers) at 15 days after treatment application.


Root


MS


Primary tiller buds/tillers

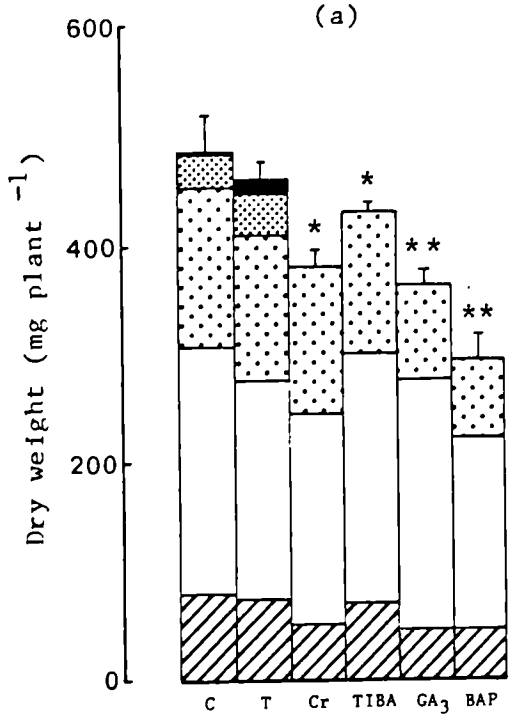

Secondary tiller buds/tillers

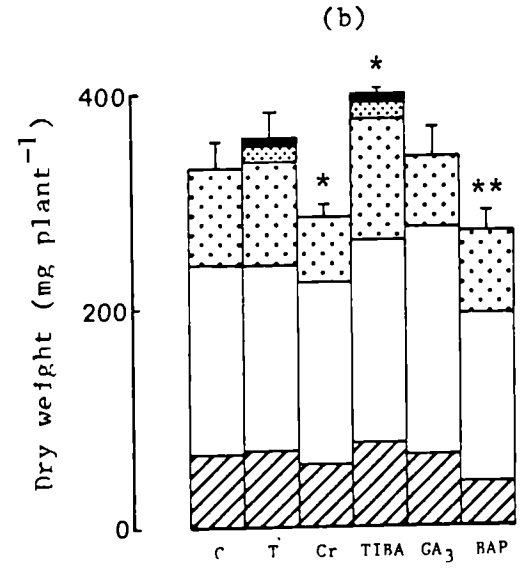

Tertiary tiller buds/tillers

Nutrient supply level:

(a) 100% (b) 20%

Vertical bars represent ±SE.


(a)
600
400
200
0
Dry weight (mg plant^{-1})
*
*
**
**
C
T
Cr
TIBA
GA$_3$
BAP


(b)
400
200
0
Dry weight (mg plant^{-1})
*
*
**
C
T
Cr
TIBA
GA$_3$
BAP

plants (Fig. 3.7)

At the high nutrient level, Terpal, TIBA and BAP had no effect on shoot:root dry weight ratio (Table 3.7). This ratio was increased by the Cerone and GA_3 treatments due to the reduced dry weight of the root system. At the low nutrient level Terpal, Cerone, TIBA and GA_3 had no effect on the shoot:root ratio whereas it was increased by BAP again reflecting the reduced dry weight of the root system. With the exception of BAP, shoot:root ratio was reduced at the low nutrient level in all plants reflecting the greater allocation of dry weight to the root system. The shoot:root ratio of BAP treated plants was similar at both nutrient levels (Table 3.7).

Table 3.7 Effect of PGR and nutrient treatments on shoot:root dry weight ratio at 15 days after application

Nutrient level	PGR treatment					
	Control	Terpal	Cerone	TIBA	GA_3	BAP
100%	5.1	5.2	6.5*	5.3	6.7*	5.3
20%	4.0	4.2	3.9	4.1	4.3	5.6*

DISCUSSION

Although apical dominance is not thought to exert a major influence during the early phase of tillering in plants grown at high nutrient levels, the application of certain PGRs (Terpal, Cerone and TIBA) promoted the development and outgrowth of tiller buds and modified their early growth as emerged tillers. Leaf appearance rate was also increased and this facilitated a higher production of tiller buds since it provided more axil sites for buds. In contrast the application of GA_3 inhibited the outgrowth of tiller buds. Growth in a low nutrient regime also reduced tiller bud production and tiller emergence, and in particular the response to Terpal and Cerone. The significance of these observations in terms of the internal control of bud development and early tiller growth will now be discussed.

The promotory effect of Terpal and Cerone on the growth and development of tiller buds was accompanied by a marked decline in the growth of the MS. Thus it may be concluded that the retardation of MS development, which is known to be a primary effect of these PGRs (Jensen and Andersen, 1981; Herbert, 1982; Hill et al., 1982) may change apical dominance either by modifying the hormonal balance between the MS and axillary tiller buds or by allowing a greater supply of resources such as carbohydrate and nitrogen to become available for tiller bud growth and development. As ethephon, an ethylene releasing compound, is common to both Terpal and Cerone it seems likely that the characteristic rapid stimulation of tiller bud production and growth is due to an increase in the internal levels of ethylene. In pea, Andersen (1976) showed that ethephon application reduced apical dominance, particularly in conditions where apical dominance was already diminished, for example, high irradiance and/or high CO_2. Burg (1973, in Phillips, 1975) showed that ethylene reduced apical dominance but only if applied as a pulse

lasting from 2 to 24 hours. Harrison and Kaufman (1982) reported that ethylene stimulated tiller bud development in oat stem segments and suggested that it promoted the swelling of the bud during the onset of bud growth rather than overcoming a dormancy mechanism. There is some evidence that an increase in the level of ethylene may inhibit polar basipetal transport of auxin in cotton (Gossypium hirsutum L.) (Morgan and Gausman, 1966) and in pea (Burg and Burg, 1967) and that ethylene may reduce auxin biosynthesis in the apical meristem of Coleus blumei (Ernest and Valdovinos, 1971). Thus ethylene-releasing PGRs may promote tiller bud outgrowth by interfering with an auxin mediated system of relatively weak apical dominance. This view is supported by the results obtained with TIBA, an auxin transport antagonist. As in other experiments with grasses and cereals (Leopold, 1949; Jewiss, 1972; Langer et al., 1973) the application of this compound promoted tiller bud outgrowth, but in contrast to the Terpal and Cerone treatments this was not generally accompanied by a reduction in the growth of the MS. Thus the retardation of MS growth is not an essential requirement for the promotion of tiller bud outgrowth, and as such a wholly hormonal control system regulating bud outgrowth largely independent of assimilate/nutrient supply from the MS is possible. In this respect the TIBA treatment appeared to be more effective in promoting the elongation of tiller buds at the low as opposed to the high nutrient regime.

The supply of auxin to tiller buds from the MS apex may, therefore, be important in imposing apical dominance in the early stages of plant development in the classical manner described for dicotyledonous plants (Phillips, 1975; Rubenstein and Nagao, 1976). The relationship between auxin and ethylene described above, is further implicated in apical dominance since the inhibition of bud outgrowth after IAA application to plants appears to be brought about by an auxin-induced release of

endogenous ethylene (Burg and Burg, 1967, 1968; Fuchs and Lieberman, 1968; Abeles, 1973; Blake et al., 1983; Hillman, 1984). Burg and Burg (1968) reported that the inhibition of bud growth in pea plants and the intensity and duration of ethylene production were exactly correlated at all levels of IAA application. Furthermore, continuous exposure of intact plants to ethylene alone inhibited bud growth and also the growth of the terminal meristem. The latter response maybe an example of a direct growth inhibition as ethylene is known to inhibit cell division in meristematic tissues in pea plants, perhaps by antagonizing the synthesis of DNA (Apelbaum and Burg, 1972; Kang and Burg, 1973). Indeed in the present experiment it can be suggested that there was a direct inhibitory effect of ethylene on cell division or cell enlargement since the application of Cerone resulted in an overall growth retardation; the length and dry weight of the MS and roots were reduced. Also the reduced growth of the tiller buds, particularly the secondary tiller buds, after their initial stimulation by release from apical dominance, could be due to a direct inhibitory effect of ethylene. Thus ethephon application to plants illicits both direct inhibitory effects on meristematic growth and indirect effects by interference with auxin production and transport. It is likely that the stimulatory effect on lateral bud outgrowth of a brief period of ethylene treatment, either as a pulse for up to 24 hours or as an application of ethephon, derives from an interuption of auxin transport from the apical meristem. From evidence in the literature it appears that there may be a feedback mechanism at work between auxin and ethylene in the plant, since IAA application increases ethylene production and increased ethylene concentrations are known to depress auxin production and transport. Exogenous applications of either of these growth substances may disrupt the balance between them in favour of, or against, lateral bud growth.

However, as well as its interference with auxin, there is some evidence that ethylene may also interact with gibberellin action (Scott and Leopold, 1967; Valdovinos et al., 1967; Goldschmidt et al., 1977). As GA_3 promotes stem elongation and leaf extension in grasses and cereals then the reduction in elongation of the MS and the corresponding increase in tiller bud development following Terpal and Cerone application, may also reflect some antagonism of GA_3 action. In the case of Terpal however, as well as ethephon the mepiquat chloride component may also directly block GA_3 biosynthesis (Jensen and Andersen, 1981) and so retard MS growth. There was some evidence in the present experiment that Terpal reduced the elongation of the MS and primary tillers to a greater extent than Cerone. There was little difference in the degree of tiller bud stimulation between these PGRs but Terpal tended to promote the outgrowth of secondary tiller buds whereas Cerone characteristically promoted T5 and CT. With respect to the mepiquat chloride component of Terpal it is pertinent to note that formulations of the closely related compound chlormequat chloride (CCC), a gibberellin biosynthesis inhibitor, but without any ethylene producing capacity, also stimulate tillering as well as temporarily retarding the growth and development of the MS (Tolbert, 1960; Humphries et al., 1965; Koranteng and Matthews, 1982). This well documented response suggests that the accelerated outgrowth of tillers is related to a change in assimilate/nutrient availability within the plant, as a result of reduced competition between the developing MS and tiller buds.

In contrast to this response and in complete opposition to the physiological response to additional ethylene, the application of GA_3 reduced the growth and development of tiller buds, especially those at the high nutrient level, and accelerated the growth of the MS. Similar observations of reduced tillering following GA_3 application to plants

have been widely reported (Jewiss, 1972; Phillips, 1975; Johnston and Jeffcoat, 1977; Cottrell et al., 1982; Isbell and Morgan, 1982). It can be suggested that by promoting the growth of the MS and emerged tillers GA_3 accentuates resource competition between the MS and newly developing tiller buds such that the latter are suppressed. Jewiss (1972) reported that arrested tiller buds in GA_3 treated plants could not be induced into growth by the direct application of sucrose; this indicates that some factor other than carbohydrate supply restricted bud development. On the other hand there is the possibility that GA_3 may promote auxin transport (Pilet, 1965; Valdovinos et al., 1967) and this could account for the enforced apical dominance observed after GA_3 application. Experiments with peas have shown that a more complete inhibition of lateral buds by application of auxin and GA_3, compared to auxin alone, resulted in higher amounts of IAA in the immediate vacinity of inhibited buds (Jacobs and Case, 1965).

Although synthetic and endogenous cytokinins, applied generally to whole plants or locally to suppressed buds, have been found to promote lateral bud outgrowth (Jewiss, 1972; Langer et al., 1973; Field and Jackson, 1974; Clifford and Langer, 1975; Johnston and Jeffcoat, 1977; Sharif and Dale, 1980a; Isbell and Morgan, 1982) there was relatively little effect of BAP on tiller bud growth and development in the present study. The greatest response was shown by the coleoptile bud, and particularly at the low nutrient level. It can be suggested that the timing of BAP application may have been coincident with a critical stage of development of this bud. Sharif and Dale (1980a) found that applications of cytokinins to leaves of barley seedlings were ineffective in promoting bud outgrowth, and there is some evidence that the poor transport of BAP from leaf to bud may limit its physiological action (Johnston and Jeffcoat, 1977). Nevertheless there was a marked effect of BAP application in this experiment as the dry weight of both

the MS and roots were significantly reduced. A similar response has been observed by other workers (Langer et al., 1973; Johnston and Jeffcoat, 1977; Richards, 1980; Sharif and Dale, 1980a).

The response to the low nutrient regime, where tiller bud outgrowth was reduced thereby increasing the degree of apical dominance, followed the well defined pattern for plants growing with a restricted supply of nitrogen (Phillips, 1975; McIntyre, 1977; Wareing, 1983). Similarly the shoot:root dry weight ratio was altered in favour of root growth as observed in other experiments (Drew et al., 1973; Brouwer, 1983). The simplest explanation for this overall response is that competition for nutrients between developing axes and buds increases and as a result the growth of the MS and roots are maintained at the expense of axillary growth (McIntyre, 1977). Thus the development of secondary tillers is greatly restricted. On the other hand, nutrient deficiency is known to have a marked effect on the levels of endogenous growth substances (Wareing, 1983). There is evidence that both auxin and GA_3 levels are reduced in the shoot apices of nitrogen-deficient tomato (Rajagopal and Rao, 1974) and that low nutrient levels reduce cytokinins in leaves, buds and roots of sunflower (Helianthus annuus) (Salama and Wareing, 1979). In the present study, Terpal and Cerone treated plants responded in a similar way to control plants to the low nutrient supply with bud number and tiller outgrowth greatly decreased at the lower nutrient level. However, the effects of TIBA, GA_3 and BAP on buds at GS 15 were the same at both levels of nutrient supply. This latter observation may be related to reductions in endogenous growth substances at low nutrient levels. TIBA applicaton may have diminished already low auxin levels at the 20% nutrient level, resulting in the greater (relative to control plants) increase in bud production and growth. In GA_3 treated plants, bud production and growth were also greater, in comparison to controls, at the lower nutrient level. The

inhibitory effect of GA_3 on lateral buds would be expected to be smaller at the low nutrient level if it is assumed that endogenous GA_3 was diminished. The relationship between BAP application and nutrient supply was not clear.

Studies of tiller bud outgrowth such as that described here are of practical importance in manipulating crop yield. We now know that auxin and GA_3, and their antagonists, TIBA, ethylene and mepiquat chloride, are central to an understanding of the factors controlling bud outgrowth. From the present study it was not possible to separate the effects of auxin and ethylene. It is possible that ethylene is more important because it is known that apical dominance is weak in young plants (Rubenstein and Nagao, 1976) and it has been suggested that auxin has little influence on tillering at this stage.

CHAPTER 4

TILLER DEVELOPMENT AND SURVIVAL

INTRODUCTION

As tiller productivity is a major yield-determining factor an understanding of the pattern of tiller development is important, especially in view of potential manipulation by fertilizer and growth regulator applications. One significant feature of tiller life history is that tiller production is suspended during the final stages of MS stem elongation (Thorne, 1962; Bunting and Drennan, 1966; Cannell, 1969a; Chapter 2, present thesis). The size of a tiller at this time is considered important in determining its survival (Garcia del Moral et al., 1984). This pre-ear emergence decline in tiller number is less marked (Thorne, 1962) or virtually absent (Aspinall, 1961) with an increased supply of nutrients at regular intervals. Another feature of the pattern of tillering is that a hierarchical relationship exists between the MS and tillers (Rawson, 1971; Fraser et al., 1982; Chapter 2, present thesis) resulting from the outgrowth of buds from MS leaf axils in a time sequence. This hierarchy is maintained during tiller growth and development by competition between the meristems. Management of this internal competition offers an opportunity to enhance tiller productivity. A greater nutrient supply weakens the dominance of the MS over the tillers (Wareing, 1983) resulting in a more synchronous development of MS and tillers (Aufhammer, 1980). Uniformity of ear emergence and ear size is a desirable characteristic, although it may not result in an overall yield increase. Similar effects on tiller hierarchy have been obtained after applications of growth retardants. For example, increased synchrony of tiller development in barley has been reported after application of CCC (Koranteng, 1981; Koranteng and Matthews, 1982) and mepiquat chloride (Cartwright and Waddington, 1982).

The aim of the following experiments, conducted on single plants in

pots, was to gather detailed information on the development and fate of individual tillers, after the onset of bud growth, and to determine how far this can be manipulated, especially by the application of PGRs. This approach may indicate the way that internal control mechanisms act in regulating tiller growth, development and survival.

EXPERIMENTAL

Experiment 4.1 Preliminary glasshouse experiment.

In this experiment the behaviour of spring barley plants was studied to obtain basic information on tillering in spaced plants grown under glasshouse conditions with and without the addition of nutrients at the time of MS ear emergence.

MATERIALS AND METHODS

This experiment, and the following experiments (Experiments 4.2 to 4.6), were conducted under glasshouse conditions at Pen-y-Ffridd Field Station, UCNW, Bangor. Experiments 4.1, 4.2, 4.3 and 4.6 were undertaken in the "old" glasshouse suite with a minimum temperature of 18°C during the photoperiod; the temperature was often several degrees above this value but was controlled by the operation of extractor fans when the glasshouse temperature reached 21°C. At night the temperature was maintained at 17°C. Natural daylight was supplemented by 400 watt mercury vapour lamps to give a 16 hour daylength.

Seeds of spring barley, cv. Triumph, were sown individually on 14 January, 1982 in plastic pots (11.25cm diameter x 8.75cm depth) containing steam sterilized John Innes No.1 potting compost. This compost was made up of loam, peat and coarse sand in the ratio 7:3:2 respectively plus Vitax Q4 complete fertilizer at 3.6g per litre of compost, pH was adjusted to 6.5 by the addition of lime. The top 2cm was sieved and levelled to provide consistency throughout the pots for seedling establishment. The pots were placed on a wire mesh bench at an approximate density of 20 plants m^{-2}. Such spacing allowed the plants to tiller freely and simplified observation and data collection. The pots were watered twice daily with tap water at soil level with a fine

spray. After emergence of the MS ear half of the plants were supplied with 100 cm^3 pot^{-1} of full strength Long Ashton nutrient solution (described in Hewitt, 1966) every 2 to 3 days. During the final stages of grain ripening no water or nutrient solution was supplied. Sprays of Benlate (0.05 g dm^{-3} + wetting agent) were applied as required to control infections of mildew (Erysiphe graminis). Emerging tillers were identified and ringed with coloured plastic as before (Chapter 2) and their growth and development was monitored throughout the duration of the experiment. Tillers and all leaves of 10 replicate plants were identified and counted 2 to 3 times weekly until anthesis and weekly thereafter, and at final harvest ears and grains per ear were counted.

RESULTS

Due to adverse external conditions tillering did not commence until 7 weeks after sowing and then continued for 19 days, after which no more tillers were produced unless nutrients were supplied. The end of tillering coincided with a phase of rapid MS stem elongation (Fig. 4.1). The inhibition of tillering during this period was alleviated by the application of nutrients. Within 4 days of the first nutrient application tillering resumed and continued until watering was stopped during the final stages of grain ripening 17 weeks after sowing (Fig. 4.1). Where no additional nutrients were applied tiller death began between 22 and 28 days after tiller production had ceased, around 13 weeks after sowing. This coincided with MS ear anthesis and early grain filling (Fig. 4.1). The addition of nutrients delayed the onset of tiller death by about a week (Fig. 4.1). At final harvest the plants supplied with additional nutrients had produced about 4 times as many tillers as control plants (Fig. 4.1 and Table 4.1). Also the plants supplied with additional nutrients had almost 7 times as many ear-bearing tillers than control plants (Table 4.1). Tiller survival was increased from 51% to 69% by the addition of nutrients. In control

Fig. 4.1

Tillering pattern of spring barley grown under glasshouse conditions and the effect of nutrient solution applied at MS ear emergence.

○ Control (without nutrients)

● With nutrients

—— Total tiller number

----- Dead tiller number

A : Rapid MS stem elongation

B : MS ear emergence

C : MS anthesis

Vertical bars represent ±SE.

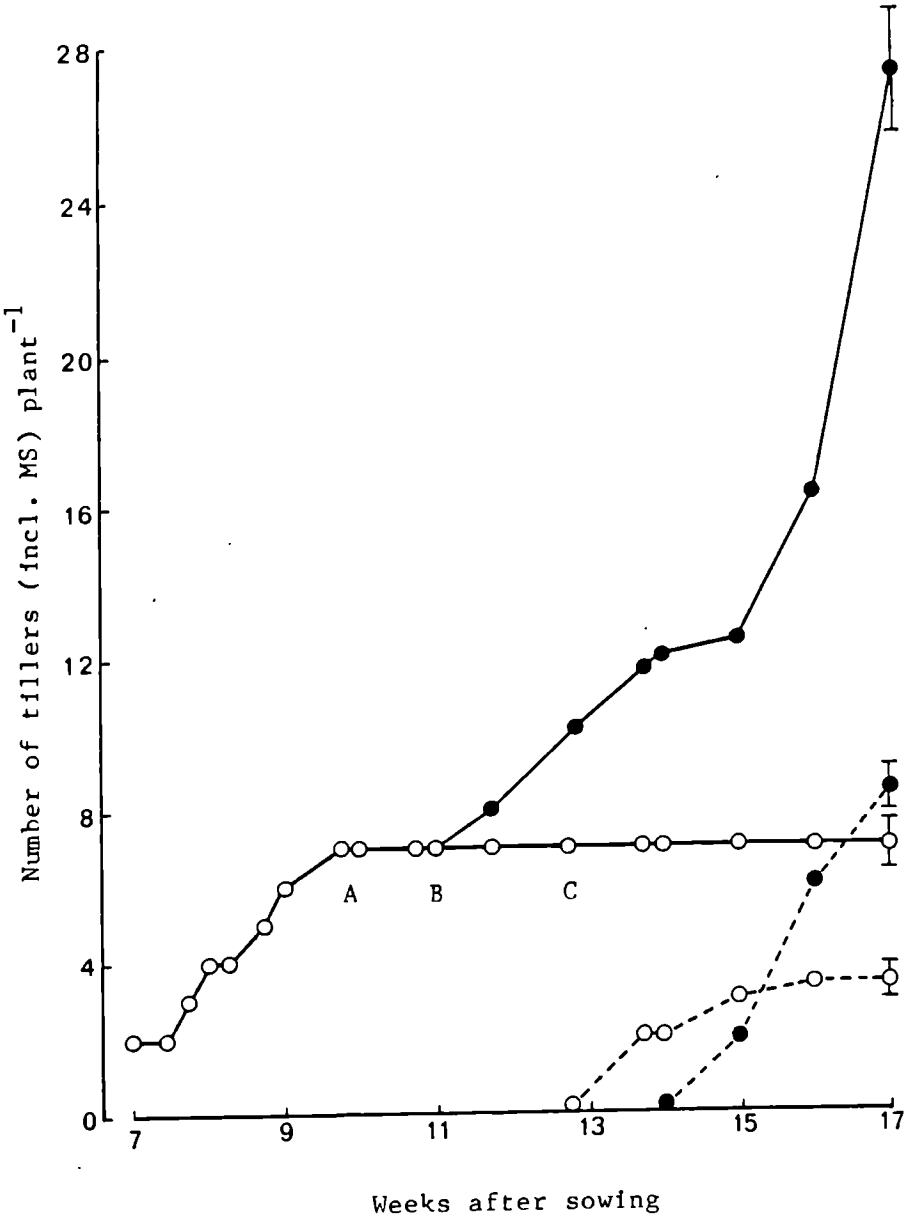

28
24
20
16
12
8
4
0
Number of tillers (incl. MS) plant^{-1}
A
B
C
7
9
11
13
15
17
Weeks after sowing

Table 4.1 Effect of additional nutrients on percentage tiller production, tiller lifespan, percentage of tillers bearing ears and grain number per ear.

Tiller identity (in order of appearance)	% emerged tillers	Mean tiller lifespan (weeks)	% ear-bearing tillers	Mean number grains ear^{-1}
(a) Without additional nutrients:				
CT	70	6	20	10.0±0.0
T1	100	10	100	20.6±2.0
T2	100	9	80	15.0±1.3
T1P	100	5	20	11.0±0.0
CTP	20	4	0	
T3	100	5	40	14.0±1.0
T1,1	40	4	0	
T2P	40	4	0	
T4	30	4	0	
Total (excl. MS)	6.0±1.1		2.6±0.5	
(b) With additional nutrients:				
CT	80	10	80	20.0±0.8
T1	100	10	100	25.0±0.8
T2	100	9	100	22.6±0.8
T1P	100	9	100	20.0±0.0
CTP	80	8	80	15.0±1.1
T3	100	8	100	21.2±1.0
T1,1	100	8	100	14.0±1.0
T1,2	100	6	70	10.0±0.0
T4	100	6	100	20.0±0.0
T2P	100	6	100	22.0±0.0
T3P	100	6	100	10.0±0.0
T1P,1	100	5	90	<5.0
T2P,1	100	5	80	"
T2,1	100	5	80	"
T3P,1	100	4	70	"
T4P	100	4	80	"
CTP,1	100	3	60	"
T2,2	100	3	60	"
T1,3	90	2	50	"
T4P,1	80	2	60	"
T3,1	100	2	40	"
CT,1	90	2	30	"
T1P,2	90	2	30	"
T3,2	70	2	0	0
T2P,2	70	2	0	0
T4,1	60	2	0	0
CT,2	50	2	0	0
CTP,2	60	2	0	0
T1P,3	40	2	0	0
T1P,4	40	2	0	0
Total (excl. MS)	26.0±2.4		17.6±1.6	

plants all non-flowering tillers died during the time of grain filling whereas when nutrients were supplied about 23% of these tillers were still alive when watering was stopped prior to final harvest. In control plants tillers that survived to produce ears had a lifespan of at least 5 weeks. When additional nutrients were supplied tiller lifespans were increased. Also many higher order tillers with lifespans of less than 6 weeks survived to produce ears although these were very small with only 1 to 5 grains per ear (Table 4:1). The extra nutrients increased the number of grains per ear of all primary tillers and reduced the difference between them (Table 4.1). Unfortunately samples were lost from the drying oven before dry weights could be determined.

Consistent with the findings of Chapter 2 there was a distinct order of tiller appearance and tiller death. The majority of the plants had coleoptile tillers, these emerged first along with T1. The order of appearance was then as follows: T2, T1P, CTP, T3, T1,1, T2P, and T4 (Table 4.1). On dissection other buds were found, for example, T1,2, T2,1, T1,3, and T1P,1, but these did not grow out unless nutrients were added (Table 4.1). Generally it was the last tillers to appear, mostly secondary tillers, that died first. However, the coleoptile tillers although emerging first, died first. As in Chapter 2, a hierarchy of tiller size was evident, with the earliest emerged tillers being larger than the later emerged tillers (Table 4.2). The addition of nutrients resulted in the increased length of MS, T1, T2, and T3 stems by the final harvest and a decrease in the difference between the MS and T3 (Table 4.2).

Table 4.2 Effect of additional nutrients on tiller height at final harvest ±SE.

Tiller	Tiller height (mm)	
	Control	+Nutrients
MS	527.2± 16.9	617.2±24.6
T1	449.6± 71.4	579.2±16.1
T2	421.2± 32.9	511.5±20.4
T3	166.4+101.9	437.7+13.0

MS leaf production continued until about 11 weeks after sowing when 9 leaves had been produced, the addition of nutrients did not increase MS leaf production further (Fig. 4.2a). MS leaf senescence began at 9 weeks after sowing, this corresponded to L6 becoming fully expanded. Senescence continued until all 9 leaves were dead 15 weeks after sowing towards the end of grain ripening. After the addition of nutrients the rate of MS leaf senescence declined and senescence was complete one week later than in control plants (Fig. 4.2a). Tiller leaf production followed a similar pattern to tiller production for the first 10 weeks, with the production of leaves stopping around the time of rapid MS stem elongation which was also when tiller leaf senescence began (Fig. 4.2b). However, during the time when tiller production had stopped but before the onset of tiller death, leaf production increased rapidly (Fig. 4.2b). When nutrients were added, leaf production continued after it had stopped in control plants and the production of leaves was almost doubled. Leaf senescence was reduced by almost 50% until watering was stopped; senescence then increased rapidly (Fig. 4.2b). In control plants tillers that survived to ear production had produced all of their leaves by 12 weeks after sowing which corresponded to one week before MS ear emergence (Fig. 4.3a). Tillers with leaves expanding after this time did not survive. With the exception of CT, percentage tiller survival was correlated to final leaf number, for example, T1

Fig. 4.2

Pattern of leaf production and the effect of nutrient solution applied at MS ear emergence (week 11).

(a) MS leaf number.

(b) Tiller leaf number.

○ Control (without nutrients)

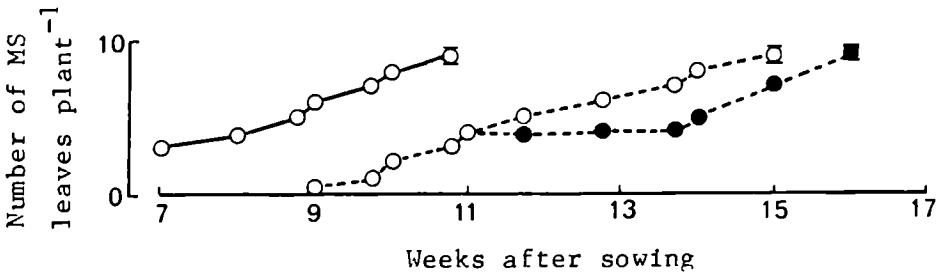
● With nutrients

—— Total leaf number

---- Dead leaf number

Vertical bars represent ±SE.

(a)


Number of MS leaves plant^{-1}
10
0
7
9
11
13
15
17
Weeks after sowing

(b)

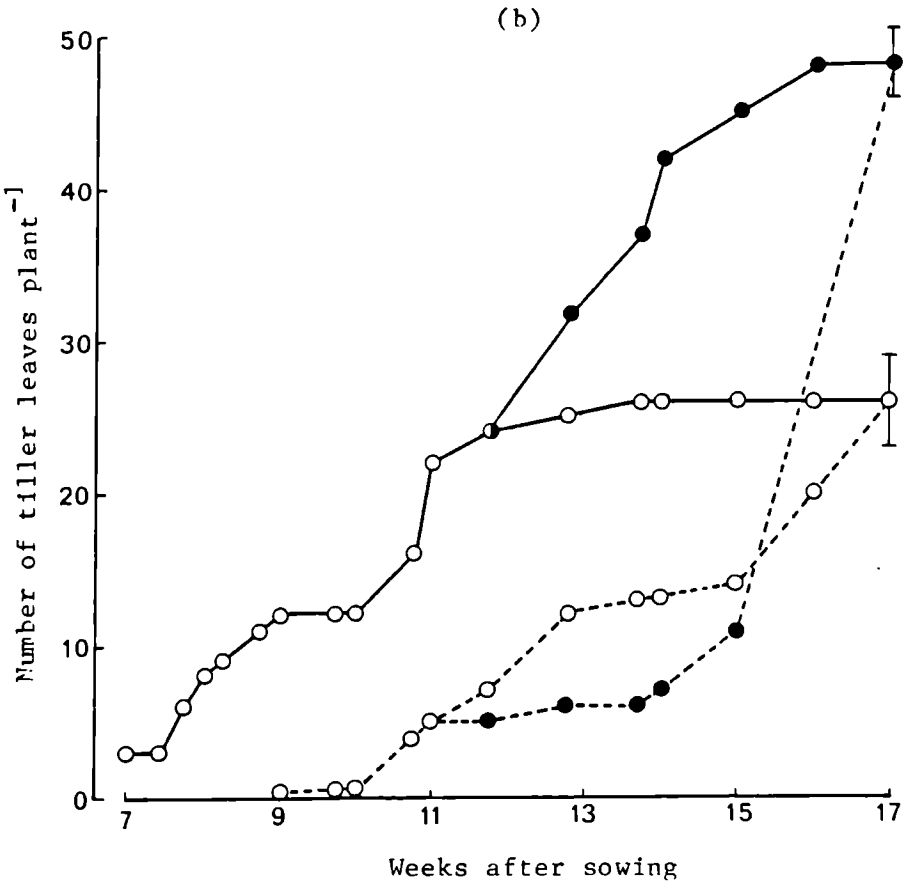

Number of tiller leaves plant^{-1}
50
40
30
20
10
0
7
9
11
13
15
17
Weeks after sowing

Fig. 4.3

Leaf production by individual tillers and the effect of nutrients applied at MS ear emergence (week 11).

(a) Control (without nutrients)

(b) With nutrients

Tiller identity, unless otherwise indicated on figure:

○ T1

● CT

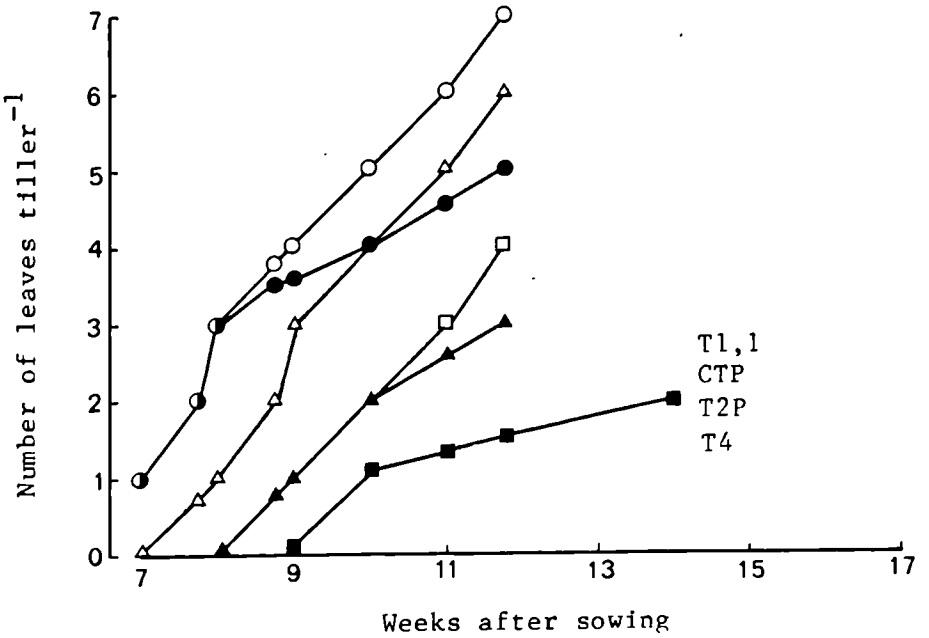
△ T2

▲ T1P

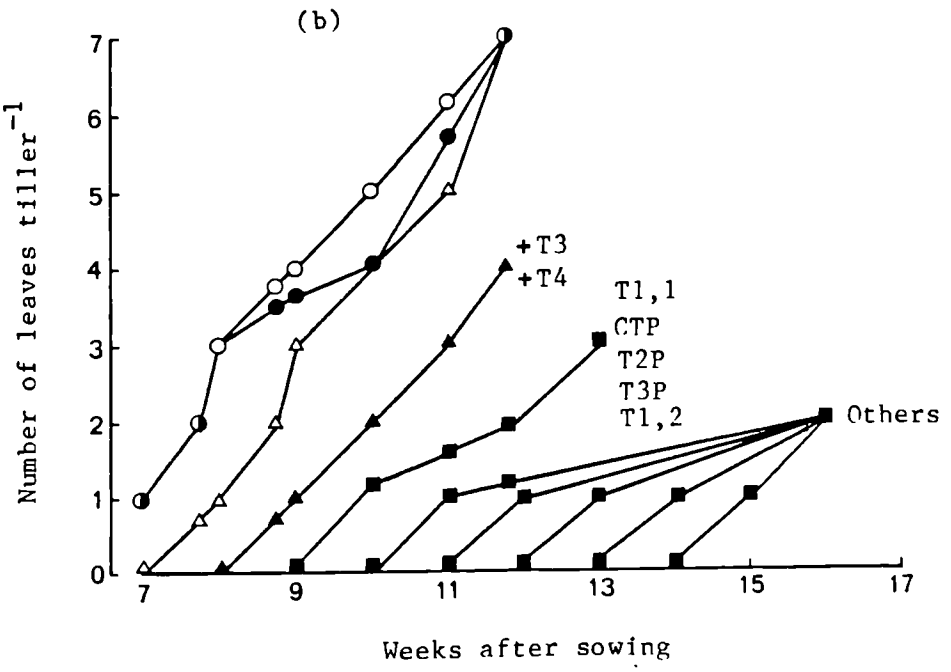
□ T3

■ All others

(a)


Number of leaves tiller^{-1}
0
1
2
3
4
5
6
7
7
9
11
13
15
17
Weeks after sowing
T1,1
CTP
T2P
T4

(b)


Number of leaves tiller^{-1}
0
1
2
3
4
5
6
7
7
9
11
13
15
17
Weeks after sowing
+T3
+T4
T1,1
CTP
T2P
T3P
T1,2
Others

had the highest percentage tiller survival and the highest number of leaves. CT survival was only 29% although it had more leaves than T2 and T3 both of which had greater tiller survival rates, that is, 80% and 40% respectively (Fig. 4.3a and Table 4.1). Tillers with less than 3 leaves did not survive. On addition of nutrients all tillers, except T1 and T3, produced more leaves. Unlike control plants, tillers with leaves emerging after 12 weeks after sowing survived to produce ears, although only tillers with at least 3 fully expanded leaves produced ears with more than 5 grains (Fig. 4.3b).

Experiment 4.2 Effects of growth retardants on tiller development.

There is evidence from Chapters 2 and 3 that Terpal can increase tiller production and modify development. Furthermore it has been found that Cerone (ethephon) can also increase early tiller bud outgrowth (Chapter 3) suggesting that it is the ethephon component of Terpal that is important in this respect. It was decided therefore to investigate the effects on tillering of 2 other stem shortening compounds that do not contain ethephon, namely CCC and Ancymidol. The following experiment sets out to describe and compare the effects of Terpal, CCC and Ancymidol on tiller development.

MATERIALS AND METHODS

Seeds of spring barley, cv. Triumph, were sown on 24 March, 1982 and grown as in Experiment 4.1. The pots were randomly assigned to 4 blocks, each block consisting of 3 replicates of 4 treatments. The treatments applied were; Terpal (2.5 dm^3 ha^{-1}) and CCC (4.2 dm^3 ha^{-1}) as a foliar spray, using a laboratory spray gun, until runoff and Ancymidol (2.5 μg pot^{-1}) as a root drench. An equivalent volume of water was applied to control plants. The treatments were applied at GS

14 when T1 and T2 were emerging. Tiller production and MS height were monitored weekly. Six replicate plants were also harvested 4 weeks after treatment application and at grain ripening for dry weight determination.

RESULTS

MS height was measured to indicate activity of the compounds; all 3 shortened the MS significantly ($p<0.05$) after only one week of application (Fig. 4.4a). Terpal had the most significant effect ($p<0.01$), reducing MS height by 34% at final harvest. The maximum height of these plants was reached 2 weeks later than in the other treatments (Fig. 4.4a). CCC had the least effect and by 4 weeks after treatment application there was no significant effect of CCC on MS height. Ancymidol reduced MS height by about 11% and this effect was significant until final harvest (Fig. 4.4a).

Tiller production began at GS 13 and continued until MS ear emergence, and was very high in this experiment. Terpal significantly ($p<0.01$) increased tiller production within one week after application and at final harvest had increased tiller production by 33% (Fig. 4.4b). Additional tillers in Terpal treated plants were due to the emergence of more T2, T3 and T4 tertiary tillers, particularly those arising from prophyll tillers. However, these extra tillers did not survive to ear production. Overall there was no significant effect of Terpal on the number of ear-bearing shoots per plant (Table 4.3). In contrast to Terpal, CCC significantly ($p<0.05$) reduced tiller production by 3 weeks after application by about 17% and this reduction was maintained until final harvest (Fig. 4.4b). At final harvest CCC significantly reduced the number of ear-bearing tillers per plant by 12% (Table 4.3). Ancymidol had no significant effect on tillering or on tiller survival (Fig. 4.4b and Table 4.3).

Fig. 4.4

Effect of growth retardants with time on:

(a) MS height and

(b) tiller number.

- ○ Control
- ● Terpal
- △ CCC
- ▲ Ancymidol

Vertical bars represent ±SE.

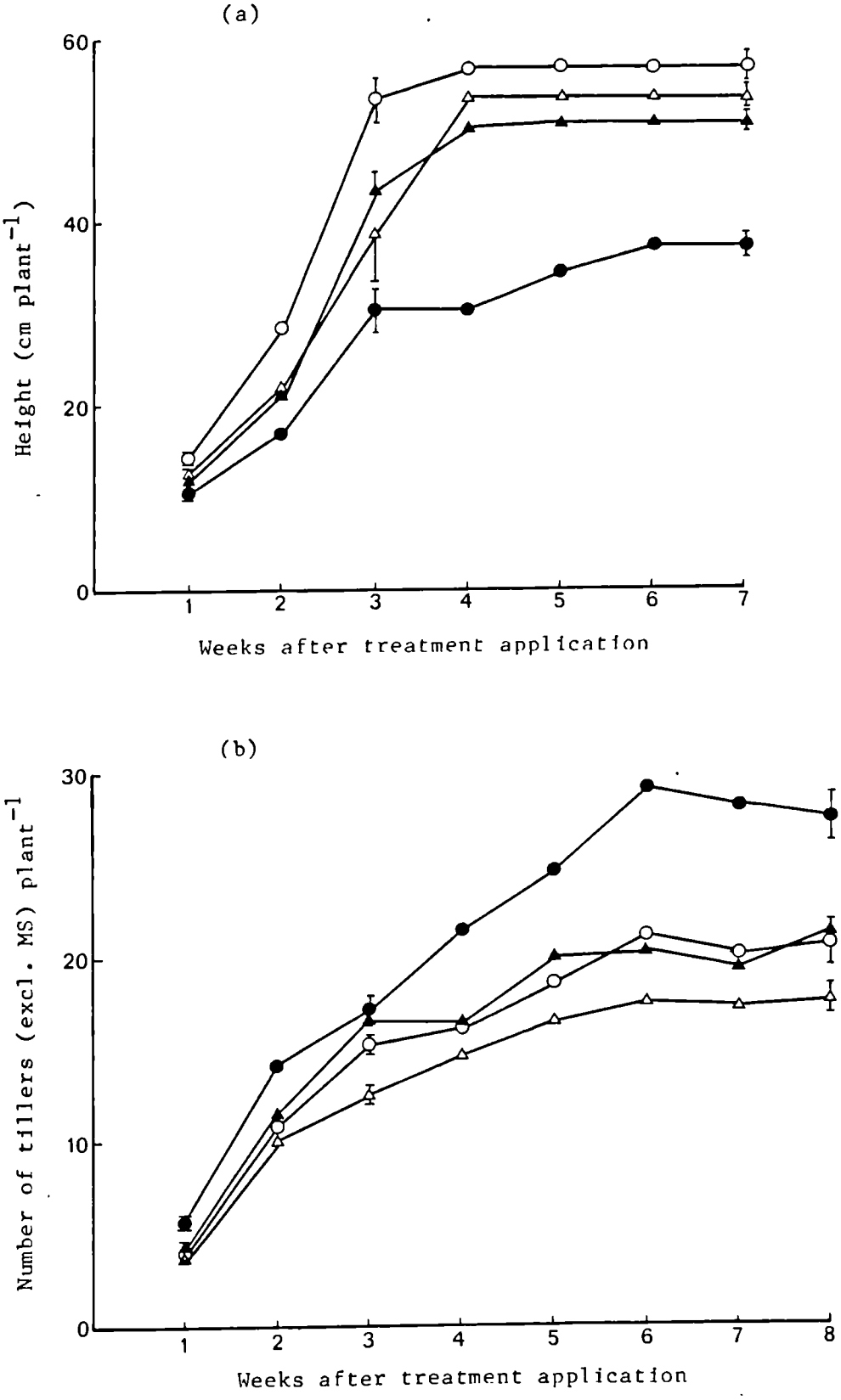

(a)
Height (cm plant^{-1})
60
40
20
0
1
2
3
4
5
6
7
Weeks after treatment application
(b)
Number of tillers (excl. MS) plant^{-1}
30
20
10
0
1
2
3
4
5
6
7
8
Weeks after treatment application

Table 4.3 Effect of growth retardants on the number of ear-bearing tillers per plant ±SE.

Treatment	Number of ears per plant
Control	18.17 ± 0.48
Terpal	17.67 ± 1.08
CCC	16.00 ± 0.52 *
Ancymidol	16.83 ± 1.20

Four weeks after application, Terpal, CCC and Ancymidol had all modified the normal hierarchical pattern of dry weight distribution between the MS, T1, T2, T3 and T4 (Fig. 4.5a). Terpal had the greatest effect, and in contrast to the control plants, there was little difference between the weights of T1, T2, T3 and T4 in the Terpal treated plants. Terpal significantly reduced the dry weights of the MS, T1 and T2 and increased that of T4 and the total dry weight of the secondary and tertiary tillers (Fig. 4.5a). Although CCC appeared to reduce the difference between the dry weights of MS, T1 and T2 (Fig. 4.5a) this is likely to be only a reflection of the more obvious effect of CCC which was to reduce ($p<0.05$) the dry weight of all tillers (Fig. 4.5a). Ancymidol had little effect on the dry weight of primary, secondary and tertiary tillers but it did seem to modify the distribution of dry weight between the tillers by significantly reducing the weights of MS and T1 ($p<0.01$ and $p<0.05$ respectively) (Fig. 4.5a). Terpal, CCC and Ancymidol all reduced total plant dry weight but only the effect of CCC was significant ($p<0.01$) (Fig. 4.5b).

By final harvest there was no significant difference in total plant dry weight between any of the treatments (Table 4.4). Terpal modified dry weight distribution by reducing the ear weights of all shoots except

Fig. 4.5

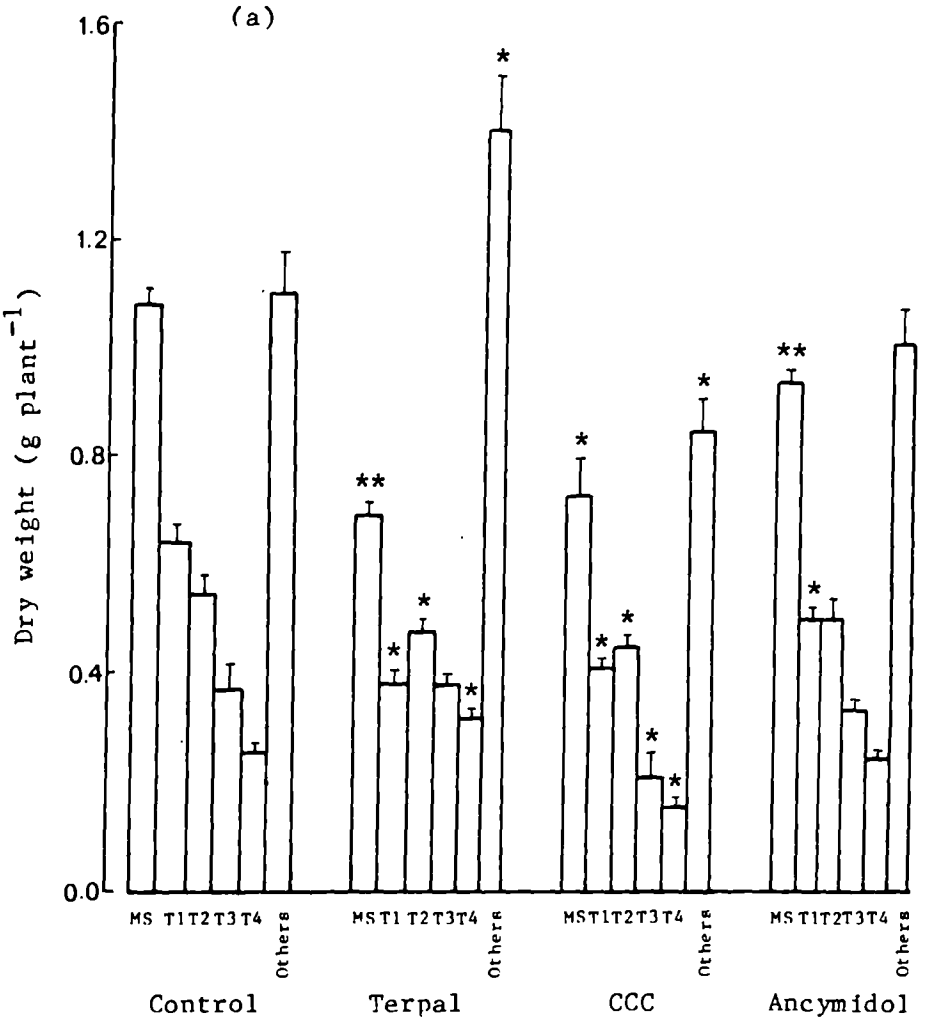
Effect of growth retardants at 4 weeks after application on:

(a) dry weight distribution between MS and tillers,

(Others = all secondary and tertiary tillers)

(b) total plant dry weight

Vertical bars represent ±SE.


(a)
Dry weight (g plant^{-1})
1.6
1.2
0.8
0.4
0.0
MS T1 T2 T3 T4 Others
Control
Terpal
CCC
Ancymidol

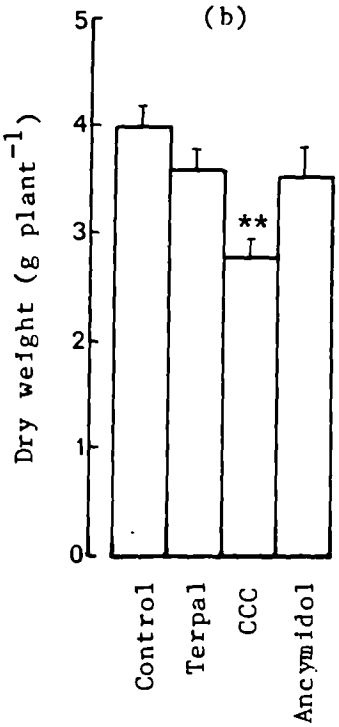

(b)
Dry weight (g plant^{-1})
5
4
3
2
1
0
Control
Terpal
CCC
Ancymidol

Table 4.4 Effect of growth retardants on dry weight distribution at final harvest ±SE.

Treatment	Ear weight (g)						Infertile tiller weight(g)	Total plant weight (g) (inc. straw)
	MS	T1	T2	T3	Others	Total		
Control	1.32±0.05	1.18±0.02	1.13±0.07	1.15±0.05	8.87±0.36	13.65±0.31	1.24±0.34	24.72±1.38
Terpal	1.00±0.07*	0.99±0.09	0.89±0.06*	0.86±0.05*	7.65±0.25*	11.39±0.87*	3.47±0.31**	23.28±1.03
CCC	1.29±0.05	1.12±0.04	1.08±0.04	0.99±0.04	8.96±0.38	13.44±1.03	0.63±0.20	23.11±2.03
Ancymidol	1.10±0.10	1.08±0.12	1.03±0.07	0.94±0.07*	7.51±0.30*	11.66±1.08*	1.35±0.56	22.58±2.17

T1, and increasing the distribution of dry weight to unproductive (non-surviving tillers) (Table 4.4). CCC had no effect on dry weight distribution, whereas Ancymidol reduced the dry weight of all ears except MS, T1 and T2; this reduction in ear weight was not enough to significantly reduce total plant dry weight (Table 4.4).

Experiment 4.3 A further investigation of the effects of Terpal on tiller development.

Of all the PGRs examined in the previous experiment, Terpal had the most profound effect on tillering. It was decided to investigate this response in more detail by conducting frequent harvests on plants during both the initial and late stages of tillering.

MATERIALS AND METHODS

This experiment was conducted as 2 sequential experiments. The first (Experiment A) was concerned with the initial phase of tiller development, and the second (Experiment B) with the later phase. Both were undertaken between April and July, 1983. Seeds of spring barley, cv. Triumph, were sown and grown as in Experiment 4.1. Terpal was applied as before at GS 13 to half of the plants; an equivalent volume of water was applied to control plants. The pots were randomly assigned along the bench. In Experiment A, plants were harvested at 2 to 3 day intervals over an 11 day period commencing immediately after Terpal application. In Experiment B, harvesting took place at approximately 6 day intervals after Terpal application and continued until the commencement of grain filling. Tiller production, MS height and dry weight of component plant parts of 6 replicate plants were measured. In Experiment B, roots were also excavated and a sample of the plants was harvested after grain ripening to assess tiller survival and yield.

RESULTS

Experiment A : Early tillering phase (GS 13 to 16)

As before Terpal caused a rapid increase in the number of tiller buds growing out and this effect was significant ($p<0.05$) after only 3 days following application (Fig. 4.6a). By GS 16 (11 days after application) Terpal had increased tiller production by 72%. This was due to the enhanced emergence of T2,1, T4, T3P, CT,1, CTP and CTP,1 tillers which had not emerged in control plants by GS 16.

Terpal significantly ($p<0.05$) reduced MS height at 3 days after application and by 11 days after applicaton it was reduced by 28% (Fig. 4.6b). There was no effect of Terpal on MS leaf number. Terpal decreased MS dry weight but this effect was not significant until 9 days after application; by 11 days after application it was reduced by 21% (Fig. 4.6c). The relative growth rate (RGR) of the MS was also reduced by Terpal at 9 and 11 days after application although this was not statistically significant (Fig. 4.7).

Generally total plant dry weight was unaffected by the Terpal treatment although it was significantly ($p<0.05$) reduced at the 9 day harvest (Fig. 4.6c). The RGR of the whole plant and of all tillers was significantly increased by the Terpal treatment between 3 and 6 days after application (Fig. 4.7). After this burst of growth the RGR either fell to below control rates (T1 and T2) or fell to rates not significantly different from controls (all other tillers) (Fig. 4.7). At the first harvest, 1 day after Terpal application, the dry weight of the T1 tiller was significantly ($p<0.05$) increased (Fig. 4.8a). At the next two harvests (3 and 6 days after Terpal application) there was no significant effect of Terpal on the dry weight of T1 or of T2, and by the 9 day harvest the dry weight of these early tillers was lower than

Fig. 4.6

Effect of Terpal on:

(a) live tiller number,

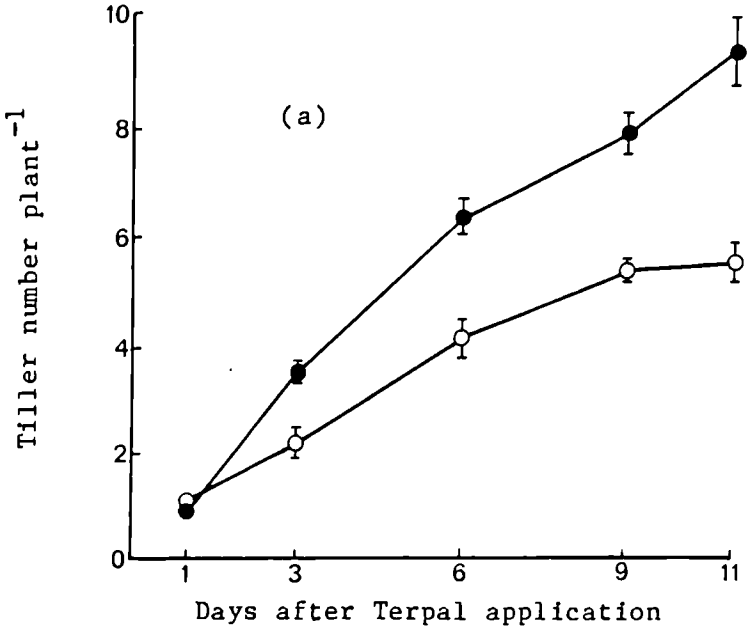
(b) MS height and

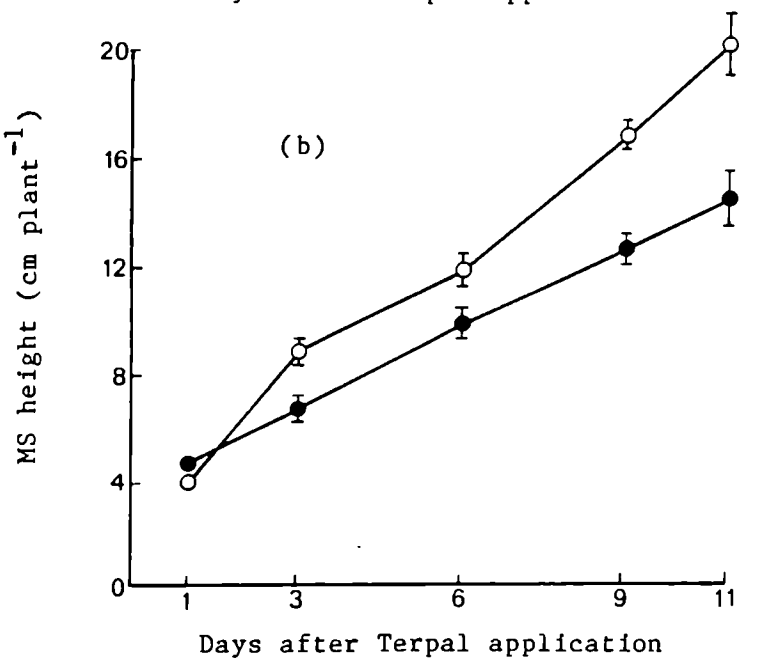
(c) dry weight, total(——) and MS (·····), between 1 and 11 days after application.

○ Control

● Terpal

Vertical bars represent ±SE.


(a)
Tiller number plant^{-1}
10
8
6
4
2
0
1
3
6
9
11
Days after Terpal application


(b)
MS height (cm plant^{-1})
20
16
12
8
4
0
1
3
6
9
11
Days after Terpal application

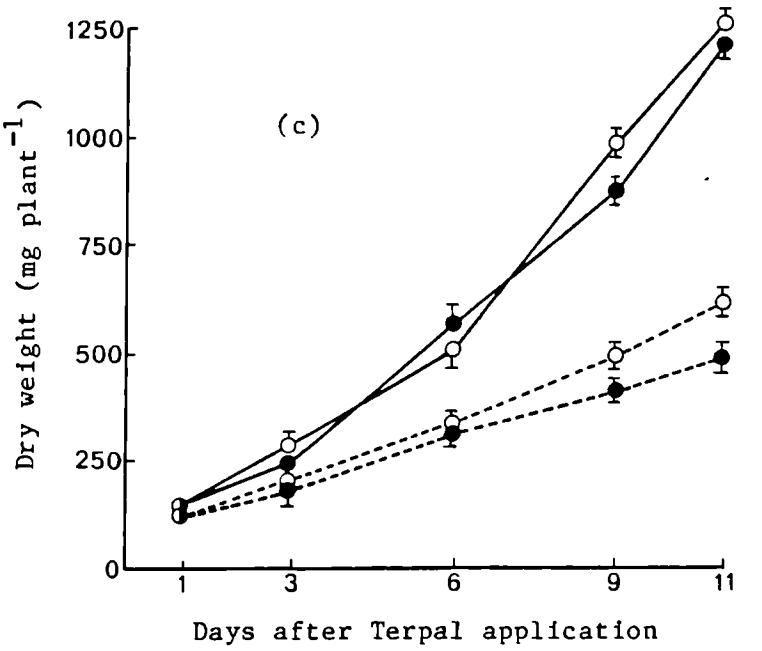

(c)
Dry weight (mg plant^{-1})
1250
1000
750
500
250
0
1
3
6
9
11
Days after Terpal application

Fig. 4.7

Effect of Terpal on the relative growth rate of the total plant and of individual tillers between 1 and 11 days after application.

—— Control

------ Terpal

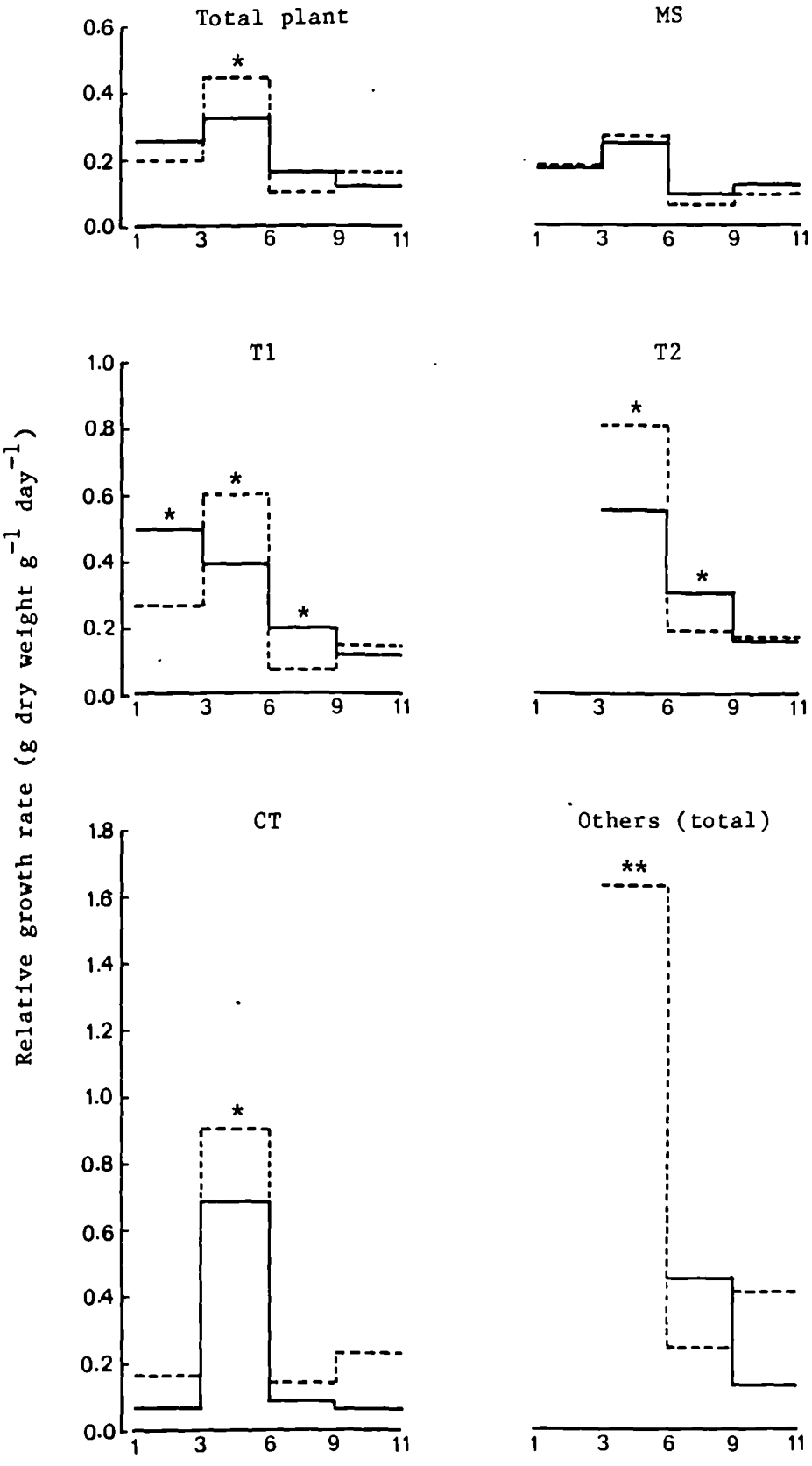

Total plant
MS
T1
T2
CT
Others (total)
Relative growth rate (g dry weight g^{-1} day^{-1})
Days after Terpal application
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
1
3
6
9
11
*
**

Fig. 4.8

Effect of Terpal on individual tiller dry weight with time.

Days after application:

(a) 1

(b) 3

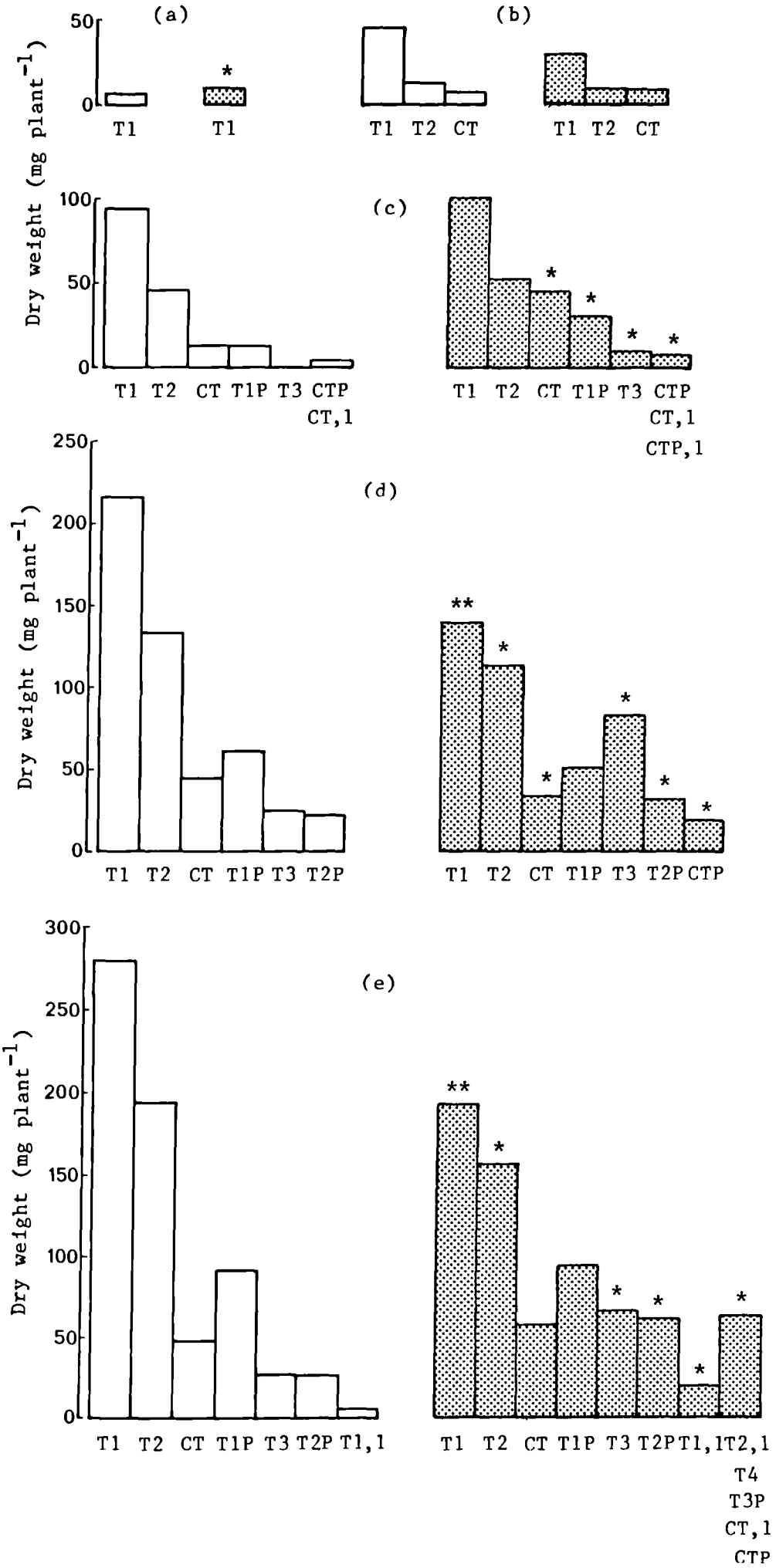
(c) 6

(d) 9

(e) 11

Control

Terpal


(a)
(b)
(c)
(d)
(e)
Dry weight (mg plant^{-1})
50
0
100
250
200
150
300
T1
T2
CT
T1P
T3
T2P
CTP
T1,1
CT,1
CTP,1
T4
T3P

in control plants; this effect was maintained to the 11 day harvest (Fig. 4.8e). By the 6 day harvest Terpal had greatly increased ($p<0.05$) the dry weight of all other tillers (Fig. 4.8c). The promotory effect of Terpal on CT and T1P diminished by the 9 day harvest so that by 11 days after treatment there was no significant difference in the dry weight of these tillers between control and Terpal treated plants (Fig. 4.8d and Fig. 4.8e). In contrast, the dry weight of the later emerging tillers continued to be significantly increased by Terpal (Fig. 4.8d and Fig. 4.8e).

Experiment B : Early to late tillering phase (GS 14 to grain harvest). Again Terpal caused a rapid increase ($p<0.05$) in tiller production which was evident 5 days after application (Fig. 4.9), by final harvest Terpal increased tiller production by 14% which was due to the enhanced production of T2P and T4 tillers. Terpal also increased the number of ear-bearing tillers at final harvest by 21% (Table 4.5) and this was due to a greater proportion of T2P and T4 tillers producing ears.

Table 4.5 Effect of Terpal on tiller numbers at final harvest ±SE.

Treatment	Number of ear-bearing tillers	Number of unproductive tillers
Control	5.33 ± 0.16	5.67 ± 0.35
Terpal	6.73 ± 0.23 **	6.07 ± 0.33

As before Terpal reduced MS height (Fig. 4.10), it also resulted in all of the shoots being of a more equal height than shoots in control plants. This was because of a reduction in the length of the first 3 emerged shoots, that is, MS, T1 and T2 and to a lesser extent, T1P and

Fig. 4.9

Effect of Terpal on tiller production with time (0 to 37 days after application).

○ Control

● Terpal

—— Total tiller number per plant

----- Dead " " "

A : Rapid MS stem elongation

B : MS anthesis

Vertical bars represent ±SE.

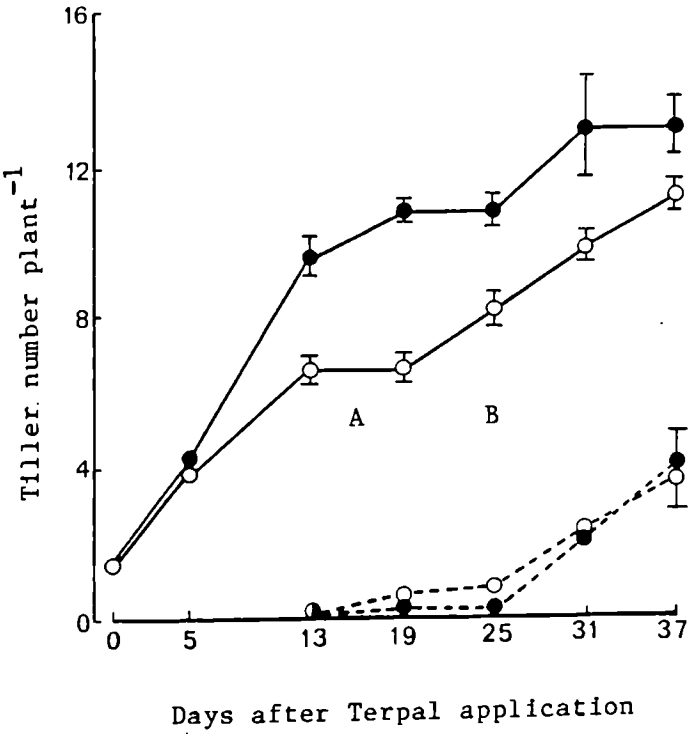

16
12
8
4
0
Tiller number plant^{-1}
A
B
0
5
13
19
25
31
37
Days after Terpal application

Fig. 4.10

Effect of Terpal on the height of the MS and individual tillers with time (5 to 37 days after application).

a) Control

b) Terpal

○ MS

● T1

△ T2

▲ T1P

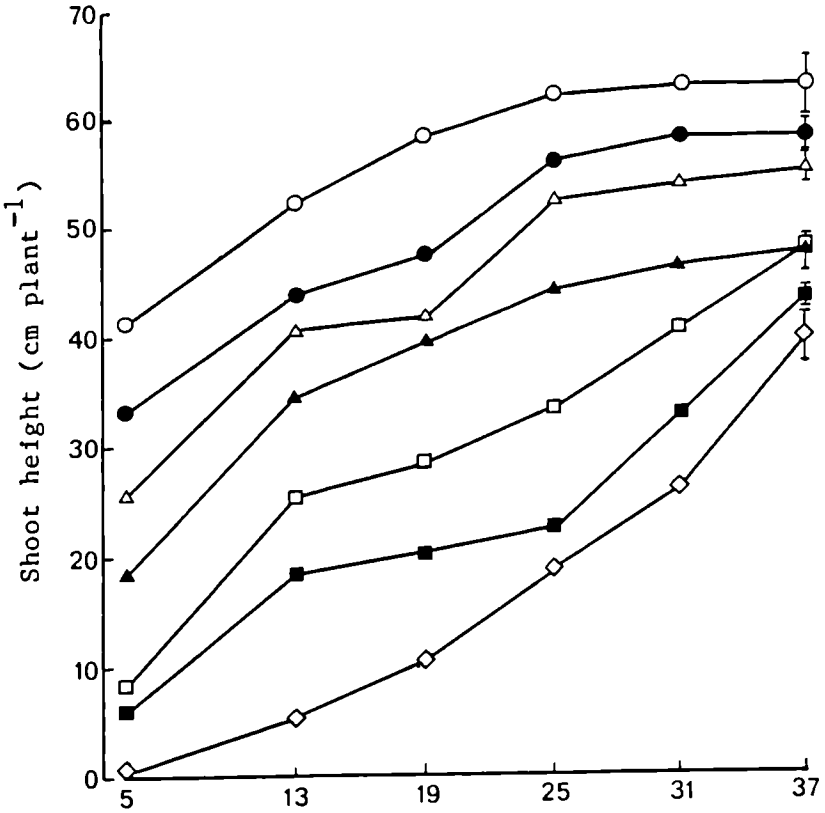
□ T3

■ T2P

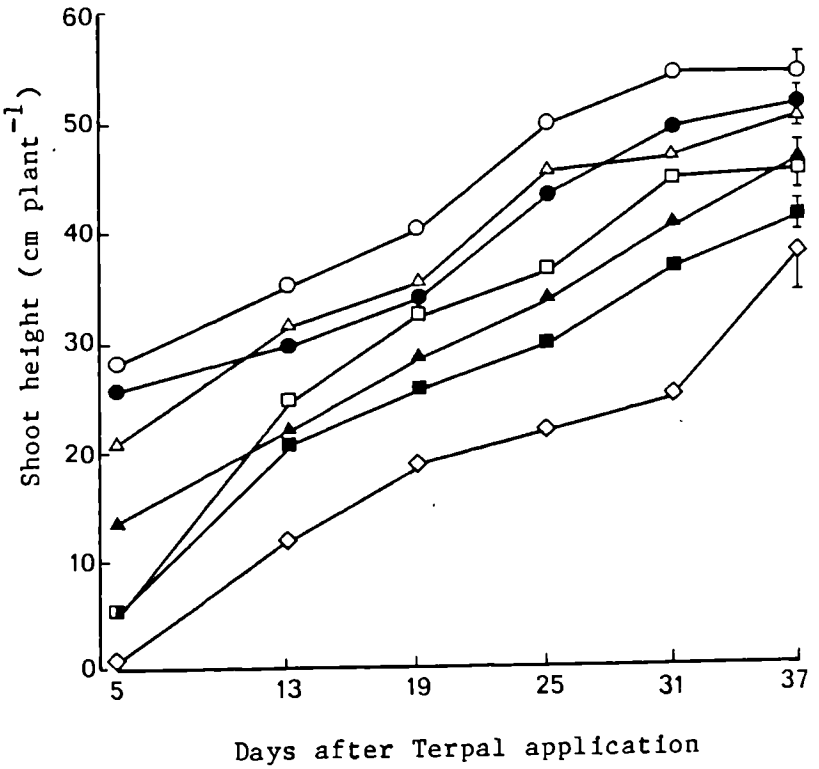
◇ T4

Vertical bars represent ±SE.

(a)


Shoot height (cm plant^{-1})
70
60
50
40
30
20
10
0
5
13
19
25
31
37
Days after Terpal application

(b)


Shoot height (cm plant^{-1})
60
50
40
30
20
10
0
5
13
19
25
31
37
Days after Terpal application

an increase in the length of the later emerged tillers, particularly during the initial phase of growth (Fig. 4.10). This pattern of growth is reflected by the effect of Terpal on dry weight distribution. Terpal significantly reduced total plant dry weight by 12% at final harvest (Fig. 4.11a) and this was due to a reduction in the dry weight of MS, T1, T2 and the roots (Fig. 4.11b and Fig. 4.12a to Fig. 4.12f). This reduction was not compensated for by the greater dry weight of the later emerged tillers, that is, T3, T2P and T4 (Fig. 4.12a to Fig. 4.12e). Terpal significantly ($p<0.05$) reduced the dry weight of MS, T1 and T2 after only 5 days from application (compared to 9 days in Experiment A) (Fig. 4.11b and Fig. 4.12a). The greater dry weight of the other tillers, particularly T3, T2P and T4, in the Terpal treated plants accompanied by the reduced dry weight of MS, T1 and T2 greatly modified the hierarchical distribution of dry weight between the tillers which was so obvious in control plants (Fig. 4.12a to Fig. 4.12f). Terpal had the greatest effect on dry weight distribution between tillers at 13 and 19 days after application (Fig. 4.12b and Fig. 4.12c). This corresponded to the final stages of MS elongation in control plants, a time when tillering stopped temporarily. In Terpal treated plants this phase was delayed and tillering continued for a further 6 days (Fig. 4.9). Fig. 4.13 shows, perhaps more clearly, that the weights of MS, T1 and T2 were much reduced relative to controls whereas the weights of T3, T4 and especially T2P were much increased by Terpal treatment between 13 and 19 days after application. The dry weight of T1P was variable, at some harvests it was increased, at others it was decreased, by Terpal treatment (Fig. 4.13). At 31 and 37 days after Terpal application, which was after anthesis, the differences in dry weight of all tillers between control and Terpal treated plants were considerably diminished (Fig. 4.13).

Fig. 4.11

Effect of Terpal on dry weight with time (5 to 37 days after application).

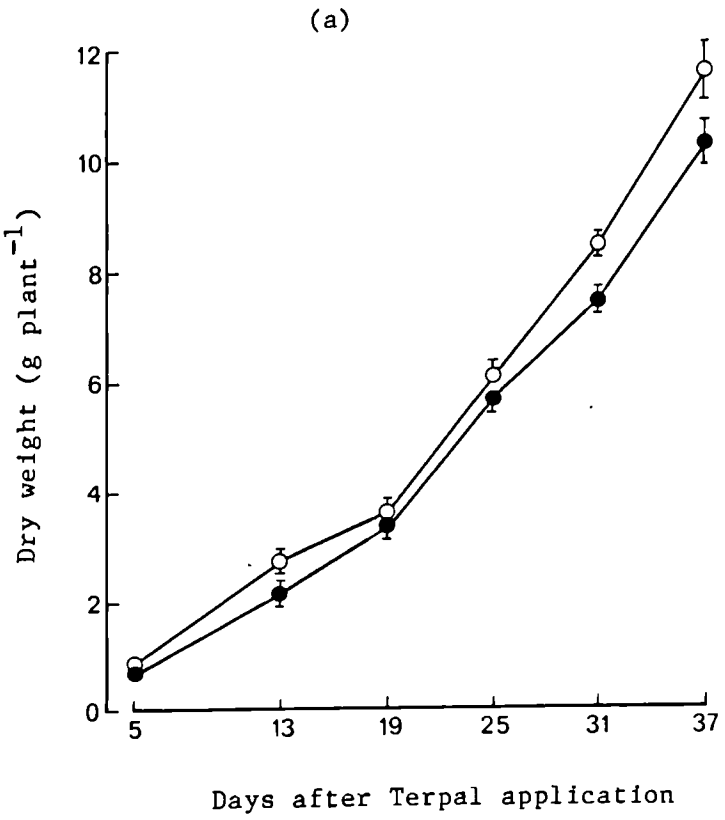
(a) Total plant dry weight.

(b) MS and root system dry weight.

○ Control

● Terpal

Vertical bars represent ±SE.


(a)
Dry weight (g plant^{-1})
0
2
4
6
8
10
12
5
13
19
25
31
37
Days after Terpal application

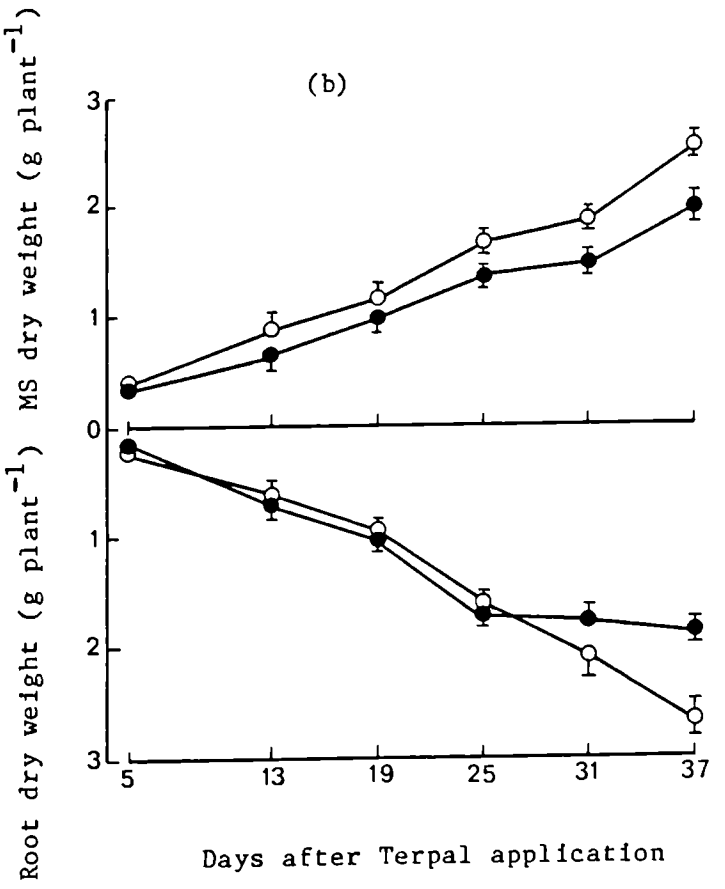
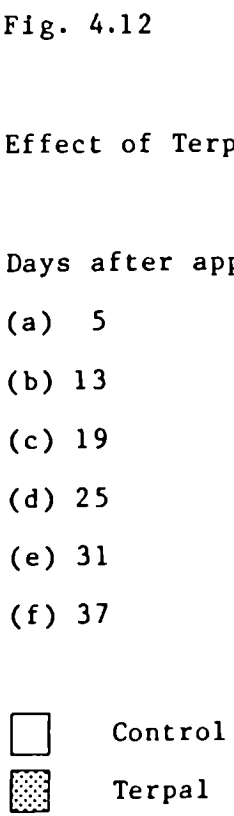

(b)
Root dry weight (g plant^{-1}) MS dry weight (g plant^{-1})
3
2
1
0
1
2
3
5
13
19
25
31
37
Days after Terpal application

Fig. 4.12

Effect of Terpal on individual tiller dry weight with time.



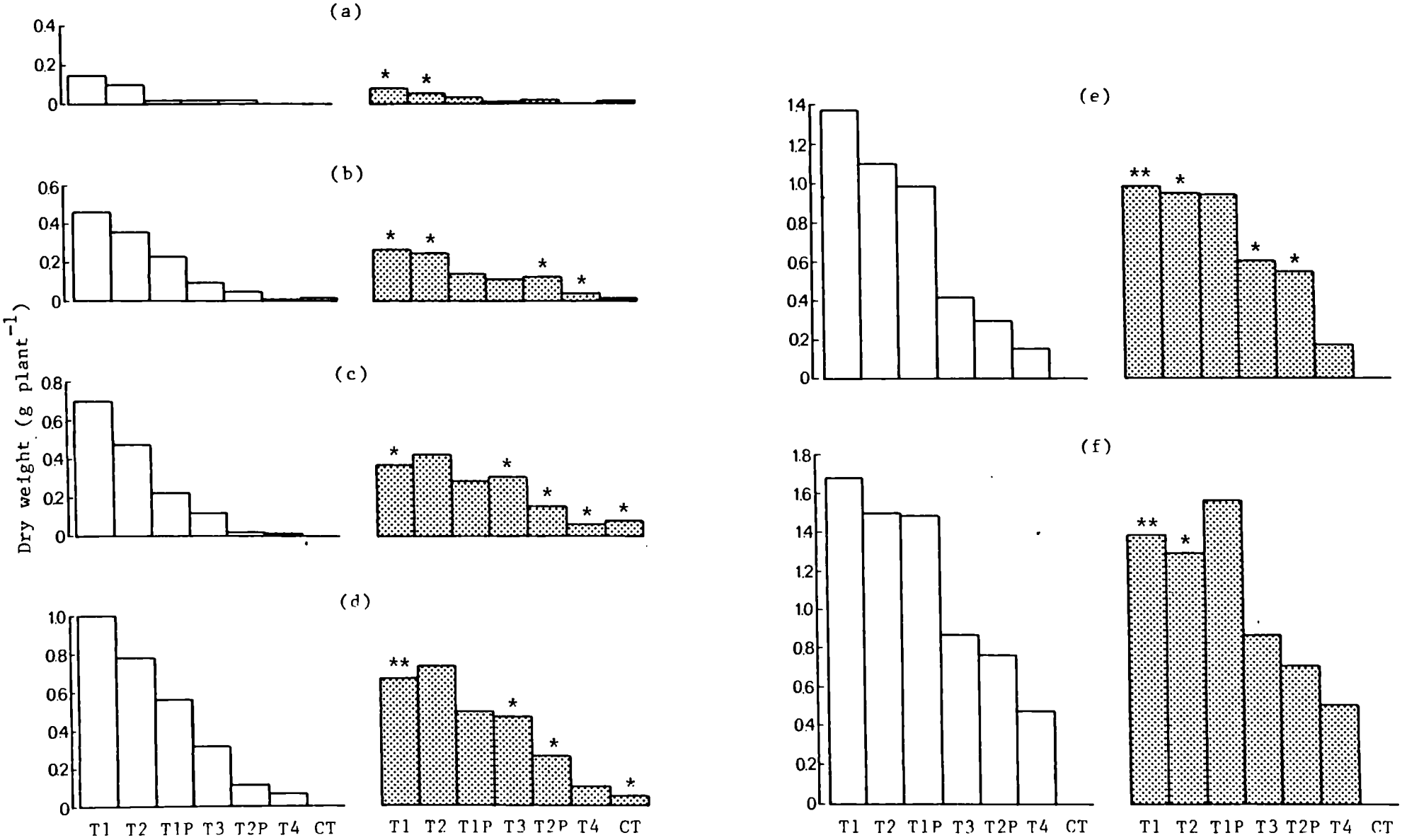

(a)
(b)
(c)
(d)
(e)
(f)
Dry weight (g plant^{-1})
T1 T2 T1P T3 T2P T4 CT
T1 T2 T1P T3 T2P T4 CT
T1 T2 T1P T3 T2P T4 CT
T1 T2 T1P T3 T2P T4 CT

Fig. 4.13

The effects of Terpal on the dry weight of each tiller over time (5 to 37 days after application) expressed as the percentage difference from control plants.

○ MS

● T1

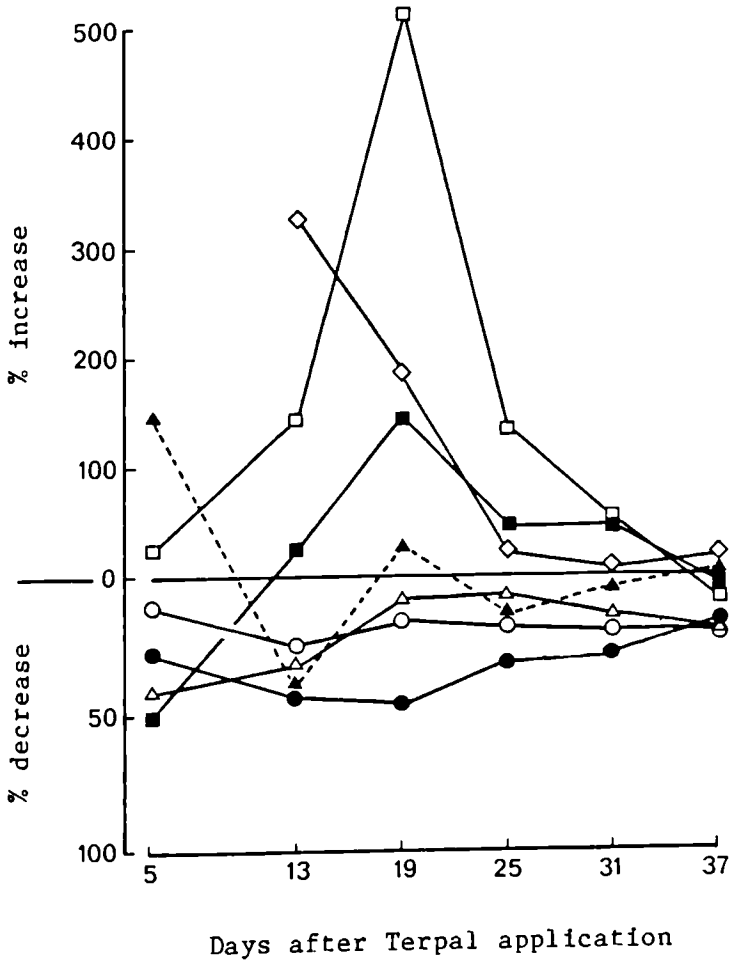
△ T2

▲ T1P

□ T2P

■ T3

◇ T4


500
400
300
200
100
0
50
100
% increase
% decrease
5
13
19
25
31
37
Days after Terpal application

A harvest of the ears of 15 treated and 15 control plants at the end of this experiment revealed that although the number of ears per plant was significantly increased by Terpal treatment ($p<0.01$) (Table 4.5), mean ear and straw weight per tiller were significantly reduced ($p<0.001$ and $p<0.005$ respectively) (Table 4.6). Thus there was no significant difference in the total ear dry weight of the plants (Table 4.6). The number of grains per ear was unaffected by Terpal treatment and since Terpal reduced ear weight it can be concluded that this was due to a reduction in grain size. The total dry weight of unproductive tillers was also unaffected by Terpal treatment (Table 4.6).

Table 4.6 Effect of Terpal on components of yield ±SE. (Differences between control and Terpal significant at: ***, $p<0.005$ level and ****, $p<0.001$ level).

Treatment	Ear weight tiller^{-1} g	Straw weight tiller^{-1} g	Grains ear^{-1}	Total ear weight g	Unproductive tiller weight g
Control	0.63±0.03	0.53±0.01	16.1±0.42	3.41±0.13	0.14±0.03
Terpal	0.48±0.02	0.47±0.01	16.6±0.45	3.12±0.10	0.19±0.05
	****	***			

Experiment 4.4 GA_3/Terpal reversal

It is unknown how Terpal has its effect on tillering. It could have either a direct effect in stimulating the outgrowth of tiller buds or an indirect effect associated with an improvement of assimilate supply to tiller buds as a result of MS retardation. Since it is well known that GA_3 has an important role in stem elongation (Jones and MacMillan, 1984) and that Terpal probably antagonizes the action of GA_3 (Jensen and Andersen, 1981), it was decided to investigate the role of GA_3 in the control of tiller production and development. A further aim of Experiment 4.4 was to determine if the effects of Terpal could be reversed by GA_3 application and vice-versa. Such information could then be used to explain the mode of action of Terpal.

MATERIALS AND METHODS

Experiments 4.4 and 4.5 were undertaken in the "new" glasshouse suite at Pen-y-Ffridd. The temperature regime was more closely controlled with a minimum temperature of 18 and 16°C during the photoperiod and the dark period respectively. Natural daylight was supplemented by high pressure sodium lamps to give a 16 hour photoperiod.

Seeds of spring barley, cv. Triumph, were sown on 21 October, 1983 and grown as in Experiment 4.1. There were 5 treatments as follows; Terpal only, GA_3 only, Terpal and GA_3 (Terpal applied first), GA_3 and Terpal (GA_3 applied first) and a control (distilled water + 0.05% v/v ethanol + 0.05% v/v Tween 20). Terpal was applied as before at GS 13. GA_3 was applied as a foliar spray at a concentration of 10^{-4}M + 0.05% v/v ethanol + 0.05% v/v Tween 20. Where both PGRs were applied to the same plant there was a 48 hour period between applications. Tiller production, MS height, MS leaf number, internode number and length, and dry weight of component plant parts of 6 replicate plants were

measured.

RESULTS

All the treatments, except the GA_3 only treatment, significantly ($p<0.05$) increased tiller production after 12 days (Fig. 4.14a). By 31 days after application the GA_3 only treatment had also increased tiller production and after 38 days all the treatments had increased tiller production by about one third (Fig. 4.14a). Over the first 19 days after application the GA_3 only treatment actually reduced ($p<0.01$) tillering by about 40% but after this time, when the MS had 7.2 leaves, tiller production began to increase rapidly. The effect of the combined Terpal/GA_3 treatments was intermediate between the Terpal only and the GA_3 only treatments from 12 to 38 days after application. The combined treatments were only significantly different to both the Terpal only and GA_3 only treatments at 19 days after application (Fig. 4.14a).

Terpal significantly reduced MS height by 20% after 5 days of application and this reduction was maintained thereafter (Fig. 4.14b). GA_3 increased MS height by 5 days after application; and the MS increased rapidly in height until 31 days after GA_3 application when it slowed down. At 38 days after application the MS height of the GA_3 treated plants was 58% greater than that of control plants (Fig. 4.14b). Both the combined Terpal/GA_3 treatments also increased MS height by 12 days after application, but not as much as the GA_3 only treatment. These combined treatments had a similar effect on MS height and by 38 days after application had increased it by almost half (Fig. 4.14b).

Analysis of plants at final harvest revealed that control plants had 5 elongated MS internodes and T1 and T2 both had 3 internodes. The last internode (below the ear) was always at least twice the length of the

Fig. 4.14

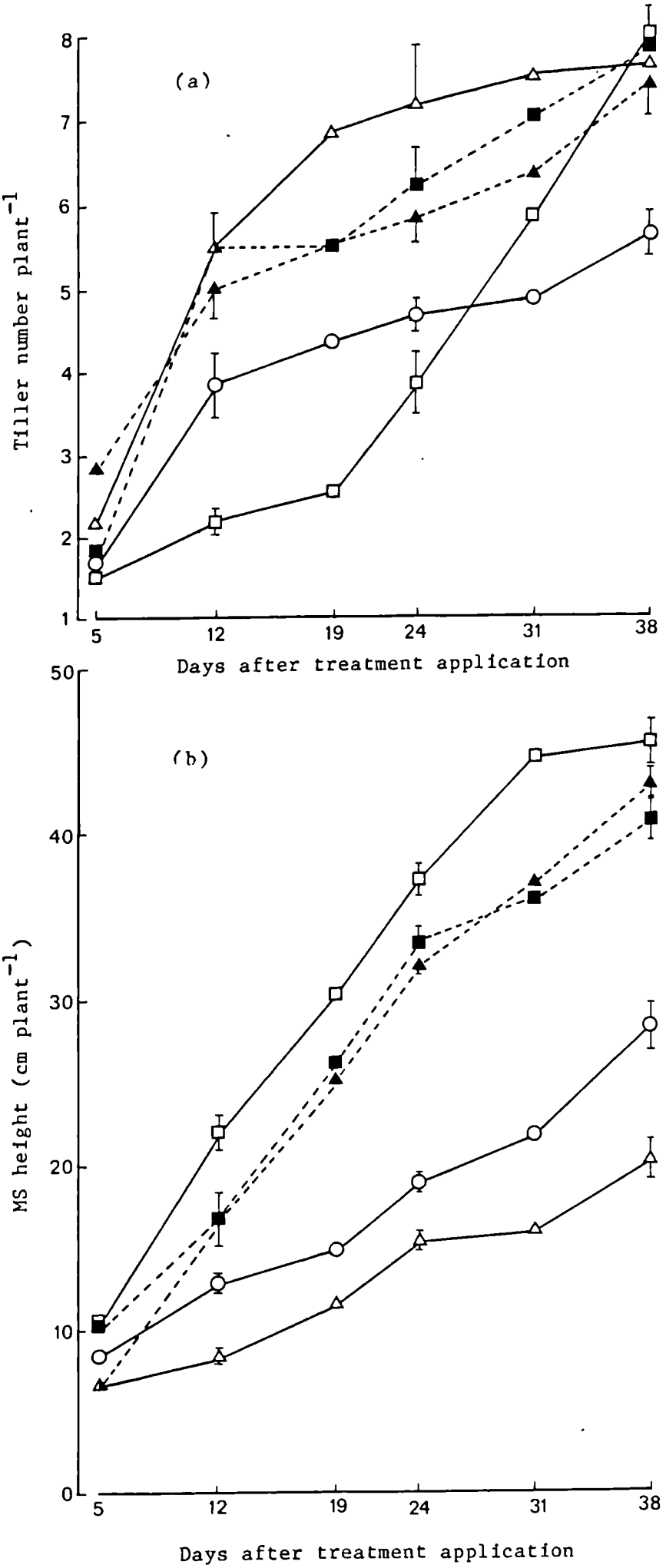
Effect of Terpal and GA_3 treatments on:

(a) tiller production with time and

(b) MS height with time.

- ○ Control
- △ Terpal
- □ GA_3
- ▲ Terpal then GA_3
- ■ GA_3 then Terpal

Vertical bars represent ±SE.


(a)
Tiller number plant^{-1}
8
7
6
5
4
3
2
1
5
12
19
24
31
38
Days after treatment application
(b)
MS height (cm plant^{-1})
50
40
30
20
10
0
5
12
19
24
31
38
Days after treatment application

others (Fig. 4.15). Terpal reduced the number of MS internodes by one, and reduced the length of the first 3 internodes by 45, 45 and 16% respectively, the length of the last internode was unaffected (Fig. 4.15). The effect of Terpal on the number and length of the T1 and T2 internodes was negligible. GA_3 increased the number of internodes of MS, T1 and T2 and also increased the length of all internodes except the last one which was unaffected (Fig. 4.15). Both the combined Terpal and GA_3 treatments had very similar effects to that of the GA_3 only treatment (Fig. 4.15).

By the end of the experiment, 38 days after spraying, the MS flag leaf was reaching full expansion in both control and treated plants. Prior to this the treatments had little effect on leaf production by the MS. Total plant dry weight was significantly reduced by Terpal and by the "GA_3 then Terpal" treatment; the other treatments had no significant effect on total plant dry weight (Table 4.7). In control plants 39% of total plant dry weight was distributed to the MS and 61% to the tillers. All of the treatments modified this pattern of dry weight distribution (Table 4.7). Overall Terpal and the "GA_3 then Terpal" treatment had similar effects, that is, the distribution of dry weight to the MS was reduced by about 27%, that to T1 and T2 were little affected and that to the remaining tillers was increased by up to 35% (Table 4.7). The effects of the GA_3 and the "Terpal then GA_3" treatments were similar, that is, the distribution of dry weight to the MS was slightly reduced, by about 13% and that to all tillers increased slightly by about 8% (Table 4.7).

Fig. 4.15

Effect of Terpal and GA_3 treatments on the MS, T1 and T2 internode number and length at 38 days after treatment application.

(a) Control

(b) Terpal

(c) GA_3

(d) Terpal then Ga_3

(e) GA_3 then Terpal

1 to 6 represent internode number, 1 = the basal internode.

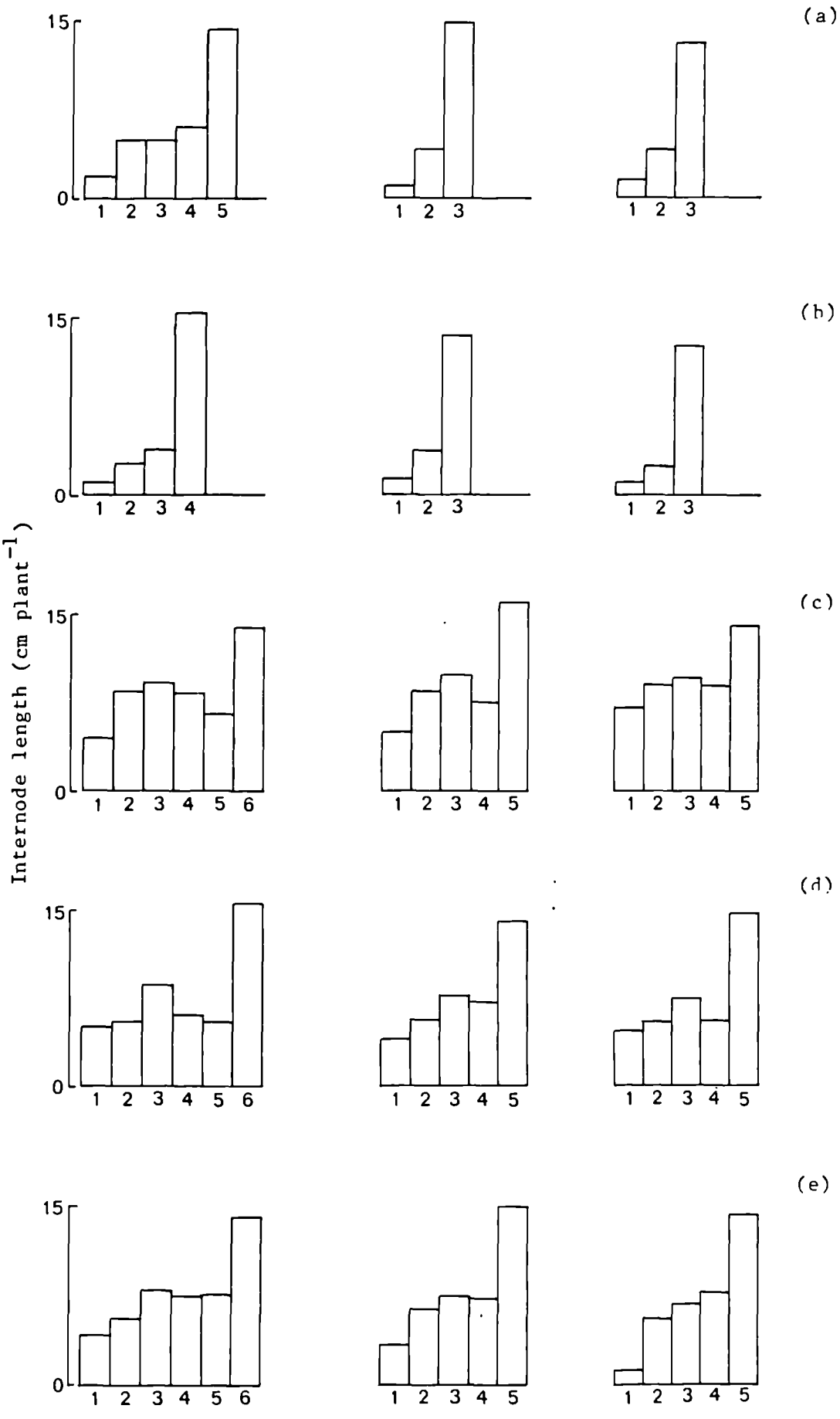

(a)
(b)
(c)
(d)
(e)
15
0
1 2 3 4 5
1 2 3
1 2 3 4
1 2 3
1 2 3 4 5 6
1 2 3 4 5
1 2 3 4 5 6
1 2 3 4 5
1 2 3 4 5 6
1 2 3 4 5
Internode length (cm plant^{-1})
Internode number
MS
T1
T2

Table 4.7 Effect of PGR treatments on total plant dry weight (g) (±SE) and percentage distribution of dry weight between the MS and tillers.

Treatment	Dry weight per plant	% Dry weight				
		MS	T1	T2	Others	Total tillers
Control	2.01±0.07	39	21	17	23	61
Terpal	1.75±0.10*	29	20	15	36	71
GA_3	1.98±0.12	35	23	18	24	65
Terpal/GA_3	1.91±0.07	33	21	23	23	67
GA_3/Terpal	1.78±0.08*	28	21	20	31	72

Experiment 4.5 Effects of PGRs on the distribution of ^{14}C-labelled assimilate.

It was thought that the role of the MS as an assimilatory organ and supplier of assimlate to developing tillers may be modified by PGR application. Any differences in assimilate distribution resulting from PGR application may reflect the modifications to tiller development described in this chapter. It was with this premise that the following experiment was undertaken in which radioactive-labelled carbon dioxide ($^{14}CO_2$) was supplied to a MS leaf of plants treated with Terpal, Cerone, TIBA or GA_3 (and control plants) 3 and 10 days after treatment application. The effect of these treatments on the distribution of the ^{14}C from the MS to the tillers is described.

MATERIALS AND METHODS

Seeds of spring barley, cv. Triumph, were sown on 17 January, 1984 and grown as in Experiment 4.1. In this experiment, however, John Innes No.1 peatless compost was used to facilitate excavation of the roots

from the pots. This compost was made up of a 7:3:2 mixture by volume of loam, "Perlite", and coarse sand with added Vitax Q4 fertilizer at 3.6g per litre of compost. PGR treatments were applied at GS 13 by foliar spray. The treatments were, Terpal (equivalent to 2.5 dm^3 ha^{-1}), Cerone (equivalent to 1 dm^3 ha^{-1}), TIBA (10^{-4}M + 0.05% ethanol + 0.05% Tween 20), GA_3 (10^{-4}M + 0.05% ethanol + 0.05% Tween 20) and control (distilled water + 0.05% ethanol + 0.05% Tween 20). At 3 and 10 days after treatment application, GS 13 and 15 respectively, plants were selected for uniformity and supplied with $^{14}CO_2$.

A MS leaf, either L1 or L2, was enclosed in a transparent polyester tubular chamber (20.5 x 3.8 cm) and supplied with the $^{14}CO_2$. This was produced by the addition of excess 1M HCl to 5 µCi (185 kBq) of an aqueous solution of $Na_2{}^{14}CO_3$. The leaf chamber was removed after 25 minutes. After 24 hours 4 replicate plants were harvested and separated into component parts, that is, tillers, roots, MS axis and leaves. These were then oven-dried at 70°C and weighed.

Samples of the dried plant tissue, <100 mg, were completely combusted in a stream of oxygen in a Harvey OX400 biological material oxidiser, with a 92% efficiency of recovery of $^{14}CO_2$. The $^{14}CO_2$ liberated was absorbed in 15 cm^3 of scintillation cocktail consisting of 46% NE233, 27% 2-phenylethylamine and 27% ethanol. This was then transferred to a glass vial. The total ^{14}C content of each solution was determined using a LKB 1215 Rackbeta II liquid scintillation counter with a window setting of 30 to 130. Quench correction was assessed by an external standard channel ratio method.

In addition an autoradiograph was made of one replicate plant per treatment. Twenty four hours after supplying the $^{14}CO_2$ these plants were separated into component parts (to prevent further translocation

of ^{14}C). The plants were then arranged as if intact in a plant press and oven-dried at 70°C for 24 hours. The plants were then mounted onto fine cartridge paper using Copydex glue and covered with thin melanex to protect the film. Autoradiographs showing the distribution of ^{14}C were then made by exposure of the mounted material to X-ray film for a period of 72 hours, and developed following standard photographic procedures.

RESULTS

There was no significant effect of PGR treatment on elongating tiller bud number at 3 days after treatment application, but Terpal significantly reduced and TIBA significantly increased MS height at this time (Table 4.8). By 10 days after treatment application tiller bud production was increased by the Terpal, Cerone and TIBA treatments and reduced by the GA_3 treatment; only the effect of Terpal was significant ($p<0.05$). Also after 10 days of treatment application MS height was significantly reduced by the Terpal, Cerone and TIBA treatments ($p<0.05$) and was increased ($p<0.01$) by GA_3 (Table 4.8). These responses are similar to those reported earlier (Chapter 3 and present chapter), although the effects on bud number are of a lower magnitude.

Table 4.8 Effect of PGR treatments on elongating tiller bud/tiller number and MS height (mm) after 3 and 10 days of application ±SE.

Treatment	Days after application			
	3 (GS 13)		10 (GS 15)	
	Bud/tiller no.	MS height	Bud/tiller no.	MS height
Control	3.0±0.00	102±2.5	5.7±0.25	139± 3.7
Terpal	3.0±0.00	93±2.1*	6.7±0.25*	116± 6.9*
Cerone	3.2±0.25	99±4.2	6.5±0.50	114± 9.8*
TIBA	3.5±0.29	112±3.3*	6.5±0.29	122± 3.9*
GA_3	2.5±0.50	104±2.6	5.0±0.00	226±13.9**

At 10 days after application Terpal and TIBA reduced MS dry weight, Cerone had little effect and GA_3 increased MS dry weight; none of these effects were statistically significant although TIBA significantly ($p<0.05$) reduced total shoot dry weight (MS and tillers) (Fig. 4.16a). Root dry weight was not modified by the treatments. Terpal and GA_3 had very little effect on the total dry weight of tiller buds and tillers whereas Cerone slightly increased and TIBA slightly decreased tiller dry weight (Fig. 4.16a). With the exception of TIBA all the treatments modified the distribution of dry weight between individual tillers (Fig. 4.16b). In control and TIBA treated plants there was a distinct hierarchical pattern of dry weight distribution with the earliest emerged tillers heavier than the later growing tiller buds and tillers. Terpal modified this pattern by reducing the dry weight of T1 and increasing that of all other tillers (Fig. 4.16b). In Cerone treated plants the dry weight of both T1 and T2 was reduced and that of all other tillers increased resulting in a much more even distribution of dry weight. The effect of GA_3 on dry weight distribution was to increase the dry weight of T1 and to reduce that of all other tillers, by at least 50%, with the exception of T2 which was not affected (Fig. 4.16b).

The amount of ^{14}C fixed per plant after 24 hours was similar (with one exception) in all treatments whether they had been applied 3 or 10 days previously. TIBA significantly ($p<0.05$) decreased the amount of ^{14}C fixed per plant 3 days after application (Table 4.9).

Fig. 4.16

Effect of PGR treatments on the distribution of dry weight at 10 days after application.

(a) Dry weight of:

 root system

 MS

 total tillers.

(b) Dry weight of individual tillers.

Vertical bars represent ±SE.

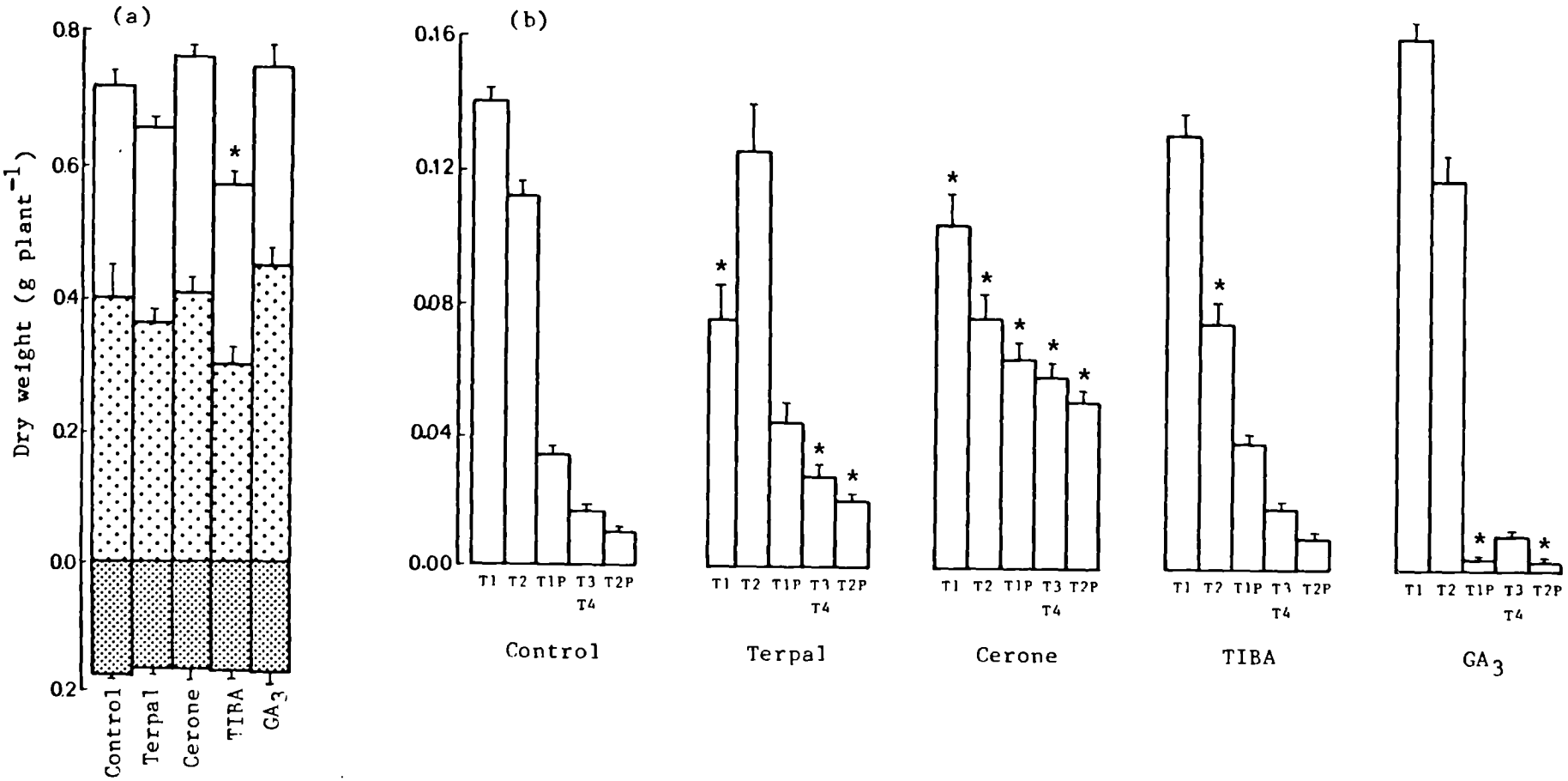

(a)
Dry weight (g plant^{-1})
0.8
0.6
0.4
0.2
0.0
0.2
Control
Terpal
Cerone
TIBA
GA$_3$
(b)
0.16
0.12
0.08
0.04
0.00
T1 T2 T1P T3 T2P
T4
Control
Terpal
Cerone
TIBA
GA$_3$

Table 4.9 Effect of PGR treatments on total ^{14}C fixed (DPM x 10^{-6}) per plant after 24 hours ±SE.

Days after application	Treatment				
	Control	Terpal	Cerone	TIBA	GA_3
3	2.97±0.20	2.91±0.19	3.14±0.27	2.32±0.13*	3.10±0.30
10	2.62±0.44	2.08±0.47	2.46±0.35	2.78±0.23	2.60±0.38

Three days after treatment application about 40% of the ^{14}C supplied to control plants was recovered from the fed MS leaf after the 24 hour period for translocation (Table 4.10). Of the 60% that was exported from the fed leaf about one third was translocated to the rest of the MS, one third to the roots and one third to the tillers (Table 4.10a and Fig. 4.17a). When the $^{14}CO_2$ was supplied 10 days after treatment application this pattern of distribution was quite different. Around 58% of the ^{14}C supplied to the control plants remained in the fed MS leaf and as such less ^{14}C was translocated to the rest of the plant at this later growth stage, that is, GS 15, than at GS 13. Here, the remaining MS was favoured over the roots and the tillers. Of the 42% of the ^{14}C that was exported about half was translocated to the rest of the MS and only about 15% was supplied to the roots and about 30% to the tillers (Table 4.10b and Fig. 4.17b).

None of the treatments had any great influence on the proportion of ^{14}C retained in the fed leaf. Three days after application Cerone significantly increased, and TIBA significantly decreased that retained, but these effects were small. GA_3 appeared to reduce the amount of ^{14}C leaving the fed leaf at both 3 and 10 days after application but this effect was not statistically significant (Table 4.10). The treatments did not significantly modify the proportion of ^{14}C translocated to the rest of the MS, whereas that exported to the roots was reduced by all of the treatments although only the effects of

Table 4.10 Effect of PGR treatments on the percentage distribution of the total ^{14}C recovered from the plant after a 24 hour period for translocation.

(a) At 3 days after treatment application ±SE.

Treatment	% distribution of ^{14}C			
	Fed MS leaf	MS	Roots	Tillers
Control	40.8±0.4	19.9±1.3	22.5±1.5	16.8±0.8
Terpal	40.9±3.1	17.8±2.6	21.8±3.1	19.5±1.5
Cerone	42.9±0.9*	17.9±0.3	19.1±1.9	20.1±2.7
TIBA	38.4±0.9*	16.9±1.2	16.6±1.7*	28.1±0.1**
GA_3	46.7±4.2	23.1±4.1	16.2±2.4*	14.0±2.2*

(b) At 10 days after treatment application ±SE.

Treatment	% distribution of ^{14}C			
	Fed MS leaf	MS	Roots	Tillers
Control	58.8±2.0	21.5±2.0	6.5±2.3	13.2±1.5
Terpal	56.1±2.2	25.2±2.2	2.9±0.6	15.8±1.2
Cerone	54.3±5.8	28.6±3.9	2.4±0.5	14.7±1.5
TIBA	55.2±3.2	27.7±2.4	3.3±0.9	13.8±1.9
GA_3	65.6±4.2	20.4±3.5	3.5±0.4	10.5±1.1

Fig. 4.17

Effect of PGR treatments on the percentage distribution of ^{14}C-labelled assimilate exported from the MS fed leaf at:

(a) 3 days after treatment application.
(b) 10 " " "

to component plant parts:


Root system

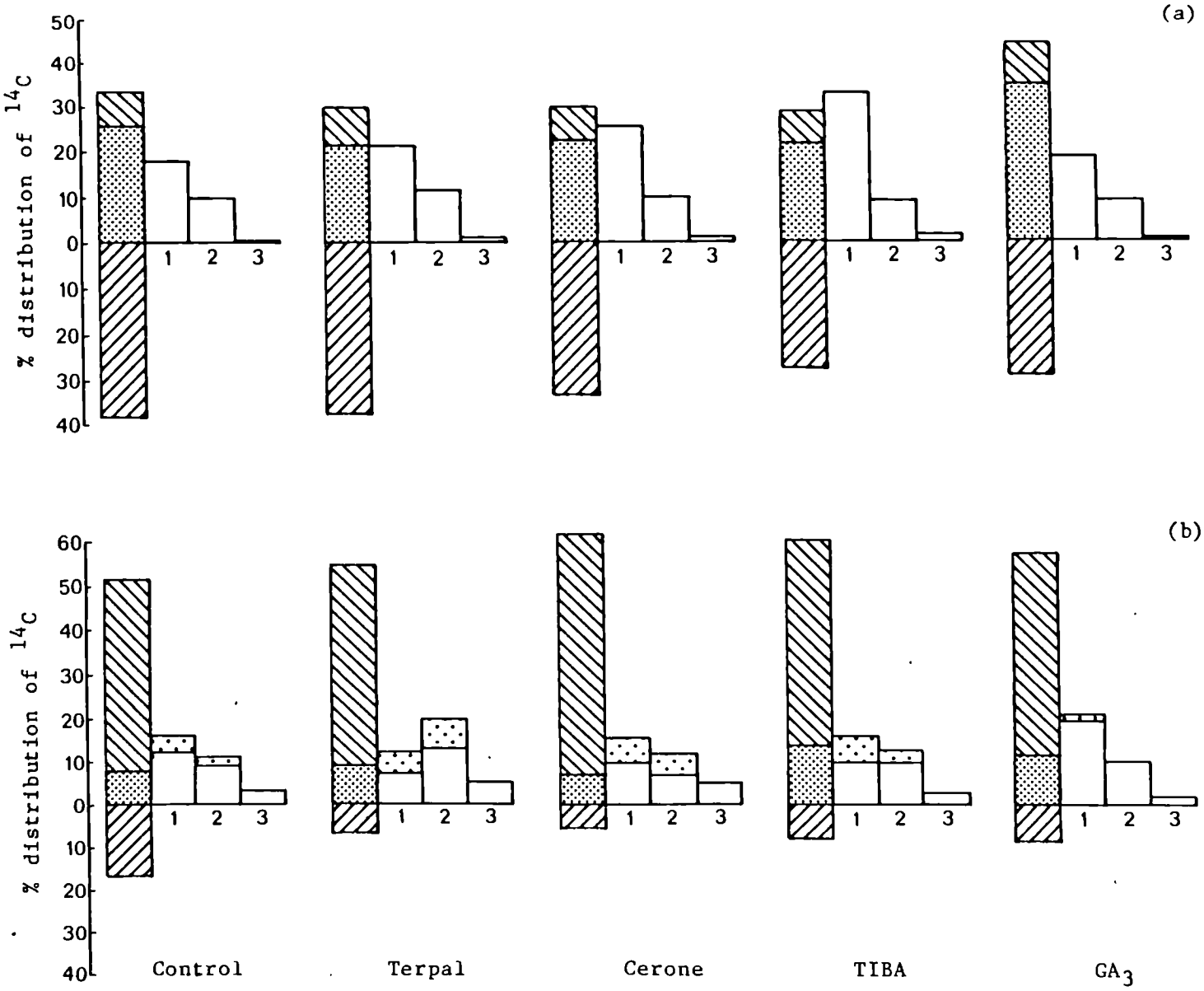

MS (stem and unemerged leaves)


MS leaves (other than fed leaf)


Primary tiller buds and tillers


Secondary tiller buds and tillers

1 T1 + T1P
2 T2 + T2P
3 T3 + T4


(a)
% distribution of ^{14}C
50
40
30
20
10
0
10
20
30
40
1 2 3
(b)
% distribution of ^{14}C
60
50
40
30
20
10
0
10
20
30
40
1 2 3
Control
Terpal
Cerone
TIBA
GA_3

TIBA and GA_3 were significant ($p<0.05$) at 3 days after treatment application (Table 4.10 and Fig. 4.17). In general, the PGR effects on ^{14}C distribution to the tillers reflected those on tiller growth described earlier in this thesis (Chapters 2, 3 and 4), with Terpal, Cerone and TIBA increasing and GA_3 decreasing the percentage distribution of ^{14}C to the tillers (Table 4.10). However, these effects were small, particularly at 10 days after treatment application. The increased distribution of ^{14}C to tillers in the Terpal, Cerone and TIBA treatments after 3 days was mainly due to an increased export of ^{14}C to T1 from the fed MS leaf rather than to T2 or T3 (Fig. 4.17a). In contrast 10 days after the application of the treatments, this increased distribution of ^{14}C to tillers in the Terpal and Cerone treatments was mainly due to an increased proportion of ^{14}C exported to the secondary tillers (Fig. 4.17b). The percentage distribution of ^{14}C to T1 was also reduced 10 days after treatment application by Terpal and Cerone. It can also be seen from Fig. 4.17b that GA_3 treatment resulted in an increased amount of ^{14}C in T1 and a reduced amount of ^{14}C assimilate in the secondary tillers.

From the results of this experiment presented so far it is difficult to compare the effects of the treatments directly since the dry weight of the MS and tillers was considerably modified by the treatments (Fig. 4.16) and furthermore, different proportions of the total ^{14}C in the plant were exported from the MS fed leaf, particularly in the case of GA_3 (Table 4.10). To facilitate data interpretation the results have also been expressed in relation to the dry weight of the component plant parts. Although overall, less ^{14}C was found in tillers of low dry matter content, the concentration of ^{14}C per mg dry weight (DPM mg^{-1}) was higher in the smaller tillers (Fig. 4.18b). In control plants, 3 days after treatment application, the highest concentration of ^{14}C was in T2 which was just emerging at this time. The treatments modified

Fig. 4.18

Effect of PGR treatments on the amount of ^{14}C-labelled assimilate (DPM mg^{-1} dry weight) at:

(a) 3 days after treatment application.
(b) 10 " " "

in component plant parts:


Root system

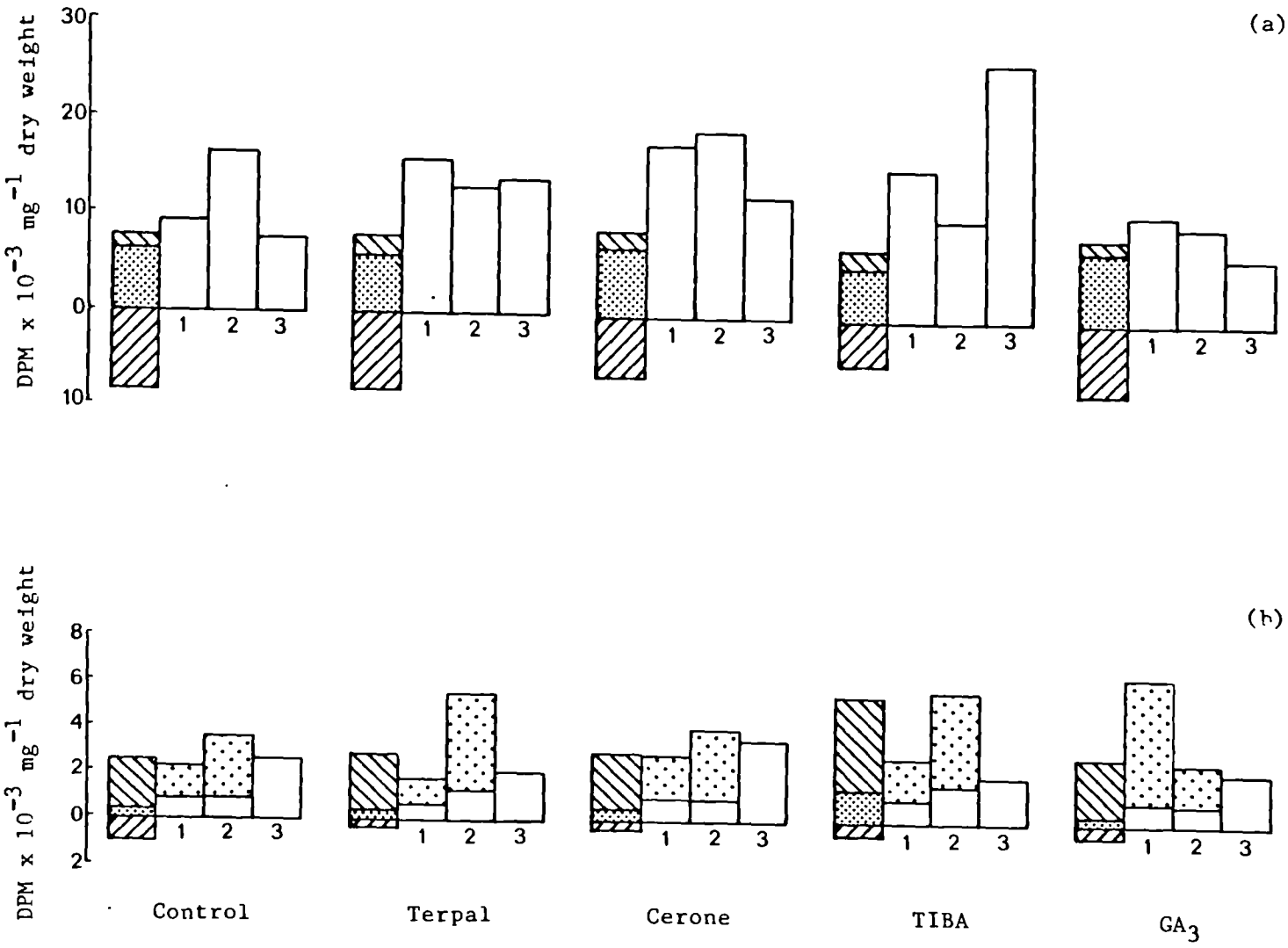

MS (stem and unemerged leaves)


MS leaves (other than fed leaf)


Primary tiller buds and tillers


Secondary tiller buds and tillers

1 T1 + T1P
2 T2 + T2P
3 T3 + T4


(a)
DPM x 10^{-3} mg^{-1} dry weight
30
20
10
0
10
1 2 3
(b)
DPM x 10^{-3} mg^{-1} dry weight
8
6
4
2
0
2
1 2 3
Control
Terpal
Cerone
TIBA
GA_3

this, Terpal and Cerone more or less evened out the ^{14}C concentration between the tillers, particularly between T1 and T2; TIBA increased the concentration in T3 whereas GA_3 resulted in T1 having a higher concentration than T2 and T3 (Fig. 4.18a). Ten days after treatment application it can be seen that the ^{14}C concentrations were much reduced in the now larger T1 and T2 (Fig. 4.18b). The highest concentrations of ^{14}C were found in the newly emerging T2P, T3 and T4 tillers. Terpal, Cerone and TIBA all increased the concentration in T2P; GA_3 reduced this amount. In the GA_3 treated plants the ^{14}C concentration in T1P was increased, it is likely that this tiller was just emerging at this time since GA_3 slowed down the rate of tiller production.

The effects of Terpal, Cerone and GA_3 described in this chapter are illustrated by the photographs in Plate 4.I. Autoradiographs that accompany these photographs (Plate 4.II) indicate the distribution of ^{14}C to all tillers at 10 days after treatment application and show the localization of ^{14}C in the growing and emerging leaves and at the root tips. The autoradiograph of the GA_3 treated plant indicates a reduced translocation of ^{14}C from the MS to the tillers.

Experiment 4.6 Effect of PGR and other treatments applied at GS 39 on tiller production and survival.

In all the experiments described previously the PGR treatments were applied early in the life of the plants, mostly at GS 13. It was decided to investigate the effect of PGR applications later in the life cycle of the plant, that is, at GS 39. This is the time when the MS is undergoing rapid elongation, tillering is suppressed, and the onset of

Plate 4.I

Effect of PGR treatments on the morphology of glasshouse grown spring barley plants at 10 days after application. Treatments applied at GS 13:

A Control

B Terpal

C Cerone

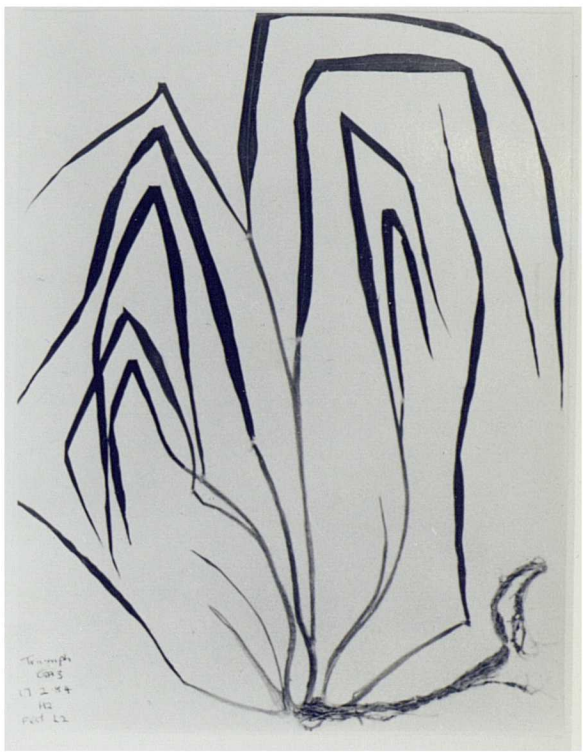
D GA_3

Photographs show the promoted tiller production and reduced MS height of both the Terpal and Cerone treated plants and the increased height of the MS, T1 and T2 in the GA_3 treated plant.

A

B

C



D

Plate 4.II

Effect of PGR treatments on the distribution of ^{14}C-labelled assimilate in glasshouse grown spring barley plants at 10 days after treatment application. Treatments applied at GS 13:

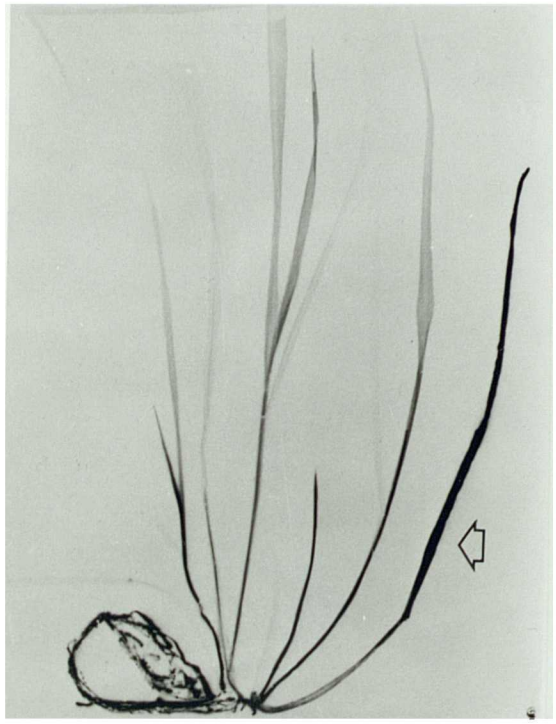
A Control

B Terpal

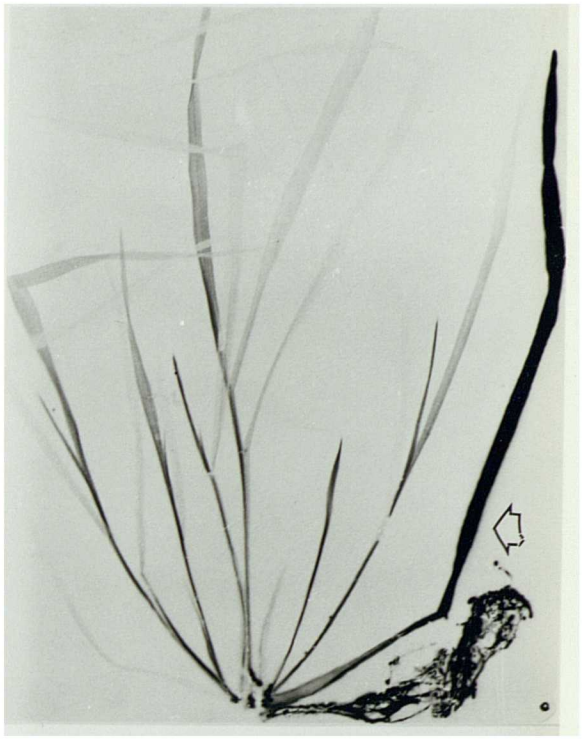
C Cerone

D GA_3

Photographs show autoradiographs of plants in Plate 4.I indicating localization of ^{14}C in all tillers (except in GA_3 treated plant), emerging leaves and roots. ^{14}C applied to MS L2 at 10 days after PGR application (⟨).

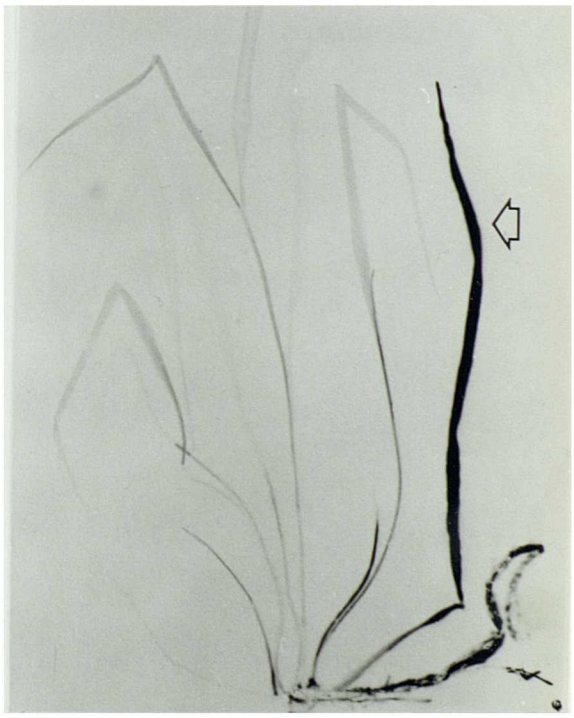


A



B

C



D

tiller death is imminent. It seems possible that the application of PGRs at this time might influence these developmental processes; in particular stimulate tillering and delay tiller senescence. Thus the effects of applications of Terpal and of other treatments during the phase of tiller inhibition (GS 39) were investigated.

MATERIALS AND METHODS

Seeds of spring barley, cv. Triumph, were sown and grown as before in the "old" glasshouse suite, as described in Experiment 4.1. At GS 39 a range of treatments were applied to 16 replicate plants (Table 4.11). A larger number of replicates than usual were used in order to reduce the variability of results previously encountered. Tillers were also counted at this stage and any that appeared to be dying, that is, with more than half the leaf area senesced and looking limp, were ringed with a plastic ring. One week after treatment application, and at weekly intervals thereafter, any changes in tiller production were monitored. The plants were then left until the grain had ripened and the ears of each plant were counted and weighed to assess tiller survival and yield potential.

RESULTS

Table 4.12 shows that about one tiller per plant was dying when the treatments were applied, dying tillers were those most recently emerged, namely T1,1 or T4 or T3P. Tiller production was relatively high in these plants. After one week a few dying tillers revived out of the 16 replicate plants in each treatment. The progression of senescence was halted in these tillers and they regained their normal erect habit and produced a new green leaf from within the older yellowing leaves. Approximately 20% of dying tillers recovered in all treatments with the exception of the Cerone treatment where two thirds of the dying tillers recovered (Fig. 4.19a). After this time there was

Table 4.11 Treatments applied at GS 39 (the onset of tiller suppression).

Control	Distilled water + 0.05% v/v ethanol + 0.05% v/v Tween 20 as a foliar spray until runoff.
Nitrate	12 mM $NaNO_3$ applied as a root drench.
Sucrose	25 mM applied as a foliar spray until runoff.
Terpal	Equivalent to recommended agricultural rate (2.5 dm^3 ha^{-1} in 220 dm^3 H_2O) as a foliar spray until runoff.
Cerone	Equivalent to recommended agricultural rate (1.0 dm^3 ha^{-1} in 300 dm^3 H_2O) as a foliar spray until runoff.
GA_3	10^{-4}M dissolved in 100% ethanol to give a concentration of 0.05% v/v ethanol in final solution + 0.05% v/v Tween 20 applied as a foliar spray until runoff.
TIBA	" " " "
BAP	" " " "
-MS	Removal of inflorescence
-Tl	" "

no further revival of dying tillers.

Table 4.12 Details of plant development at the time of treatment application (GS 39) ±SE.

MS leaf number	MS height (mm)	Number of tillers	Number of dying tillers
8.6±0.13	480.1±13.59	8.3±0.18	1.1±0.14

Terpal and Cerone promoted the outgrowth of several new tillers within the first week of application, 5.4 and 6.7 new tillers per plant respectively (Fig. 4.19b). The number of new tillers produced by control plants during this time was negligible. Of the other treatments only TIBA and the removal of the MS and T1 significantly increased the production of new tillers (Fig. 4.19b). These additional tillers emerged through leaf sheaths at the base of the plant and as such it was impossible to accurately identify them, but they were thought to originate from the secondary and tertiary tillers of CT, T1 and T2. After one week from treatment application no more tillers emerged.

At grain ripening it was found that most of the revived tillers (about 80%) survived to produce ears. None of the newly emerged tillers survived to ear production. Overall, only Terpal and Cerone significantly ($p<0.001$) increased ear production (Table 4.13) and this was because these treatments increased the survival rate of all tillers produced before GS 39 compared to a survival rate of only 56% in the same tillers of control plants. None of the other treatments had a statistically significant effect on ear production (Table 4.13). Plants which had undergone removal of the MS or T1 were able to compensate for this loss by producing an extra fertile tiller of similar size to the

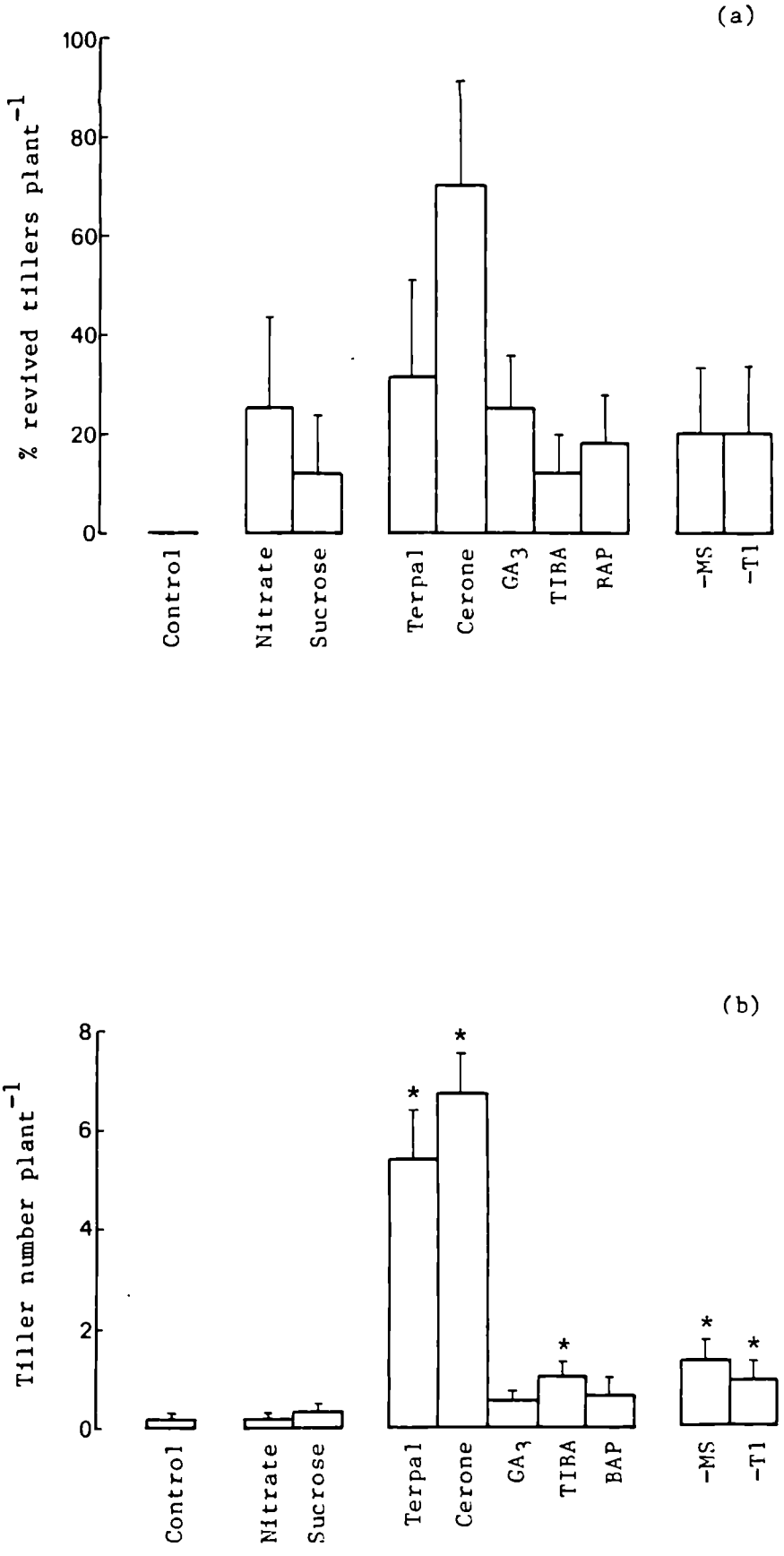
Fig. 4.19

Effect of treatments (Table 4.11) applied at GS 39 on:

(a) the percentage of dying tillers that revived one week after treatment application and

(b) the number of newly emerged tillers one week after treatment application.

Vertical bars represent ±SE.


(a)
% revived tillers plant^{-1}
100
80
60
40
20
0
Control
Nitrate
Sucrose
Terpal
Cerone
GA_3
TIBA
BAP
-MS
-T1
(b)
Tiller number plant^{-1}
8
6
4
2
0
*
Control
Nitrate
Sucrose
Terpal
Cerone
GA_3
TIBA
BAP
-MS
-T1

control MS, but tiller survival rate was not increased further. None of the treatments significantly modified ear dry weight per plant (Table 4.13). Thus, although Terpal and Cerone increased ear number per plant, individual ear weight was reduced.

Table 4.13 Effect of treatments applied at GS 39 on the number and weight (g) of fertile ears per plant ±SE (*** effect significant at $p<0.001$ level).

Treatment	Number of fertile ears plant^{-1}	Total dry weight of ears plant^{-1}
Control	5.21±0.24	3.65±0.15
Nitrate	5.43±0.25	3.82±0.12
Sucrose	5.53±0.27	3.85±0.08
Terpal	8.50±0.86***	3.42±0.09
Cerone	9.90±0.43***	3.59±0.17
GA_3	4.80±0.25	3.14±0.30
TIBA	5.36±0.22	3.85±0.14
BAP	4.93±0.15	3.52±0.19
-MS	5.60±0.33	3.43±0.27
-Tl	5.27±0.23	3.64±0.18

DISCUSSION

Observations described in this chapter demonstrate how applications of nutrients and PGRs may modify certain features of tillering behaviour. The pattern of tillering was similar to that described previously for glasshouse-grown barley (Aspinall, 1961; Laude et al., 1967) with a rapid initial phase of tillering that was followed by a steady decline, so that by the later stages of MS elongation no further tillers appeared; tiller death commenced between anthesis and grain filling. However, when mineral nutrients were supplied every 2 to 3 days (Experiment 4.1) tiller production did not stop at this time and the onset of tiller death was delayed. These observations suggest that tillering stopped and later on, tillers died, at times when the MS had a high nutrient demand. The MS is likely to require an increased nutrient supply when it is undergoing stem elongation, anthesis and grain filling. At these times the influence of apical dominance is probably greater and nutrients are likely to be diverted away from the developing tillers to the MS. Thus when additional nutrients are supplied, competition between the MS and tillers is diminished, allowing tillers to continue growth and survive longer. Kemp and Whingwiri (1980) provide some evidence that competition between tillers may be for reduced N and consider it unlikely that these shoots compete for carbohydrates; although Lauer and Simmons (1985) have recently suggested that diversion of photoassimilate from tillers of spring barley to the MS stem contributes to their premature abortion. However, in the present study even though sufficient nutrients were available, many tillers still died, or remained non-flowering (Experiment 4.1). There may have been insufficient time for certain later produced tillers to form an ear before the onset of whole plant senescence.

It appears that tiller size at the time of MS anthesis and early grain

filling, which is determined largely by the timing of individual tiller emergence, is critical in determining tiller survival or death. The greater the independence of a tiller at the time of MS anthesis, the greater are its chances of survival to ear production. Such independence could be defined by 3 fully expanded leaves in this experiment. Additional nutrients enabled small tillers to continue leaf production after this time and therefore improved their chances of survival by reducing their dependence on the MS and increasing their ability to compete for external resources. Although it is possible that these tillers may have also become better placed to compete for endogenous factors. A further consequence of the increased competitiveness of tillers was that they were more similar in size, in terms of leaf number, height and number of grains per ear. Continued tiller production after ear emergence was observed only when additional nutrients were supplied and tillering did not stop as long as nutrients were continuously supplied. These results show clearly that tillering, subsequent development, and survival were limited by nutrient availability. In the presence of an abundant nutrient supply the yield of ears per plant and grains per ear was vastly increased in this experiment. It was expected that N application would have enhanced tiller survival when applied late in the life cycle (at GS 39), but it had a small effect (Experiment 4.6). However, it has been observed that the later the nutrients are applied, the less the effect on tillering, since competition between the shoots becomes more intense with age (Aspinall, 1961). Similarly the later appearing tillers are very poorly rooted (Anderson-Taylor and Marshall, 1983) and so the majority of the nitrogen taken up may be initially accumulated by the MS.

Nitrogen, particularly if applied early, not only increases tiller *number* but also their survival and yield (Aspinall, 1961; Thorne, 1966; Ishag and Taha, 1974; Garcia del Moral et al., 1984). The uptake of

nitrogen by a given tiller during the tillering phase is extremely important in regulating its future development and productivity (Power and Alessi, 1978). However, it is also well-known that very high applications of N may be disadvantageous in that it increases the risk of lodging (Herbert, 1983). This can be overcome by either breeding semi-dwarf varieties or by using growth retardants. Undesirably high levels of endogenous gibberellins resulting from high N (Rajagopal and Rao, 1974) can be reduced by using growth retardants such as CCC or Terpal.

Of the 3 retardants used in Experiment 4.2, Terpal was found to have the greatest influence on tiller production and size. Responses were similar to those found under field conditions (Chapter 2) where tiller production was increased and the difference in size between tillers reduced. Meanwhile, although CCC application resulted in the expected MS retardation, it also inhibited the production and growth of tillers. Since these effects of CCC on tillering do not correspond with findings of promoted tiller production reported in the literature (Tolbert, 1960; Larter et al., 1965; Bokhari and Youngner, 1971a; Koranteng, 1981), it is possible that the concentration of CCC used in Experiment 4.2 was not optimal. However, there is some evidence that the developmental stage of plants at the time of CCC application determines its precise effect on growth and development. Early treatment reduces the growth rate of aerial parts without affecting tillering in spring wheat (Bruinsma et al., 1965) and in winter wheat and winter barley (Bragg et al., 1984). On the other hand, Tolbert (1960) reported a pronounced stimulation of tillering with CCC application in widely spaced wheat plants when CCC was either applied to seeds at germination or to leaves at GS 11. Further, Koranteng (1981) found that CCC applied at 3 weeks after sowing increased the number of shoots per metre row of

spring barley and resulted in a significant increase in grain yield (g m^{-2}) in winter barley cv. Igri. Ancymidol, previously reported to stimulate tiller production in grasses, for example, Agrostis stolonifera L. (Jinks and Marshall, 1982) and in sorghum (Isbell and Morgan, 1982) failed to do so in Experiment 4.2. It is possible that Ancymidol cannot promote tillering in spring barley, cv. Triumph, but since Ancymidol was applied as a root drench, poor acquisition of the compound from the soil may be to blame for the lack of response to its application. Terpal application consistently resulted in increased tiller production, MS retardation and increased synchrony in tiller development (Experiments 4.2 to 4.5). Terpal caused the earlier outgrowth of tillers and the outgrowth of additional tiller buds which did not grow in control plants. Terpal, when applied early, was unable to completely overcome the influence of apical dominance as tiller production stopped prior to anthesis. This was, however, one week later than in control plants. The application of Terpal and Cerone during the final stages of MS elongation immediately suppressed apical dominance resulting in the revival of dying tillers and renewed bud outgrowth. However, this was, a temporary effect lasting only one week (Experiment 4.6). MS height continued to be retarded in Terpal treated plants throughout (Experiments 4.2 to 4.5) and this was accounted for by both a reduction in the number of elongating internodes and a reduction in the length of the first 3 internodes (Experiment 4.4).

The results of Experiment 4.3 show clearly how Terpal diminished the normal hierarchical pattern of tiller development. The promotory effect of Terpal on primary tillers, T1 and T2, was short-lived (less than 3 days in Experiment 4.3A) and after this initial promotion, the growth of these tillers was retarded. This behaviour resulted in the MS, T1 and T2 having a more similar size than their counterparts in control plants. The accelerated growth rate of later produced tillers continued

for longer, but did eventually diminish. This latter effect may simply have been a reflection of Terpal decreasing in activity. The increased growth rate of later tillers resulted in their larger size and overall, a more synchronous pattern of tiller development than in control plants. The effect of Terpal on T1P was extremely variable; T1P was the next bud to emerge after T2 which was retarded by Terpal and it emerged before T3, T2P and T4, which were promoted by Terpal. The size of the T1P bud at the time of Terpal application is likely to be critical in determining its fate. Until the beginning of grain filling total plant dry weight was little affected by the Terpal treatment, thus the changes described above can be considered as a reallocation of dry weight. Later, plant dry weight was reduced by the Terpal treatment which was due particularly to a reduction in root dry weight.

It is speculated that the timing of rapid MS extension is critical to the amount of tillering. In control plants, tillering occurred early and ceased at the time of rapid MS stem extension. It was found in Experiment 4.4 that when this rapid extension was made to occur either earlier (with GA_3 application) or later (with Terpal application), tiller production could be increased. Until ear emergence GA_3 had an opposite effect to Terpal in that tillering was reduced and MS extension promoted, but when the rapid phase of MS elongation was complete, tillering was promoted. Tillering was also promoted at this same time in plants treated with combined Terpal and GA_3 applications. It is possible that by this time the GA_3 was no longer active although this is unlikely since it has been reported to have long-lived effects (Nothmann and Koller, 1975; Cottrell et al., 1982). On the other hand, it is possible that after MS extension some other mechanism of tiller bud control becomes active and GA_3 is no longer involved.

It has been suggested that there is some direct hormonal influence of

developing grains on tiller buds although this is thought to be only a small effect (Aspinall, 1963). Developing grains contain high amounts of auxin and other growth substances (Wheeler, 1972). However, in Experiment 4.6 the stem shortening compounds, Terpal and Cerone had a far greater effect on tiller production and survival than removal of the MS inflorescence and from other results presented in this chapter it can reasonably be concluded that MS stem elongation inhibits tiller production. This could be due to increased competiveness of the MS stem over the tillers for nutrients, but it seems unlikely that the mechanism resulting in bud inhibition during MS extension is so straight forward. There is evidence from Experiment 4.4 and in the literature to suggest that MS extension and its accompanying high nutrient demand are not the sole controlling factors of bud inhibition. In Experiment 4.4 earlier elongation of the MS was induced by GA_3 application and tiller bud outgrowth was promoted at the same time by the simultaneous application of Terpal. Tiller production was strongly inhibited at this time in the GA_3 only treatment. This evidence refutes the hypothesis that GA_3 inhibits tiller production simply by promoting stem extension and thereby utilizing resources required by tiller buds, unless, of course, nutrient absorption is enhanced by the combined Terpal/GA_3 treatments. Tiller bud outgrowth was, however, diminished in these treatments when the MS had between 6 and 7 leaves and had reached approximately 50% of its final height. Since GA_3-promoted stem extension may not directly inhibit early tiller bud outgrowth, it seems possible that the enhancement of apical dominance by GA_3 is due to a direct effect of GA_3 on tiller buds. It therefore follows that the effect of Terpal on tiller buds may also be a direct one since mepiquat chloride is thought to interfere with GA_3 biosynthesis; it could therefore relieve the buds of the inhibitory influence of GA_3. Alternatively the ethylene component of Terpal may exert such a direct effect. Also, it was shown in this experiment that Terpal rapidly

increased tiller production even if the MS was elongating, further supporting the idea that this PGR has a direct effect on tiller buds. In other studies, Morgan et al. (1977) and Isbell and Morgan (1982), a range of GA_3 concentrations were employed such that one treatment was low enough to prevent tiller bud outgrowth without significant promotion of stem extension. This confirms the findings of the present study that GA_3 does not have its effect by increasing the competiveness of the MS over the tiller buds and may therefore have a more or less direct inhibitory effect on tiller buds. Also Jewiss (1972) found that GA_3-inhibited buds were not released by direct application of sucrose, indicating that some factor other than carbohydrate starvation probably limited bud growth.

The Terpal and GA_3 applications did not entirely reverse the effects of each other. Terpal was not expected to affect exogenous GA_3, since its action is thought to be by way of biosynthesis antagonism. Thus Terpal would diminish only the endogenous production of GA_3 and so the combined treatments ilicited an intermediate response. GA_3 did not overcome the promotory effect of Terpal on tiller buds, suggesting again that Terpal had some effect on buds other than by blocking GA_3, for example, via ethylene action.

The pattern of ^{14}C assimilate distribution from the MS to the developing tillers (Experiment 4.5) was generally similar to that previously described for Lolium multiflorum (Marshall and Sagar, 1968), L. temulentum (Ryle and Powell, 1972), Poa pratensis (Nyahoza et al., 1973) and L. perenne (Colvill and Marshall, 1981). Each developing primary tiller was supplied with ^{14}C-assimilate as were the first produced secondary tillers. In Experiment 4.5 it was shown that as T1 and T2 increased in size, and therefore assimilatory capacity, their import of assimilate declined. It is likely that these tillers would

have reached a stage where they became independent of the MS in terms of their carbon economy. However, in a previous study (Marshall and Sagar, 1968), it was found that such independence was never absolute, some radiocarbon from the MS was always detected in established primary tillers and their roots, but this was possibly because of the vascular organisation of the young tillering plant rather than any requirement for assimilate. There is evidence from Experiment 4.5 that ^{14}C-assimilate translocation from the MS to developing tiller buds and tillers was modified by PGR application. Terpal, Cerone and TIBA all had similar effects. At the first harvest (GS 13), these treatments increased the ^{14}C recovered from T1, and at the 2nd harvest (GS 15), the ^{14}C recovered from T1 was reduced, whereas that from secondary tillers was increased. These findings confirm previous observations of the effects of Terpal (Experiment 4.3) of an initial promotion of T1 prior to its retardation. GA_3 had an opposite effect, for example, at GS 15 the ^{14}C recovered from T1 and T2 was increased, whereas that of the secondary tillers was reduced. These findings corroborate with results discussed earlier of modifications of tiller development. It was not possible to determine, however, whether these responses to PGR treatment were as a direct result of application or were secondary or tertiary responses.

The highest rates of survival and dry matter yield were obtained from MS, T1 and T2 in the present study. Survival rates and tiller grain yields were related to their time of emergence and were proportional to their size before MS ear emergence. Hence later emerging, and therefore smaller tillers, did not yield as well as primary tillers. This has been previously reported by Rawson (1971) and Koranteng (1981). The MS had 5 or 6 leaves and was commencing stem elongation before many of these tillers emerged, for example, T3 and T1P emerged at this time and their survival rate was much less than that of previously emerged

tillers. Tillers emerging after this time were unlikely to have developed sufficient leaf area or roots to render them independent of the MS before the final stages of MS elongation and ear emergence. Although Terpal increased the number of ear-bearing tillers per plant, no yield increase was realised. This was because of reduced grain size, further indicating the role of Terpal in dry weight reallocation. Cerone had a similar effect, increasing the number of ears per plant but reducing their size so that total plant ear weight was unchanged. It is concluded that only simultaneous applications of N would result in significant yield increases from Terpal and Cerone applications.

CHAPTER 5

SEED TREATMENT WITH TERPAL

INTRODUCTION

There is much evidence in the literature that the treatment of seeds at the onset of germination can produce dramatic and long lasting effects on plant growth and development. Probably the most well-known example of such seed pre-treatment is that involving partial imbibition of the seed followed by exposure to low temperatures, in the process of vernalization. Many workers, including May et al. (1962), Woodruff (1969), De et al. (1982), Chatterjee and Singh (1983), Hariharan and Unnikrishnan (1983) and Singh and Banerji (1983), have obtained increased yields from various pre-sowing seed treatments. Singh and Banerji (1983) found that a pre-sowing chill treatment to a wheat cultivar that did not require vernalization for flowering, enhanced tillering and yield. They suggested that the underlying biochemical changes may involve modifications of endogenous PGR content.

There is considerable evidence, mainly from the USSR, that the drought resistance of plants can be increased by subjecting seeds to a cycle of wetting and drying before sowing. Genkel (1946, in May et al., 1962) claims that plants hardened by treatment before sowing, yield better under drought conditions. He obtained increases in yield of 10 to 25% for wheat resulting from more grains per ear (due to more spikelets) and possibly also because of a higher 1000 grain weight. Henckel (1964) suggested that such drought hardening may result from an increase in the hydrophilic property of the protoplasmic colloids thereby enhancing water holding capacity. Wetting and drying of seed prior to sowing is also considered to increase the resistance of the plant to heat and its tolerance to soil salinity (May et al., 1962). Chatterjee and Singh (1983) found that soaking barley seeds in salt solutions ($Na_2HPO_4.12H_2O$; $Al(NO_3)_3.6H_2O$ or $Co(NO_3)_2.6H_2O$) and then drying them

before sowing, produced taller plants with more tillers and greater dry weight than untreated plants grown under rainfed conditions in India. Bozhenko (1965) also reported that seed treatment with trace elements (especially Cobalt) increased ATP content of the shoot and root meristems of sunflower and that this possibly caused increased resistance to drought and high temperatures.

Miyamoto (1962) found that seed soaked in CCC (0.5% solution CCC for 14 hours) increased the resistance of wheat seedlings to high concentrations of salts and to high and low soil pH. De et al. (1982) working in India, found that by soaking wheat seeds overnight in a 0.5% solution of CCC, yield could be increased significantly over untreated controls. They reported that CCC caused more root-growth, increased stomatal resistance and produced higher leaf water potentials. Treated plants extracted more water from deeper soil layers increasing their water-use efficiency. Seed soaked with sub-lethal concentrations of the herbicide 2,4-D can also modify growth and produce some beneficial effects. Abdel-Malik et al. (1975, in Hariharan and Unnikrishnan, 1983) obtained improved growth and yield in corn (Zea mays L.) and in another study Hariharan and Unnikrishnan (1983) found that 2,4-D treatment of seed of Trigonella foenum-graecum enhanced fruit and seed development. It is obvious, therefore, from the examples cited above, that CCC and 2,4-D and maybe other similar compounds, can profoundly effect plant growth and development when applied at a very early stage.

In this chapter, seeds were treated with Terpal before sowing by allowing them to take up the growth regulator during imbibition at the onset of germination. It was thought that apical dominance might be diminished and tillering enhanced more successfully if Terpal was introduced to the plant as early on in development as possible.

EXPERIMENTAL

Experiment 5.1 Germination trial and preliminary study of the effects of Terpal seed soaking treatments.

A range of Terpal seed soaking treatments were applied to spring barley (cv. Triumph) seeds to assess their effects on germination, growth and development, and yield.

MATERIALS AND METHODS

Dry seeds, or seeds previously imbibed with aerated distilled water for 12 hours, were exposed to Terpal on moist filter paper in Petri dishes. On 27 March 1983, 3 concentrations (10, 50 and 100%) of the recommended rate of application of Terpal, were applied to dry seeds for 12, 24 and 48 hours and to imbibed seeds for 12 hours. Control seeds were soaked in distilled water only. The Petri dishes were incubated at 20°C under fluorescent lighting at a photonfluence rate of 300 $\mu E\ m^{-2}\ s^{-1}$ in a controlled environment cabinet with a 16 hour photoperiod. After exposure to the treatments the seeds were transferred to clean Petri dishes containing only distilled water for a 4 day period. The seedlings were then transferred individually to pots containing John Innes No. 1 potting compost and grown under glasshouse conditions in the "old" glasshouse suite as described in Chapter 4. Germination was recorded prior to transplanting, and thereafter tiller production and survival were monitored. MS height and dry weight at 4 weeks after soaking, and MS height and dry matter yield at grain-ripening were also measured.

RESULTS

The control treatment had the most successful germination with 96% of *seeds germinating within 3 days* (Table 5.1). Germination was defined as the first sign of emergence of the first seminal root on imbibition. When the Terpal treatments were applied the degree of germination varied according to the concentration and duration of exposure to the chemical. Those seeds treated with the lowest concentration (10%) for the shortest time (12 hours) had the highest percentage germination and this was the same as the control treatment (Table 5.1). The percentage germination of seeds treated with all the 10% Terpal treatments was not significantly different from the control treatment. On the other hand, the percentage emergence of the coleoptile of the seedlings after 3 days was greatly reduced compared with the control treatment. For example, the 10% concentration of Terpal for 12 hours reduced it by 35% (Table 5.1). The 50% concentration reduced germination, especially as the degree of exposure to Terpal increased from 12 to 48 hours; coleoptile emergence was almost completely absent in the 48 hour treatment and in imbibed seed treated with Terpal. At the 100% concentration, germination was reduced further, those seeds treated with this concentration for the longest time had the lowest percentage germination of all the treatments. Coleoptile emergence was completely retarded at this time in all but one of the 100% treatments, that is, the 12 hour Terpal treatment, where coleoptile emergence was reduced by 84%. The germination of seeds imbibed with water before Terpal application for 12 hours was reduced further (Table 5.1). Once the seed treated with the 100% Terpal concentration had been transferred to compost some additional germination was observed particularly in those seeds imbibed with water prior to exposure to Terpal. All seed that germinated continued growth and survived to grain harvest (Table 5.2).

Table 5.1 Effect of Terpal seed treatment on percentage germination and emergence of the coleoptile at 3 days after seed soaking (±SE).

Treatment	% Germination	% Coleoptile emergence
Control	96 ± 4.0	74 ± 8.1
10% Terpal 12h	96 ± 4.0	48 ± 8.6 *
" " 24h	92 ± 3.7	46 ± 6.8 *
" " 48h	90 ± 4.5	56 ± 9.3
" " Imbibed	86 ± 5.1	42 ±12.0 *
50% Terpal 12h	84 ± 5.1	44 ± 6.0 *
" " 24h	64 ± 8.7 *	12 ± 5.8 **
" " 48h	62 ±14.9 *	2 ± 2.0 **
" " Imbibed	48 ± 6.6 **	2 ± 2.0 **
100% Terpal 12h	82 ± 3.7 *	12 ± 3.7 **
" " 24h	32 ± 9.7 **	0
" " 48h	18 ± 5.8 **	0
" " Imbibed	12 ± 5.8 **	0

The pattern of tillering is shown with time for the 12 hour soaking treatments (to dry seeds) only (Fig. 5.1). The order of tiller emergence and pattern of tillering were unchanged by the seed treatments. Tillering was rapid over the first 4 weeks after soaking, but declined over the following 2 weeks up to ear emergence. Subsequently, tillering was again rapid and by anthesis the Terpal treatments had produced approximately 2 more tillers than control plants (significant at the $p<0.05$ level). Tillering declined after anthesis (Fig. 5.1). All concentrations of Terpal increased tiller production, but only the 50% concentration resulted in significant ($p<0.05$) increases prior to ear emergence. By anthesis all concentrations of Terpal had significantly ($p<0.05$) increased tiller production by about 21% (Fig. 5.1).

By the time of grain ripening, 8 weeks after soaking, all of the seed soaking treatments had increased tiller production with the exception of soaking in 100% Terpal for 48 hours (Table 5.2). The treatments that had the greatest effect on tiller production were the 10% concentration of Terpal for 12, 24 and 48 hours on dry seeds and the 50 and 100% concentrations of Terpal for 12 hours only on dry seeds; these effects were statistically significant (Table 5.2). Several of the treatments also increased the number of ear-bearing tillers per plant, these were, the 10% concentration for 12 and 48 hours on dry seed and for 12 hours on imbibed seed, the 50% concentration for 24 and 48 hours on dry seed and the 100% concentration for 12 hours on dry seed (Table 5.2). The number of ear-bearing tillers was reduced ($p<0.01$) by soaking in 100% Terpal for 48 hours. None of the treatments greatly increased the percentage tiller survival, so although ear number per plant was often increased by the Terpal seed treatments, about 25% of the tillers produced still died prematurely (Table 5.2).

Fig. 5.1

Effect of Terpal seed treatments on tiller production with time. Treatments applied for 12 hours to dry seeds only.

- ○ Control
- ● 10% Terpal
- ▲ 50% Terpal
- ■ 100% Terpal

A : MS ear emergence

B : MS anthesis

Vertical bars represent ±SE.

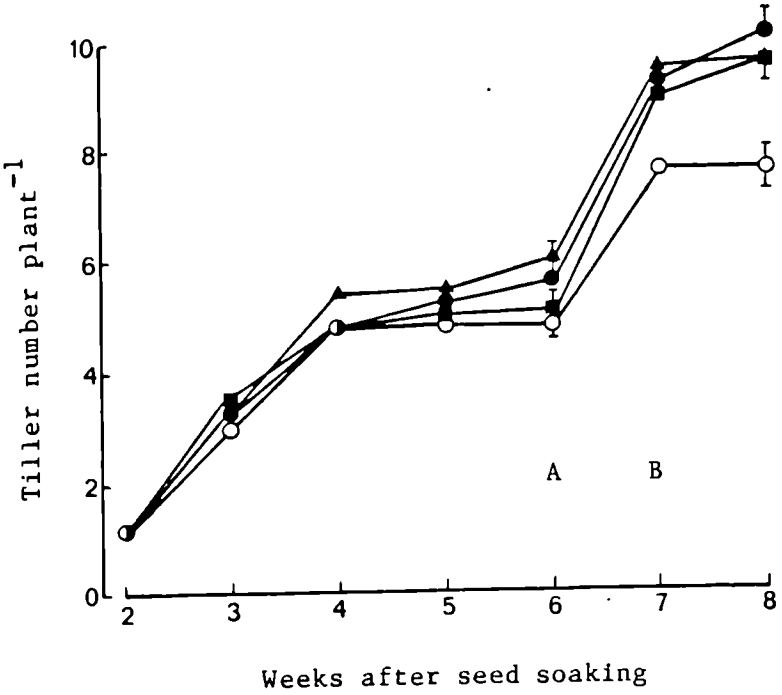

Tiller number plant^{-1}
10
8
6
4
2
0
2
3
4
5
6
7
8
A
B
Weeks after seed soaking

Table 5.2 Effect of Terpal seed treatments on tiller production and survival (including MS) at 8 weeks after soaking (final harvest) ±SE.

Treatment	Number of replicates	Tillers/ plant	Ears/ plant	% survival
Control	5	7.6±0.40	5.6±0.24	74
10% Terpal 12h	5	10.2±0.58**	7.6±0.81**	74
" " 24h	5	9.6±0.81*	6.2±0.37	65
" " 48h	5	9.4±0.81*	7.0±0.00**	74
" " Imbibed	5	9.2±0.80	6.8±0.49*	74
50% Terpal 12h	5	9.6±0.24**	6.0±0.63	62
" " 24h	5	9.2±0.66	6.6±0.40*	72
" " 48h	5	9.4±1.07	6.6±0.24*	70
" " Imbibed	5	8.0±0.83	5.6±0.24	70
100% Terpal 12h	5	9.6±0.40*	7.6±0.40**	79
" " 24h	5	8.7±1.11	5.8±0.49	67
" " 48h	2	5.0±2.00	3.0±0.00**	60
" " Imbibed	4	8.5±0.87	6.7±0.56	79

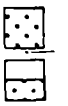
Four weeks after soaking, the Terpal treatments had little effect on MS height (Fig. 5.2). Only the 50% concentration for 48 hours on dry seed and for 12 hours on imbibed seed gave significant ($p<0.05$) reductions in MS height (31 and 35% respectively). By the final harvest there was no significant difference in MS height in any of the treatments (Fig. 5.2)

The distribution of dry weight between the shoots was little affected by the Terpal seed treatments at 4 weeks after soaking (Fig. 5.3). All concentrations of Terpal applied for 12 hours, to dry seeds, reduced the dry weight of the MS but this was not statistically significant. However, these seed treatments did have one significant effect on dry weight, that is, the dry weight of T3 and T4 was increased by around 100% (Fig. 5.3).

At final grain harvest it was found that most of the seed treatments did not affect MS ear weight or number of grains per MS ear (Table 5.3). The 10% concentration of Terpal for 12 hours on dry seed and on imbibed seed significantly ($p<0.05$) reduced the weight of the MS ear, whereas the 100% concentration for 24 hours increased ($p<0.05$) both MS ear weight and grain number. Mean tiller ear weight was reduced by all of the Terpal seed treatments although only the effects of the 10% concentration for 12 and 48 hours on dry seed, the 50% concentration for 48 hours on dry seed, and the 100% concentration for 12 hours also on dry seed were statistically significant (Table 5.3). Grain number per tiller ear was not affected by any of the treatments. Furthermore, total ear dry weight per plant was not affected (with one exception) by the Terpal seed treatments even though they had increased the number of ears per plant. Soaking in 100% Terpal for 48 hours significantly ($p<0.01$) reduced total ear dry weight reflecting the smaller ear number per plant. Total straw dry weight and as a consequence, total biomass,

Fig. 5.2

Effect of Terpal seed treatments on MS height at:



4 weeks after seed soaking

8 " " " "

12, 24, 48 : duration of seed soaking (hours) (dry seeds)

Imb : 12 hours of seed soaking (imbibed seeds)

Vertical bars represent ±SE.

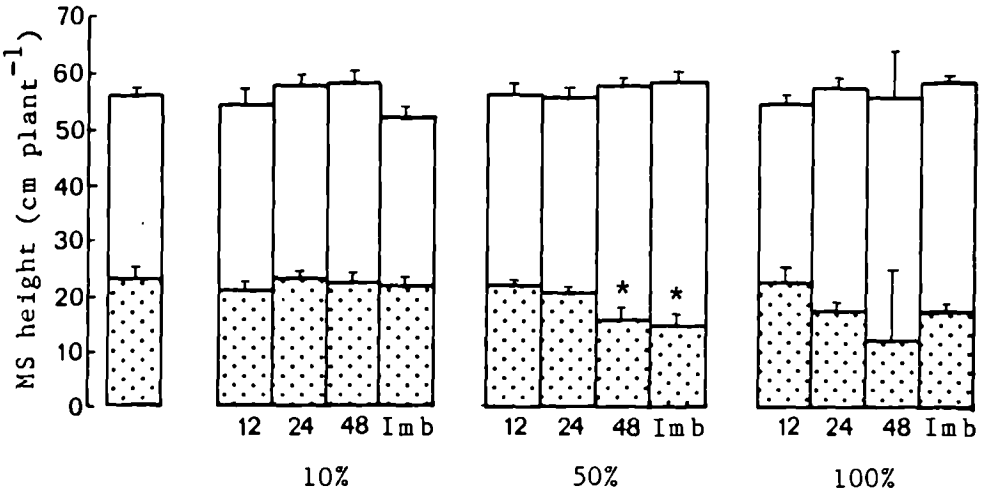

MS height (cm plant^{-1})
70
60
50
40
30
20
10
0
12 24 48 Imb
12 24 48 Imb
12 24 48 Imb
*
*
10%
50%
100%
Control
Terpal concentration

Fig. 5.3

Effect of Terpal seed treatments on the dry weight distribution between the MS and tillers at 4 weeks after soaking. Treatments applied for 12 hours to dry seeds only.

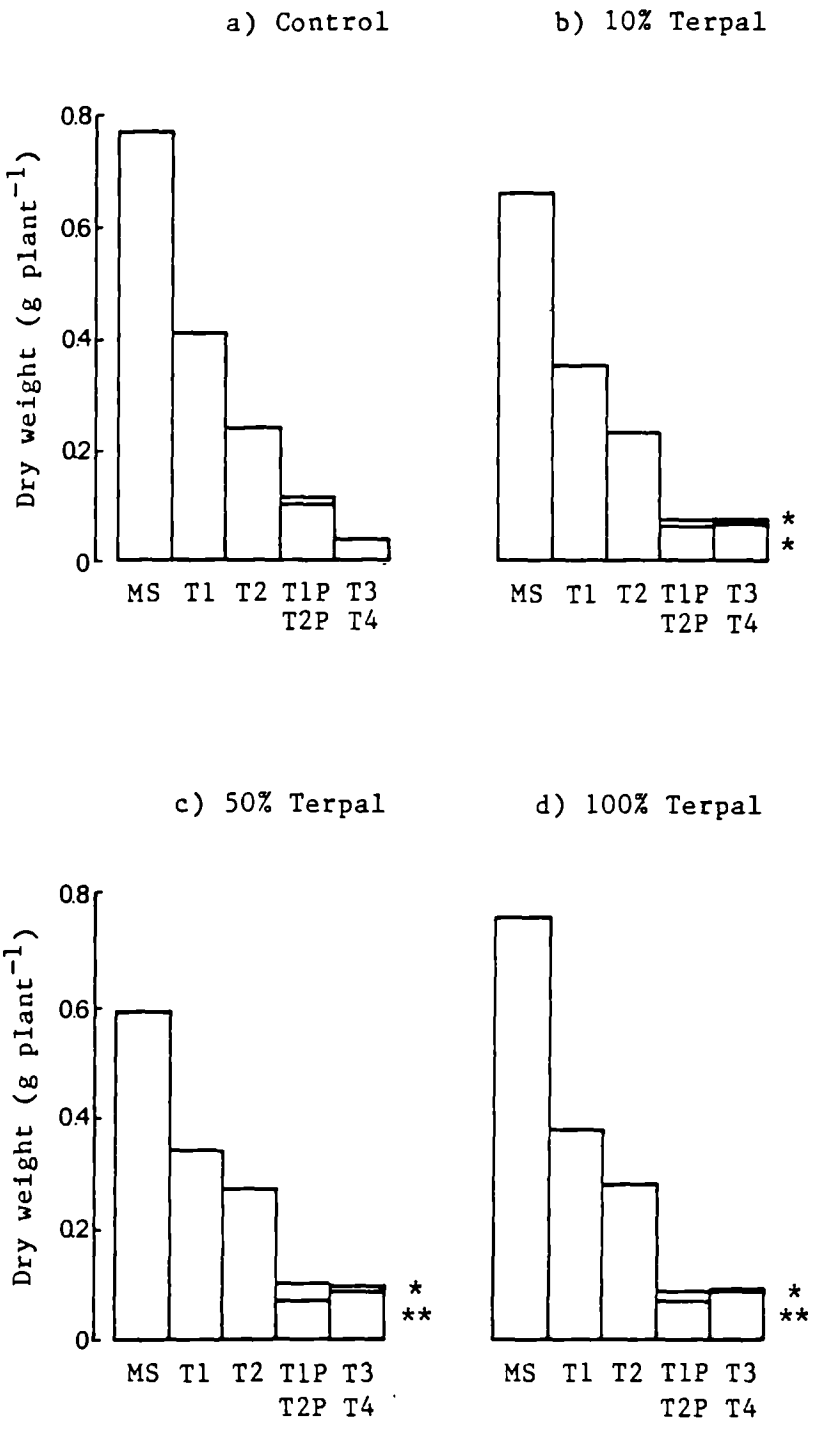

a) Control
b) 10% Terpal
c) 50% Terpal
d) 100% Terpal
Dry weight (g plant^{-1})
0.8
0.6
0.4
0.2
0
MS T1 T2 T1P T3 T2P T4
*
**

Table 5.3 Effects of Terpal seed treatment on dry matter yield (g) of component parts and grain number per ear at final harvest ±SE. (Imb.= 12h soaking of imbibed seed; DW = dry weight).

Treatment	MS ear DW	MS grain number	Ear DW tiller^{-1}	Grain no. tiller^{-1}	Total ear DW	Total straw DW	Total biomass
Control	1.39±0.03	23.0±0.45	0.83±0.04	18.5±1.20	5.14±0.13	3.09±0.13	8.24±0.15
10% Terpal 12h	1.20±0.07*	21.8±0.58	0.56±0.09*	17.9±0.89	4.90±0.20	3.44±0.09*	8.14±0.20
" " 24h	1.33±0.03	23.4±0.40	0.75±0.04	18.7±1.30	5.23±0.21	3.39±0.15	8.62±0.30
" " 48h	1.31±0.03	22.8±0.20	0.65±0.04**	19.7±1.40	5.21±0.20	3.28±0.25	8.49±0.28
" " Imb.	1.21±0.06*	21.0±1.00	0.66±0.10	18.7±1.50	5.04±0.36	3.41±0.10	8.47±0.25
50% Terpal 12h	1.40±0.06	22.8±0.37	0.78±0.03	19.1±1.70	5.30±0.28	3.18±0.09	8.25±0.25
" " 24h	1.36±0.03	22.8±0.49	0.72±0.04	19.4±0.73	5.39±0.20	3.61±0.14*	8.95±0.20*
" " 48h	1.42±0.01	23.0±0.45	0.65±0.04**	18.7±0.76	5.06±0.13	3.66±0.08**	8.72±0.20*
" " Imb.	1.40±0.06	22.4±0.98	0.78±0.03	19.6±0.72	4.99±0.28	3.18±0.09	8.17±0.20
100% Terpal 12h	1.30±0.07	22.6±0.51	0.61±0.04**	18.9±1.40	5.32±0.25	3.55±0.11*	8.92±0.26*
" " 24h	1.50±0.04*	24.4±0.40*	0.78±0.07	19.9±1.20	5.24±0.19	3.69±0.09**	8.87±0.20*
" " 48h	1.33±0.06	23.5±1.50	0.58±0.28	15.2±1.70	1.99±0.52**	1.21±0.36**	3.21±0.08**
" " Imb.	1.46±0.03	23.0±1.10	0.71±0.04	19.4±0.68	5.51±0.34	3.81±0.08**	9.32±0.25**

were generally increased by the Terpal seed treatments and this was because of the increased number of tillers per plant. This effect was not always statistically significant but was usually so at the higher Terpal concentration treatments (Table 5.3). In contrast, the 100% Terpal treatment for 48 hours significantly ($p<0.01$) reduced straw dry weight and total biomass due to the reduced number of tillers per plant (Table 5.3).

Experiment 5.2 Effects of seed soaking with Terpal on early leaf and tiller bud growth.

In order to determine how soon after soaking plant growth was modified and to define more precisely the responses observed previously, an experiment was designed in which plants were harvested at frequent intervals after the seed soaking treatment with Terpal.

MATERIALS AND METHODS

Terpal, at 10% of the recommended rate of application, was applied to dry seeds for 12 hours as described in Experiment 5.1, on 15 July 1983. After 4 days the seeds were transferred individually to pots of John Innes No. 1 potting compost and grown under glasshouse conditions in the "old" glasshouse suite as described in Chapter 4. Six replicate plants were harvested at 3 to 7 day intervals immediately after planting. Tiller bud number, length and dry weight were obtained. MS leaf number, leaf length and dry weight were also measured. Root length and dry weight were measured for the first 19 days, after this time root excavation became very inaccurate and no further observations were made on the root system.

RESULTS

Tiller production was again found to be enhanced by seed treatment with Terpal. Growing tiller bud number per plant was significantly increased ($p<0.05$) by 8 days after seed soaking and this increase was maintained thereafter (Fig. 5.4). This increase was due to the outgrowth of more secondary tiller buds, for example, T1,1 and T2P. Tiller buds also commenced outgrowth earlier in the treated plants (Table 5.4). Eight days after soaking Terpal had increased the outgrowth of T1 from 50 to 100%, 12 days after soaking the outgrowth of T2 was increased by about 600% compared to control plants and at 15 days after soaking all Terpal treated plants had growing T3 buds whereas control plants had none. By 26 days after soaking all plants had a similar percentage of growing buds (Table 5.4).

Table 5.4 Percentage frequency of growing tiller buds.

Days after soaking	Control						Terpal					
	T1	T2	T3	T1P	T2P	T4	T1	T2	T3	T1P	T2P	T4
8	50						100					
12	100	17					100	100				
15	100	100					100	100	100			
19	100	100	66	100	83	17	100	100	100	100	83	83
26	100	100	100	100	83	100	100	100	100	100	100	100

The Terpal seed treatment also significantly ($p<0.05$) increased the initial elongation (for approximately the first 11 days) of T1, T2, T3 and T4 buds (Fig. 5.5a). The length of the T3 bud was greatly increased, that is, by 150%. However, after this initial period of growth, the elongation of the T1 axis was significantly ($p<0.05$)

Fig. 5.4

Effect of Terpal seed treatment on tiller bud, and emerged tiller number with time.

○ Control

● Terpal

Vertical bars represent ±SE.

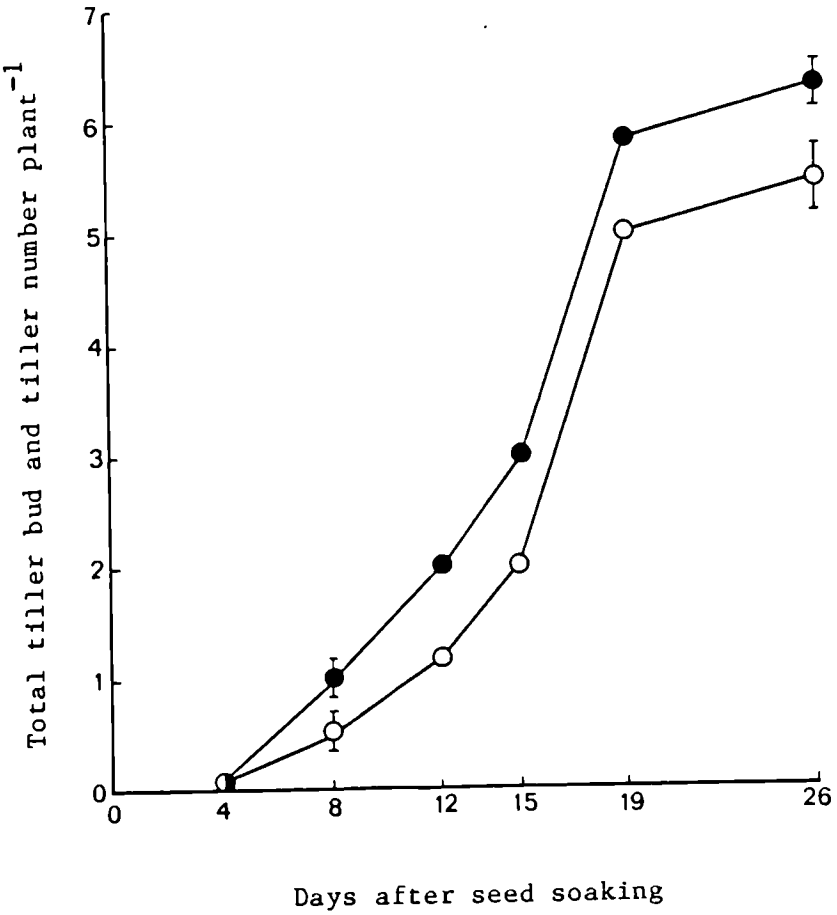

Total tiller bud and tiller number plant^{-1}
0
1
2
3
4
5
6
7
0
4
8
12
15
19
26
Days after seed soaking

Fig. 5.5

Effect of Terpal seed treatment on:

(a) tiller bud (or tiller) length with time,

(b) tiller bud (or tiller) dry weight with time.

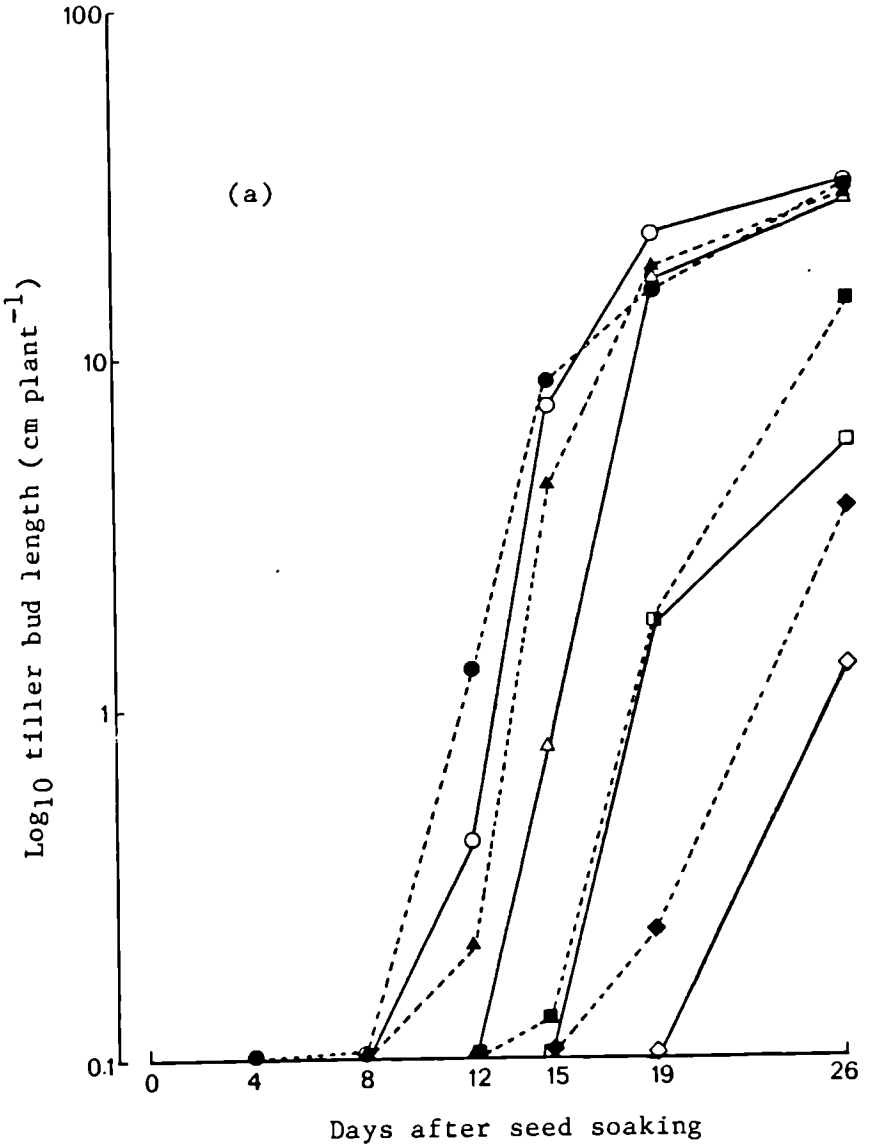
○ ● T1

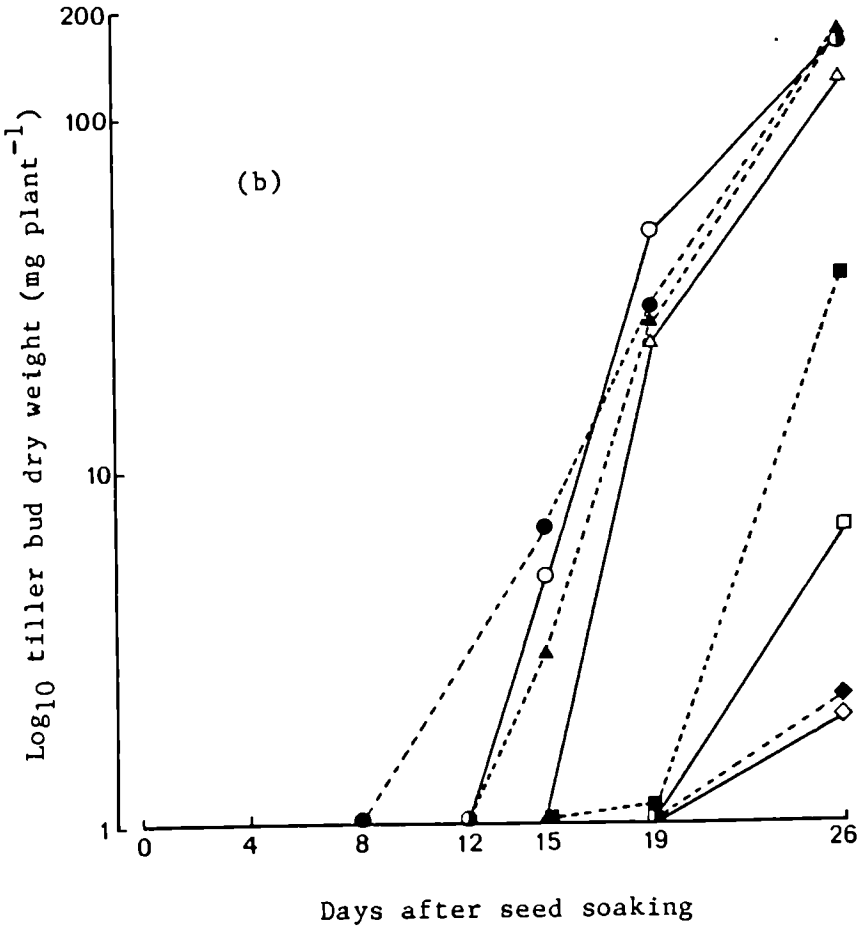
△ ▲ T2

□ ■ T3

◇ ◆ T4

Open symbols (and solid lines) represent control plants.
Solid symbols (and dotted lines) represent Terpal treated plants.


(a)
100
10
1
0.1
Log10 tiller bud length (cm plant-1)
0
4
8
12
15
19
26
Days after seed soaking


(b)
200
100
10
1
Log10 tiller bud dry weight (mg plant-1)
0
4
8
12
15
19
26
Days after seed soaking

reduced by the Terpal seed treatment. Thus, by 19 days after seed soaking the lengths of T1 and T2 were more similar in treated plants than in control plants (Fig. 5.5a). Although the T1 bud commenced growth earlier in the Terpal seed treated plants, at 19 days its dry weight was reduced compared with control plants; at 26 days after treatment its dry weight was not significantly different from that of control plants (Fig. 5.5b). The dry weights of T2 and T3 were significantly increased ($p<0.01$) by 42 and 350% respectively at 26 days after Terpal seed treatment whereas the dry weight of T4 was little affected.

MS leaf number was not significantly affected by the Terpal seed treatment; the leaf number of T1 and T2 was significantly ($p<0.05$) increased by 26 days after seed soaking but the effect was small (Table 5.5).

Table 5.5 Effect of Terpal seed treatment on the number of growing and fully expanded leaves (±SE).

Days after	Control			Terpal		
soaking	MS	T1	T2	MS	T1	T2
8	3.0 ±0.0			3.0 ±0.0		
12	4.0 ±0.0			4.0 ±0.0		
15	5.0 ±0.0			5.0 ±0.0		
19	7.0 ±0.0	3.0 ±0.0	2.2 ±0.3	7.0 ±0.0	2.7 ±0.2	2.5 ±0.2
26	7.0 ±0.0	3.2 ±0.2	3.0 ±0.0	8.0 ±2.0	3.8 ±0.2*	3.5 ±0.2*

The lengths of the MS leaves, 1 to 5, were significantly ($p<0.01$ for L1 to L4 and $p<0.05$ for L5) reduced by the Terpal seed treatment by 26 days after soaking (Fig. 5.6). Terpal had the greatest effect on L3 which was reduced by 34%, 26 days after soaking. This reduction in leaf length was obvious at the onset of elongation of L2, whereas L3, L4 and L5 were initially longer in the seed treated plants as these leaves emerged slightly earlier, the reduction in the length of these leaves was not seen until between 15 and 26 days after seed soaking. The lengths of the elongating leaves (L6 and L7) were significantly ($p<0.05$ and $p<0.01$ respectively) greater at 26 days after soaking in Terpal treated plants and this was due to their earlier emergence and initial faster growth rate (Fig. 5.6b). The dry weight of the MS leaves reflected these measurements of leaf length. The dry weight of leaves 1 to 5 was reduced by the Terpal treatment ($p<0.05$), Terpal having the greatest effect on L3 (Fig. 5.7). The dry weight of L6 was increased by the Terpal treatment ($p<0.05$). There was no significant effect of Terpal on the dry weight of L7 by 26 days after soaking (Fig. 5.7b).

The total dry weight of the MS was little affected by the Terpal treatment until 19 days after soaking when it was reduced ($p<0.01$), MS dry weight was also reduced at 26 days after soaking but this effect was not statistically significant (Fig. 5.8). The total dry weight of the tillers and total plant dry weight were not significantly affected by the Terpal seed treatment at any harvest (Fig. 5.8).

The Terpal seed treatment had no significant effect on root length or dry weight until 26 days after seed treatment when the total root system dry weight was significantly ($p<0.05$) reduced (Table 5.6). Although the results for individual root length were not significantly different, each of the 3 longest seminal roots of the Terpal treated plants was less than that of the comparable roots from control plants

Fig. 5.6

Effect of Terpal seed treatment on the length of MS laminae with time.

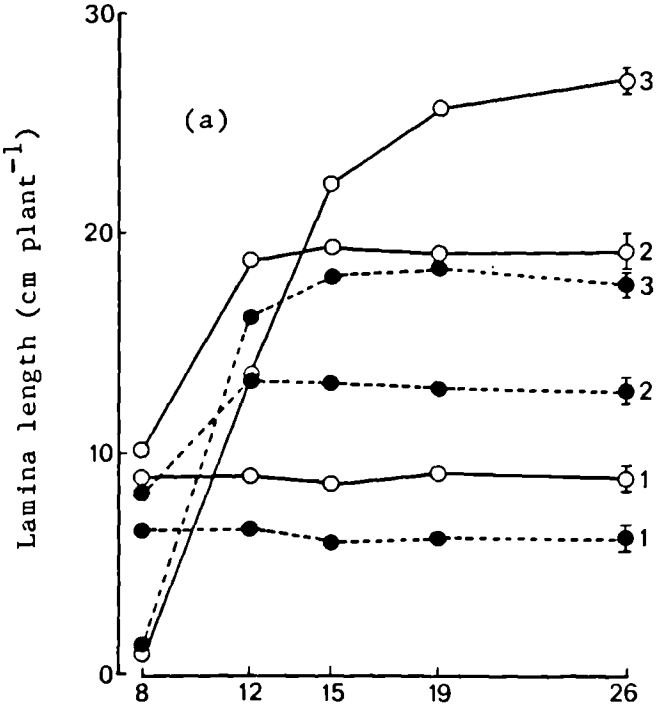
(a) MS leaves 1 to 3.

(b) MS leaves 4 to 7.

o—o Control

●···● Terpal

Vertical bars represent ±SE.


(a)
Lamina length (cm plant^{-1})
30
20
10
0
8
12
15
19
26
3
2
3
2
1
1
Days after seed soaking

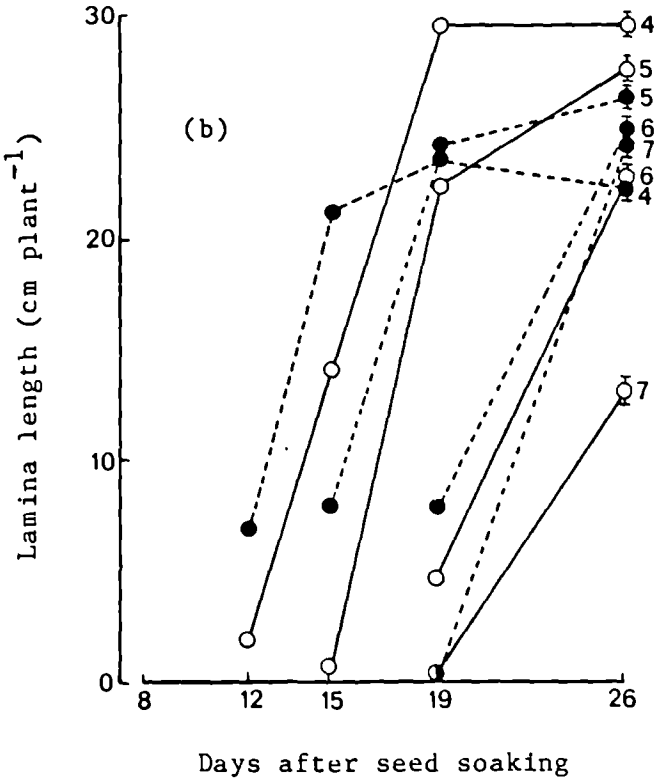

(b)
Lamina length (cm plant^{-1})
30
20
10
0
8
12
15
19
26
4
5
5
6
7
6
4
7
Days after seed soaking

Fig. 5.7

Effect of Terpal seed treatment on the dry weight of MS leaf laminae with time.

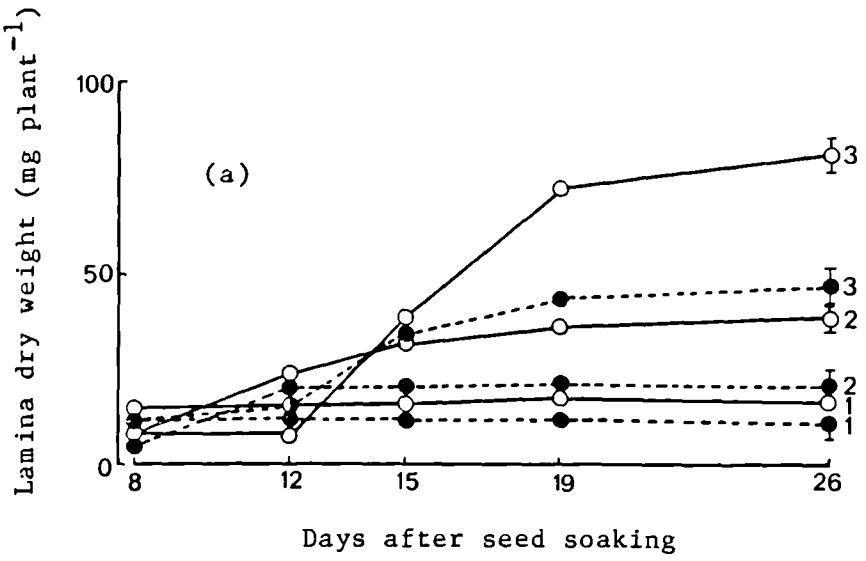
(a) MS leaves 1 to 3.

(b) MS leaves 4 to 7.

o—o Control

●···● Terpal

Vertical bars represent ±SE.


Lamina dry weight (mg plant^{-1})
100
50
0
(a)
3
3
2
2
1
1
8
12
15
19
26
Days after seed soaking

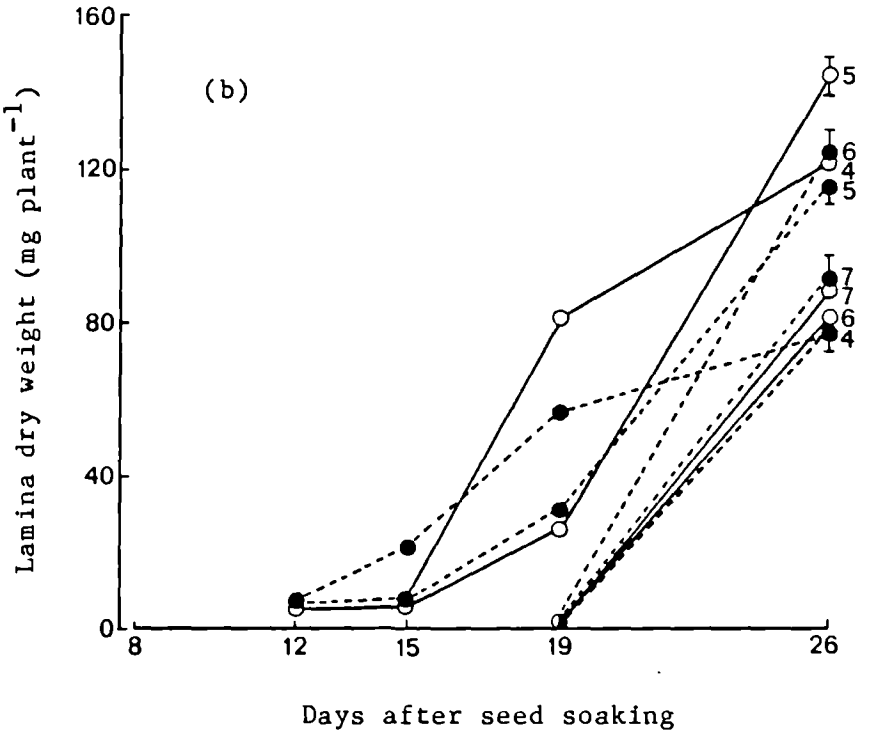

Lamina dry weight (mg plant^{-1})
160
120
80
40
0
(b)
5
6
4
5
7
7
6
4
8
12
15
19
26
Days after seed soaking

Fig. 5.8

Effect of Terpal seed treatment with time on the dry weight of:

□ ■ MS

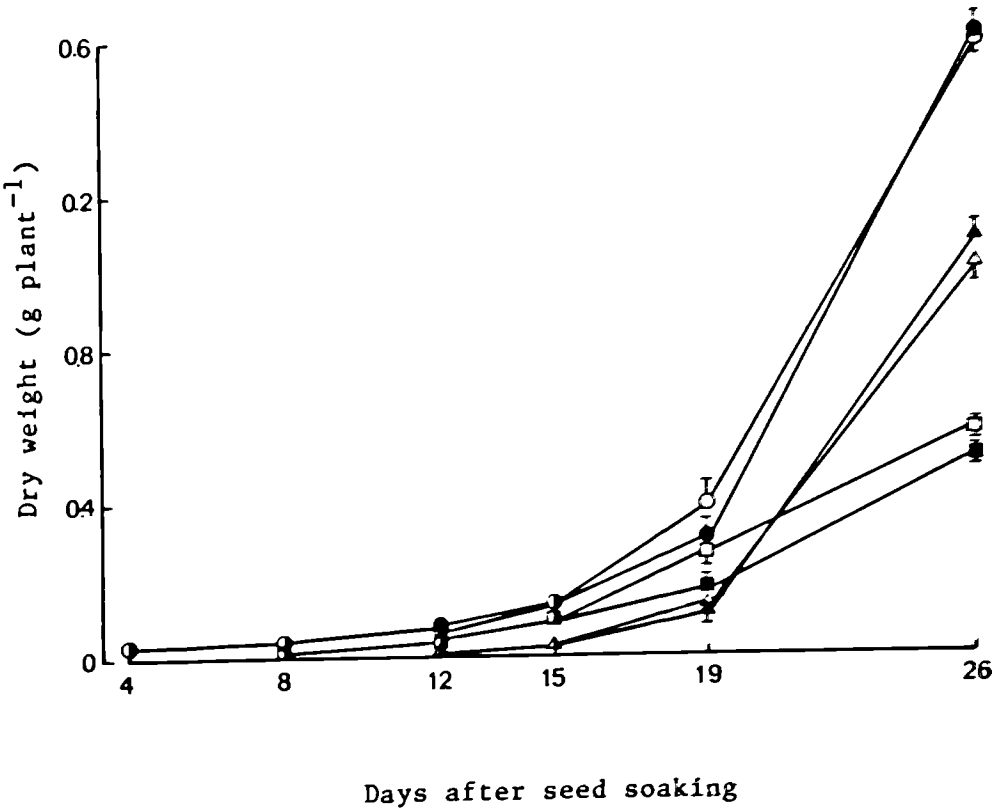
△ ▲ Total tillers

○ ● Total plant (MS + tillers + roots)

Open symbols represent control plants

Solid symbols represent Terpal treated plants

Vertical bars represent ±SE.


0.6
0.2
0.8
0.4
0
Dry weight (g plant^{-1})
4
8
12
15
19
26
Days after seed soaking

(Table 5.6) and the combined lengths of these roots was significantly ($p<0.05$) less in the Terpal treated plants.

Table 5.6 Effect of Terpal seed treatment on root length and dry weight at 26 days after seed soaking (±SE).

Treatment	Length of 3 longest seminal roots (mm)			Dry weight
	1	2	3	(mg)
Control	388.7 ±41.3	373.3 ±41.8	321.5 ±45.8	67.0 ±7.0
Terpal	366.8 ±24.4	301.5 ±11.0	285.5 ±18.1	50.0 ±3.0 *

DISCUSSION

As shown in other studies (Miyamoto, 1962; De et al., 1982; Hariharan and Unnikrishnan, 1983) the pre-sowing treatment of seed with growth regulating agents can have a marked effect on plant growth and development. Terpal applied to imbibing barley seeds significantly modified the normal pattern of apical dominance, in that the outgrowth of tillers was promoted and the growth and development of the later formed primary and secondary tillers was characteristically enhanced. The size of the first five MS leaves was also reduced, but there was generally no overall effect on total plant dry weight. This general response to Terpal is similar to that evoked by foliar application (Chapter 4) but the effects were of a lesser magnitude compared with those generated by foliar application of Terpal at GS 13. For example, after Terpal seed treatment, increases in tiller production were in the order of 25.0±5.3% (mean value), whereas tiller production was increased by 49.0±8.7% (mean value from results in Chapter 4) when Terpal was applied to leaves. Also, MS height, reduced by 27.5±2.7% (mean value from results of Chapter 4) on foliar application of Terpal, was either unaffected or reduced only slightly after seed treatment. These differences in response were presumably due to the relatively small amount of Terpal taken up in the seed treatment. Firstly, because of the smaller surface area available for absorption by a seed than a plant at GS 13, and secondly, in Experiment 5.2, because the concentration of Terpal supplied was only 10% of that normally given as a foliar spray, as the 50 and 100% concentrations were found to retard or inhibit germination in some cases.

Despite the smaller overall response to Terpal when applied to seeds there was, nevertheless, a clear response to the dose of Terpal absorbed by imbibing seeds; the higher the concentration of Terpal and

the longer the period it was applied, the more germination and early growth were retarded. These effects diminished with time and the characteristic increase in tillering was displayed. As the uptake of Terpal by the seeds was relatively low, the changes in the normal pattern of growth and development were only of limited duration. Thus from Experiment 5.2 the length of MS leaves 1 to 3 was greatly reduced by up to 44%, and L4 and L5 were reduced to a lesser extent. But in the case of seeds treated with the greatest Terpal dose (100% concentration for 48 hours in Experiment 5.1) an inhibitory effect on germination and growth was maintained and the grain yield of the few plants that emerged was severely reduced (due to the smaller number of ears per plant). Thus there was sufficient uptake of the chemical by the seed at germination to permanently retard the subsequent growth and development of the plant. It was thought that imbibition of seeds with water before Terpal application might diminish the inhibitory effect of Terpal on germination by diluting the chemical, and this was so for the 100% concentration. There was no obvious effect of this treatment with the lower Terpal concentrations.

It can be concluded from this study that it is possible to manipulate apical dominance very early in the plant's life by treating seeds with a commercial PGR. The physiological effects are transient but sufficient to modify the basic pattern of growth so that more ear-bearing tillers may be produced from plants grown from seeds treated with Terpal. Although later growth and development were not significantly impeded by Terpal the overall yield of the plant was not improved as the mean ear weight of tillers was reduced. This suggests that the modifications to growth caused by seed soaking (that is, additional tillers) are supported by redistribution of a finite pool of resources. It is therefore likely that only seed treatments of PGRs in conjunction with additional nutrients, especially nitrogen, would be

successful in increasing the yield of tillers. Nevertheless the field study of De et al. (1982) in semi-arid conditions with CCC, which acts in a similar manner to the mepiquat chloride component of Terpal, shows a marked increase in grain yield.

Besides the precise modification of plant growth and development there are other benefits to be gained from the technique of applying a PGR to dry seeds. It is a viable alternative to foliar spraying since it is relatively cheap and easy compared to foliar spraying methods, that is, sophisticated spraying machinery is not required, and application is independent of weather conditions. The technique may be particularly advantageous in arid regions since seed treatment economises on water use (De et al., 1982). Seed soaking may also result in a more uniform application of the chemical thus reducing the variability of response. On the other hand, this technique may be disadvantageous in that the concentrations of the chemical needed to evoke a response may reduce the rate of germination and establishment, as indicated in the present study, and thereby make the crop more susceptible to interference by weeds.

CHAPTER 6

MANIPULATION OF TILLER BUD GROWTH IN UNICULM CEREALS

INTRODUCTION

There is evidence that the growth and development of the main shoot may be restricted by competition for assimilates and nutrients by developing tillers (Aspinall, 1963; Kirby, 1973a; Mohamed and Marshall, 1979). In particular the potential size of the MS ear may be reduced as developing tillers will be supplied with assimilates by the MS leaves at the same time as the MS apex itself is initiating spikelet primordia. Even when the tillers have several expanded leaves they may still receive assimilates from the MS, and during the final stages of grain filling some tillers are still supplied with assimilates by the flag leaf and other MS leaves (Rawson and Hofstra, 1969; Thorne, 1982). As many tillers die prematurely and some make little contribution to yield, their production can be considered to be wasteful of the plant's resources (Jones and Kirby, 1977; Power and Alessi, 1978; Aufhammer, 1980). In addition to the carbon economy of the MS and tillers water lost by transpiration through unproductive tillers may be particularly significant under dryland conditions (Winward et al., 1983). In experiments where leaf area was reduced by detillering the rate of early water use was diminished and this led to an increase in grain yields in water stressed wheat (Richards, 1983). Unproductive tillers may also intercept light which would otherwise fall on fertile shoots. Correspondingly in view of these adverse aspects of tillering the development of a cereal phenotype with a single shoot (uniculm) and a large ear has been proposed as a viable alternative to current freely tillering cultivars (Donald, 1968).

Although there appears to be a strong argument in favour of uniculm or low tillering cultivars, it must be remembered that the production and maintenance of several tillers per plant is a significant feature of the biology of temperate cereals as it allows adaptation to a range of conditions, for example sowing density, and it helps compensate for

pests, disease and any unfavourable conditions which may adversely affect crop development. Consequently the tillering habit has been fostered, especially as the results of several experiments show little effect of infertile tillers on potential yield. For example, Bremner (1969) found that in wheat, competition from unproductive tillers of Yeoman and Cappelle cultivars was not serious. Yeoman which had many unproductive tillers, yielded the same as Cappelle, which had fewer unproductive tillers. Bremner (1969) also noted more rapid growth after the death of unproductive tillers and it was thought that this was either because of transfer of materials to surviving shoots from dying shoots or because of the removal of the source of competition (Bunting and Drennan, 1966). Thorne (1962) found that when tillers died the growth of the whole plant was not checked. It was also established that N content per plant did not change during the period when tillers died as that of surviving shoots increased sufficiently to compensate for the loss by dying shoots (Thorne, 1962). Rawson and Donald (1969) suggested that when high order tillers died there was a remobilization of most of their N to fertile shoots. Recently Russelle et al. (1984) have demonstrated that barren maize tillers translocate substantial amounts of phosphorus to the MS.

In the single stem plant or uniculm all of the plant's resources are directed towards the single stem and ear. Some investigations of the yield potential of single shoot plants have been undertaken with mechanical detillering of wheat and barley (Kirby and Jones, 1977; Mohamed and Marshall, 1979; Islam and Sedgley, 1981; Kemp and Whingwiri, 1980; Winward et al., 1983). It has been found that if young tillers are removed the growth and yield of the MS can be greatly enhanced. Mohamed and Marshall (1979) found that the earlier the tillers were removed the greater the increase in yield due to the increase in number of grains per spikelet. As mentioned previously,

detillering can also improve water-use efficiency defined as grain yield per unit water loss (Jones and Kirby, 1977). All this supports the idea that developing tillers compete with the MS for a limited supply of resources.

The potential benefits of a uniculm habit were discussed by Donald (1968) in his description of a crop ideotype for temperate cereals. The ideotype was defined as, "a biological model which is expected to perform or behave in a predictable manner within a defined environment" (Donald and Hamblin, 1976). Other features of Donald's ideotype are a short strong stem, few small erect leaves, and a large erect ear with awns. Donald considered that crop breeders would develop such an ideotype by the progressive adoption of individual model characters until the total model had evolved. He thought it unlikely that the ideotype would ever arise in standard breeding programmes based on selection for yield under present agronomic practices.

Uniculm and very restricted tillering lines of barley have been studied for some time, particularly uniculm mutants of Proctor and Kindred (Bokhari and Youngner, 1971b; Kirby, 1973a, 1973b; Kirby and Jones, 1977). The potential yield increase from these mutants has not yet been shown because of abnormalities in ear development (Kirby, 1973b). Until recently few studies on uniculm wheat have been possible because of the lack of suitable genotypes. However, a number of uniculm and very restricted tillering lines of wheat have been developed in Israel (Atsmon and Jacobs, 1977). These possess "Gigas" characteristics, that is, large thick leaves, thick stiff straw, a large ear with long awns and many grains, and a high harvest index. Uniculm mutants of wheat derived from selections of Atsmon and Jacobs (1977), and of barley (Donald, 1979), are now specifically bred and grown in parts of semi-arid Australia and are subject to research into their yield potential.

Marshall and Boyd, (1985) have demonstrated that the growth and development of the MS can be enhanced in the absence of competing tillers in uniculm and biculm wheat plants. The MS of these plants had a greater number of grains and these were larger than those of the MS ear of tillering varieties. However, this increase in the size of the MS was insufficient to compensate for the grain contributed by tillers as the yield of the tillering varieties was 30% greater than that of the uniculm and biculm plants.

The mechanism of tiller bud suppression in uniculm cultivars is unknown. Uniculm selections of wheat may tiller freely in certain environments; Atsmon and Jacobs (1977) refer to a thermophotoperiodic control of tiller bud development in their material. The hormonal background of this response has not been investigated. In a uniculm barley mutant Bokhari and Youngner (1971b) found that applications of CCC stimulated tiller production, and this may implicate the involvement of endogenous gibberellins in regulating tiller bud outgrowth. On the other hand, Kirby (1973b) found no effect of CCC on Proctor and Kindred uniculm mutants of barley. The use of uniculm selections allows investigations of the hormonal factors influencing tillering to be conducted in a far more critical way than is possible with existing cultivars; such material also allows a unique assessment of the growth of the MS in the absence of competition with developing tillers. The present study investigated the regulation of tillering in uniculm wheat, derived from the restricted tillering lines of Atsmon and Jacobs (1977) and recently described by Marshall and Boyd (1985), and a uniculm barley selection (Donald, 1979). Seed and foliar applications of a range of PGRs were made in an attempt to promote the outgrowth of tiller buds. Application to seed ensured the earliest possible entry of the PGR into the plant, thus maximising any influence on bud outgrowth.

EXPERIMENTAL

Experiment 6.1 Preliminary observations on uniculm barley and wheat selections.

In this experiment seedlings of uniculm selections and tillering cultivars were grown in a growth cabinet or in glasshouse conditions to determine both the degree of tillering and the expression of the uniculm habit.

MATERIALS AND METHODS

Due to lack of space in the growth cabinet the study was conducted in two parts: an experiment with the wheat genotypes commenced on 9 March, 1983 and a similar experiment with the barley genotypes commenced on 14 April, 1983. Seed of the uniculm selections and tillering cultivars of spring barley and wheat (the tillering cultivars were Triumph and Broom, for barley and wheat respectively) were sown in John Innes No.1 compost in the "old" glasshouse suite or germinated on moist filter paper in the growth cabinet. The latter were subsequently transferred to pots containing nutrient solution. After emergence half of those seedlings germinated in the glasshouse and growing in compost were transferred to the growth cabinet and half the plants germinated in the growth cabinet and growing in the nutrient solution were transferred to the glasshouse. In this manner four different conditions for growth were established. The growing conditions of the growth cabinet are described in Chapter 3 as is the nutrient solution and culture method; glasshouse conditions are described in Chapter 4. Tiller numbers and identities were recorded in all regimes after 33 days.

RESULTS

Both the uniculm wheat and barley selections produced tillers under all 4 growing regimes, but this occurred to a much lesser degree in barley than in wheat. In both the glasshouse and growth cabinet about 40% of the barley plants produced at least one tiller, that is, 60% of the plants were uniculm (Table 6.1). Of the plants that tillered a mean of 1.3 tillers per plant were produced (Table 6.2), these were T1 and sometimes T2. In contrast in wheat all individuals produced tillers in 3 of the 4 growing conditions; only in solution culture in the glasshouse was this reduced to 33%, that is, 66% of the plants were uniculm (Table 6.1). The plants that tillered produced up to 4 tillers (usually the first two primary tillers and T1P and T2,1), but the degree of tillering was significantly greater in the growth cabinet environment than in the glasshouse (a mean of 3.2 tillers compared with 1.1 in the glasshouse) (Table 6.2). The tillering cultivar of wheat also produced significantly more tillers in the growth cabinet, in the order of 30%, whereas tillering in the barley types was very similar in both environments (Table 6.2). Normal patterns of tillering (see Chapter 4) were observed in both tillering cultivars under the 4 growing conditions, about 6 tillers per plant were produced by 33 days after sowing (Table 6.2).

Experiment 6.2 Effect of PGR seed treatments on tiller bud outgrowth in uniculm barley and wheat grown in growth cabinet and glasshouse conditions.

It was obvious from the results of Experiment 6.1 that the uniculm selections were capable of limited tillering. To afford better understanding of the control of this tiller production it was decided to examine the effects of applied PGRs, and to apply them as early as

Table 6.1 Percentage plants with one or more tillers grown under the 4 growing regimes.

Treatment	% plants with one or more tillers			
	Barley		Wheat	
	Uniculm	Triumph	Uniculm	Broom
Glasshouse				
:compost	40	100	100	100
:solution	37	100	33	100
Cabinet				
:compost	44	100	100	100
:solution	44	100	100	100

Table 6.2 Number of tillers of tillering plants ±SE.

Treatment	Mean number of tillers per plant			
	Barley		Wheat	
	Uniculm	Triumph	Uniculm	Broom
Glasshouse				
:compost	1.00±0.00	6.00±0.00	1.12±0.24	5.83±0.17
:solution	1.30±0.28	6.20±0.20	1.00±0.00	5.20±0.37
Cabinet				
:compost	1.30±0.24	6.20±0.41	2.37±0.20	7.83±0.41
:solution	1.50±0.25	6.60±0.34	4.00±1.04	7.67±0.62

possible in relation to tiller development. Thus PGRs were applied to seeds in order to maximise their influence on the outgrowth of the tiller buds.

MATERIALS AND METHODS

Seeds of uniculm barley and wheat were soaked for 12 hours in solutions of Terpal (10 and 50% of the recommended rate of application), BAP (10^{-4}M), TIBA (10^{-4}M) or in distilled water (control) on filter paper in covered Petri dishes and incubated in the growth cabinet. After this the seeds were transferred to Petri dishes containing distilled water only. Germination was monitored after 4 days. After 6 days of soaking (6 June, 1983) the seedlings were either potted individually into John Innes No.1 compost and grown in the "old" glasshouse suite (described in Chapter 4) or put into pots containing nutrient solution and grown in the growth cabinet (described in Chapter 3). Tiller number was counted weekly commencing 3 weeks after the initial PGR soaking treatment. After 6 weeks the plants grown in solution in the cabinet were harvested. Those grown in the glasshouse were harvested at grain ripening after 10 weeks. In all treatments the MS height, leaf number and dry weight of 6 replicate plants were measured, and in addition in glasshouse grown plants the number of fertile ears per plant was counted and MS and tiller ears were oven-dried and weighed.

RESULTS

Germination was defined as the appearance of the first seminal root after imbibition. The soaking treatments had little effect on percentage germination with the exception of the 50% Terpal and BAP treatments on barley which almost completely inhibited germination at 4 days after soaking (Table 6.3). Most of the soaking treatments severely retarded the growth of the first seminal root and to a lesser extent the coleoptile after 4 days, particularly the 50% Terpal and BAP

treaments in both barley and wheat (Table 6.3).

Table 6.3 Effect of seed soaking treatments on germination (% Germ.) and elongation of the first seminal root and the coleoptile of uniculm barley and wheat seeds at 4 days after soaking ±SE.

Treatment	Barley			Wheat		
	% Germ.	Root (mm)	Coleoptile (mm)	% Germ.	Root (mm)	Coleoptile (mm)
Control	95	5.5±0.3	5.5±0.3	100	5.5±0.3	5.5±0.3
10% Terpal	98	1.0±0.0	4.5±0.2	85	3.0±0.3	4.5±0.2
50% Terpal	2	<1.0	<1.0	98	<1.0	1.0±0.0
BAP	2	<1.0	<1.0	92	<1.0	<1.0
TIBA	72	1.5±0.2	5.0±0.3	100	2.5±0.2	5.0±0.3

Most tillers were produced by 3 weeks after soaking, after this there was little change in tiller number per plant. At 6 weeks after soaking tiller production by the control barley plants was negligible, no tillers were produced under glasshouse conditions and only a mean of 0.5±0.2 tillers per plant were produced in the growth cabinet (Fig. 6.1). In contrast, many more tillers were produced by the control wheat plants, up to 1.5 tillers per plant were produced under glasshouse conditions and in the growth cabinet tiller production was appreciably greater, that is, up to 3 tillers per plant (Fig. 6.1). In those plants that tillered the order of appearance was T1, CT, T2 and T3; no secondary tillers were produced. These findings are similar to those of Experiment 6.1.

The seed treatments did not significantly affect the tiller production of barley plants grown in the glasshouse or growth cabinet, except in the case of plants grown in the growth cabinet and treated with 50%

Fig. 6.1

Effect of seed soaking treatments at 6 weeks after soaking on:

A) tiller and ear production (including MS) by plants grown under glasshouse/compost conditions.

total number of tillers plant^{-1}

number of ear-bearing tillers plant^{-1}

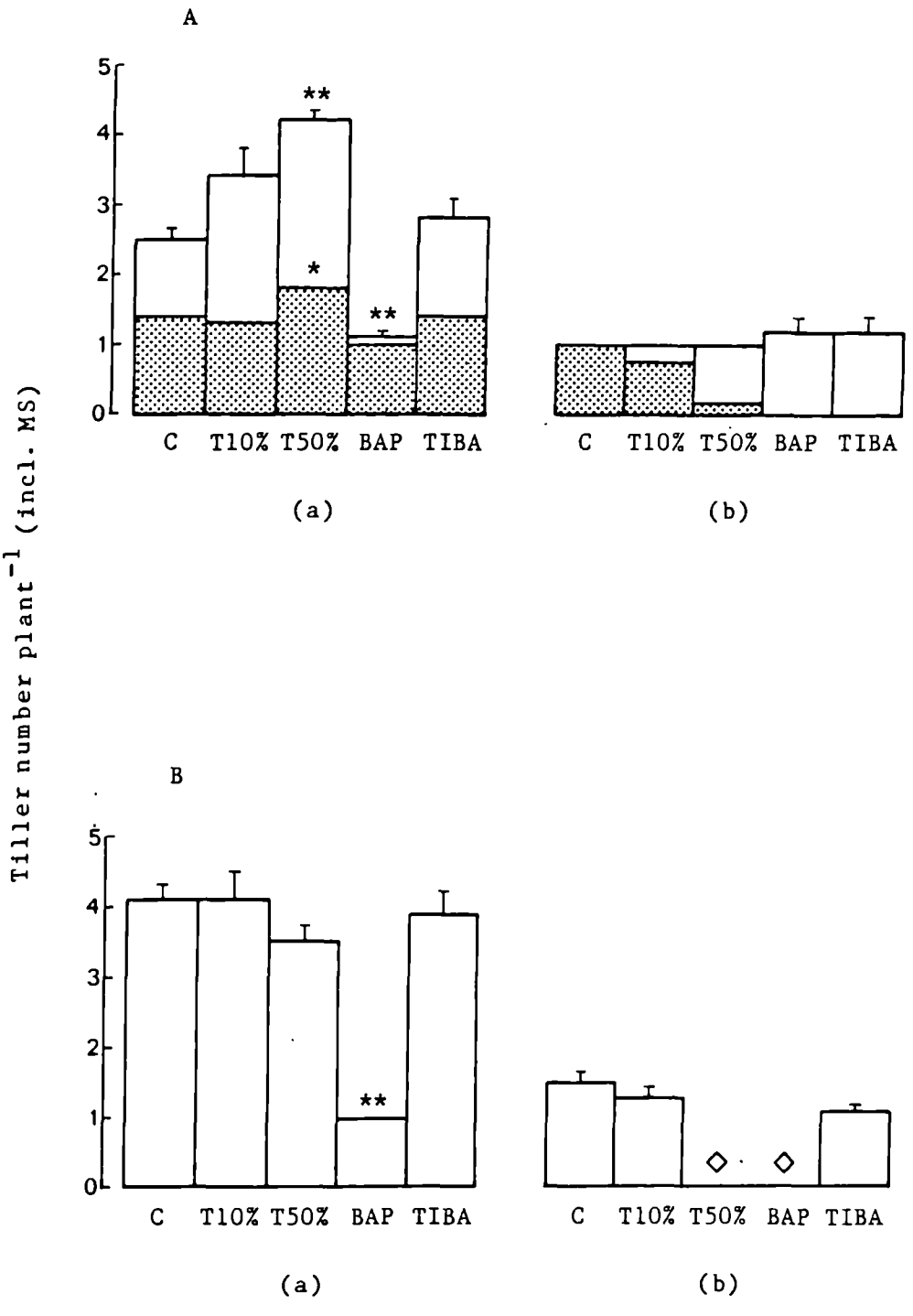
B) tiller production (including MS) by plants grown under growth cabinet/nutrient solution conditions.

◇ insufficient data.

a) Uniculm wheat

b) Uniculm barley

Vertical bars represent ±SE.


A
5
4
3
2
1
0
**
*
**
C T10% T50% BAP TIBA
(a)
C T10% T50% BAP TIBA
(b)
Tiller number plant^{-1} (incl. MS)
B
5
4
3
2
1
0
**
C T10% T50% BAP TIBA
(a)
◇ ◇
C T10% T50% BAP TIBA
(b)

Terpal and BAP. In these cases establishment was almost completely inhibited and it was not possible to collect sufficient data for presentation (Fig. 6.1B). Under glasshouse conditions tillering of wheat plants was increased by the Terpal seed treatments by about 60% with the 10% concentration and by about 100% by the 50% concentration, the effect of the latter being statistically significant ($p<0.01$) (Fig. 6.1A). This effect is shown in Plate 6.I. TIBA did not significantly modify tiller production whereas BAP significantly ($p<0.01$) reduced tiller production by 94% essentially reducing the plant to a single MS (Fig. 6.1A). When the wheat plants were grown in the cabinet none of the treatments, with the exception of BAP, had a significant effect on tiller production; BAP again significantly ($p<0.01$) reduced tillering (Fig. 6.1B).

Ear production of barley plants grown in the glasshouse was greatly inhibited by the 50% Terpal, BAP and TIBA seed treatments, none of the BAP and TIBA treated plants produced an ear, this was because of poor germination and emergence and stunted plant growth. Control barley plants produced one ear per plant, that is, the MS ear; the 10% Terpal treatment did not change this (Fig. 6.1A). Ear production was slightly higher by the control wheat plants, 1.4 ± 0.2 ears per plant were produced. The 10% Terpal and TIBA seed treatments did not modify this, but the 50% Terpal treatment significantly ($p<0.05$) increased ear production and the BAP seed treatment significantly ($p<0.05$) reduced the number of fertile ears per plant (Fig. 6.1A).

The MS height of barley plants grown in the cabinet 6 weeks after seed soaking was significantly reduced by the 10% Terpal and TIBA treatments. The MS height of the wheat plants was significantly reduced by the 50% Terpal treatment but was unaffected by the other treatments (Table 6.4). The MS leaf number of barley plants grown in the cabinet

Plate 6.I

Effect of Terpal on the morphology of uniculm wheat. 50% strength Terpal applied to seeds at germination; plants grown under glasshouse conditions. Photograph shows promotion of tiller emergence and reduction of MS height in Terpal treated plant (B) compared to control plant (A). Both plants 6 weeks old.


A
B

was significantly increased by the 10% Terpal treatment and was unaffected by TIBA 6 weeks after soaking. Only the BAP treatment affected MS leaf number of the wheat plants, and in this case leaf number was significantly reduced (Table 6.4).

Table 6.4 Effect of seed treatments on MS height and leaf number 6 weeks after soaking in cabinet/solution grown plants ±SE (◇ insufficient data).

Treatment	Barley		Wheat	
	Height (cm)	Leaf number	Height (cm)	Leaf number
Control	16.8±0.66	10.0±0.26	13.8±0.71	7.7±0.26
10% Terpal	13.9±0.33**	11.2±0.26**	12.2±0.51	8.1±0.12
50% Terpal	◇	◇	10.9±0.43**	8.5±0.29
BAP	◇	◇	14.7±0.33	7.0±0.00*
TIBA	15.1±0.54*	9.6±0.36	13.4±0.70	8.0±0.00

Shoot and root dry weight of barley and wheat grown in the cabinet was significantly reduced by all the seed treatments at 6 weeks after soaking, with only 2 exceptions (Table 6.5). The effects of TIBA on barley root dry weight and of 10% Terpal on wheat shoot dry weight were not statistically significant (Table 6.5). The shoot:root dry weight ratio of the barley plants was little affected by the seed treatments whereas that of the wheat plants was increased particularly in the 50% Terpal and TIBA treatments, reflecting a greater sensitivity to the treatments of root growth compared with shoot growth (Table 6.5).

Table 6.5 Effect of seed treatments on shoot and root dry weight and shoot:root dry weight ratio (S:R) 6 weeks after soaking in cabinet/solution grown plants ±SE (◇ insufficient data).

Treatment	Dry weight (mg)					
	Barley			Wheat		
	Shoot	Root	S:R	Shoot	Root	S:R
Control	913± 70	288±30	3.2	1085±117	422±30	2.6
10% Terpal	535± 50**	155±20**	3.5	813±80	264±40**	3.1
50% Terpal	◇	◇	◇	555±70**	127±20**	4.4
BAP	◇	◇	◇	355±60**	114±20**	3.1
TIBA	619±100*	211±60	2.9	714±50*	181±10**	4.0

The Terpal seed treatments had no effect on the MS height and the MS leaf number at grain ripening in glasshouse grown barley, whereas BAP and TIBA significantly reduced MS height and leaf number. None of the treatments had any effect on the MS height of wheat grown in the glasshouse, but MS leaf number was significantly increased by the 10 and 50% Terpal treatments by 18% and 31% respectively. (Table 6.6).

Table 6.6 Effect of seed treatments on MS height and leaf number at grain ripening in glasshouse/compost grown plants ±SE.

Treatment	Barley		Wheat	
	Height (cm)	Leaf number	Height (cm)	Leaf number
Control	33.0±2.1	11.2±0.43	52.9±1.6	7.1±0.11
10% Terpal	36.1±4.0	11.0±0.87	48.7±1.3	8.4±0.17**
50% Terpal	30.8±4.2	12.5±0.68	45.4±1.5	9.3±0.17**
BAP	16.9±6.2*	6.3±0.91**	52.5±1.7	6.7±0.15
TIBA	12.5±6.5**	4.2±1.12**	54.9±2.1	7.4±0.16

The 10% Terpal treatment increased the dry weight of the MS ear of the barley plants but reduced straw weight (Table 6.7). Very few barley plants treated with the other PGRs produced ears (Fig. 6.1A), and the straw weight of these was much reduced. The 10 and 50% Terpal and BAP treatments all significantly reduced the dry weight of wheat MS ear, but TIBA had no effect. BAP also significantly reduced the weight of MS straw (Table 6.7). There was no difference in tiller ear dry weight, with the exception of BAP; BAP seed treatment inhibited the production of ear-bearing tillers in the wheat plants (Fig. 6.1A). Although the 50% Terpal treated plants yielded more ear-bearing tillers (Fig. 6.1A), no overall yield increase was realised since MS ear weight was reduced by this treatment.

Table 6.7 Effect of seed treatments on MS ear and straw and tiller ear dry weight at grain ripening in glasshouse/compost grown plants ±SE (◇ insufficient data).

Treatment	Dry weight(mg)					
	Barley			Wheat		
	MS ear	MS straw	Tiller ears	MS ear	MS straw	Tiller ears
Control	256±30	1572± 85	0	824±42	1939±227	174±72
10% Terpal	406±30**	1371± 18*	0	672±41*	1671±175	121±61
50% Terpal	◇	1179± 15**	0	522±34**	1853±172	166±45
BAP	◇	206±111**	0	670±54*	1117±104**	0
TIBA	◇	293±157**	0	876±30	1892± 99	131±52

Experiment 6.3 Vegetative growth and development and fate of tiller buds in seed treated uniculm barley and wheat plants.

This experiment was undertaken to investigate in more detail the effect of seed soaking with Terpal and TIBA on tiller bud outgrowth in uniculm barley and wheat.

MATERIALS AND METHODS

Uniculm barley and wheat seeds were soaked for 12 hours in Terpal (50% of the recommended rate of application) and in TIBA (10^{-4}M) on filter paper in sealed Petri dishes. After 12 hours the seeds were transferred to Petri dishes containing distilled water. Control plants were treated by soaking in distilled water only. After a further 4 days (28 October, 1983) a sample of the best germinated seedlings were potted up individually in John Innes No.1 compost and grown in the "new" glasshouse suite (described in Chapter 4). During the first 32 days of growth plants were harvested at regular intervals and tiller buds were dissected out, and where possible identified, measured and weighed. Thirty two days after soaking MS height and dry weight, root system length and dry weight, and the lengths of the MS laminae 1 to 5 inclusive were measured.

RESULTS

a) Uniculm wheat.

Data presented in Table 6.8 represent a summary of the fate of tiller buds during the first 32 days after soaking. The number of visible buds, elongating buds, emerged tillers and ear-bearing tillers are the maximum number observed during the 32 day period. On dissection all plants were found to possess a bud in the axil of L1 and 80% of the plants a bud in the axil of L2 (Table 6.8). All of the Terpal treated plants and 60% of the TIBA treated plants also had buds in the L3 axil

by 32 days after soaking. Besides increasing the number of buds visible to the naked eye, Terpal and TIBA also increased the number of elongating buds (Table 6.8). However, many of these buds, including all of T2 and T3 buds, stopped elongation and so did not emerge as tillers. Only T1 buds became tillers in both control and treated plants. In the latter the elongation of buds not destined to be tillers stopped about 21 days after germination. Overall 60% of the control plants were uniculm phenotypes. Tiller production in this experiment was low when compared to that in Experiment 6.2 with no plant producing more than one tiller by 32 days after seed soaking. Terpal increased tiller production so that 100% of the plants produced a T1 tiller. TIBA had little effect on tiller production, and if any it was to decrease it (Table 6.8). Terpal increased the number of ear-bearing tillers but reduced percentage tiller survival so that only 55% of emerged tillers produced an ear compared to 83% in control plants. Although TIBA reduced the number of ear-bearing tillers, all tillers that emerged produced ears, that is, 20% (Table 6.8).

Table 6.8 Fate of tiller buds during development in seed treated uniculm wheat plants (percentage value from all replicates).

Treatment	Buds visible to the naked eye			Buds elongating		
	T1	T2	T3	T1	T2	T3
Control	100	80	0	60	0	0
Terpal	100	100	100	100	100	0
TIBA	100	100	60	80	20	0

	Buds developing into emerged tillers			Ear-bearing tillers		
Control	40	0	0	33	0	0
Terpal	100	0	0	55	0	0
TIBA	20	0	0	20	0	0

T1 buds commenced growth 3 days earlier in the Terpal treated plants (Fig. 6.2) and they attained a significantly greater length (350% greater than control T1) and dry weight by 32 days after seed soaking. The length of the T2 buds was also significantly increased by the Terpal seed treatment (Table 6.9). Seed treatment with TIBA delayed the outgrowth of T1 and did not significantly affect tiller bud length or dry weight (Fig. 6.2 and Table 6.9).

Table 6.9 Effect of seed treatments on mean tiller bud and tiller length 32 days after soaking of uniculm wheat seeds ±SE.

Treatment	Tiller length (mm)		
	T1	T2	T3
Control	64.6±61.7	0.8±0.2	
Terpal	289.8±16.5**	2.8±0.4**	1.0±0.0
TIBA	66.4±62.8	1.0±0.0	0.6±0.2

The Terpal seed treatment reduced the length of all MS leaves measured, that is, L1 to L5. This reduction in length was similar for all leaves, that is, about 25% and was statistically significant. TIBA seed treatment had no significant effect on MS leaf length (Table 6.10).

Table 6.10 Effect of seed treatments on MS leaf length (mm) 32 days after soaking uniculm wheat seeds ±SE.

Treatment	MS leaf number				
	L1	L2	L3	L4	L5
Control	133.6±12.1	239.8±13.2	289.8±11.7	325.4±11.5	371.8±8.7
Terpal	98.8± 4.2*	167.0± 2.7**	219.0± 3.9**	254.0± 1.7**	297.0±6.6**
TIBA	142.0±15.5	251.0±14.0	319.0±14.9	324.0±11.3	363.8±3.6

Fig. 6.2

Effect of seed soaking treatments on:

a) length of T1 and

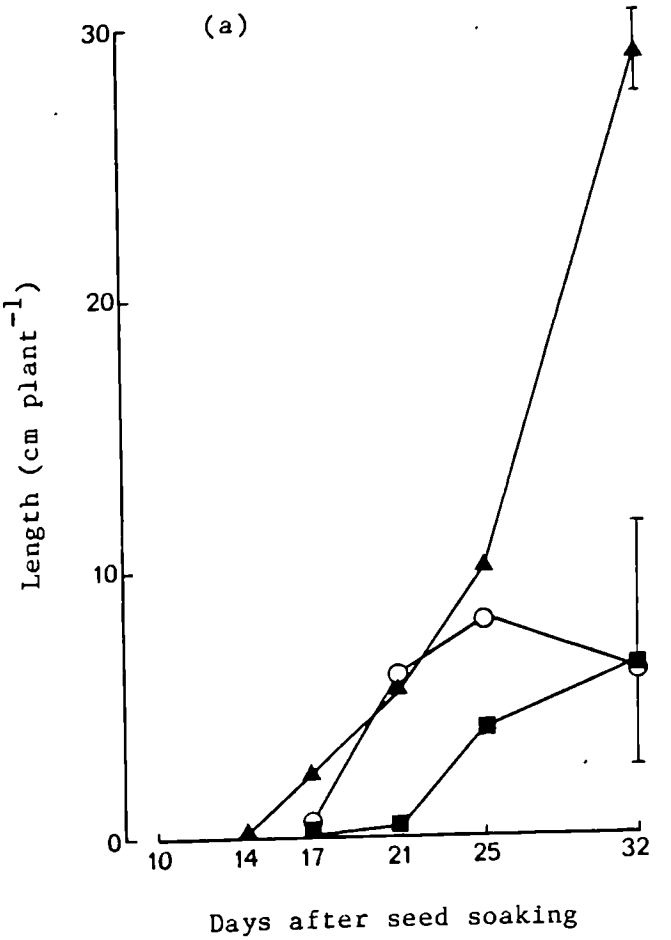
b) dry weight of T1 of uniculm wheat plants with time.

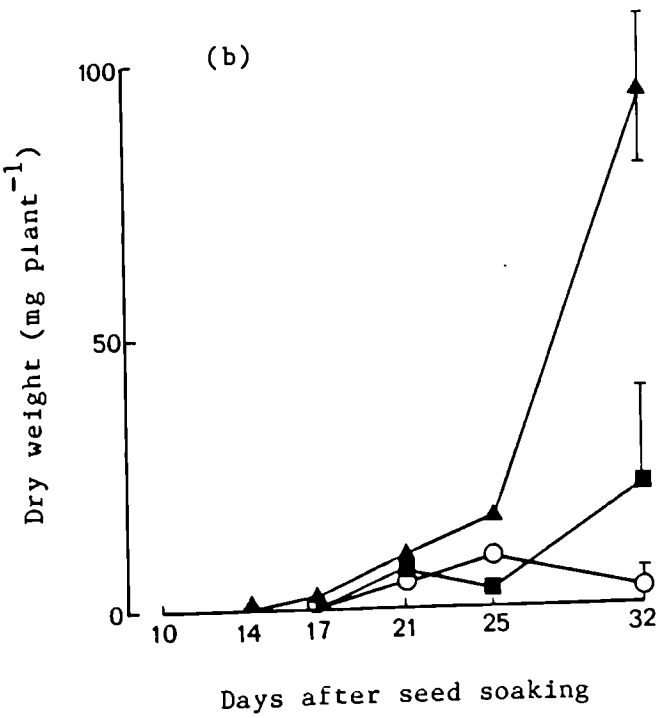
○ Control

▲ Terpal

■ TIBA

Vertical bars represent ±SE.


(a)
30
20
10
0
Length (cm plant^{-1})
10
14
17
21
25
32
Days after seed soaking


(b)
100
50
0
Dry weight (mg plant^{-1})
10
14
17
21
25
32
Days after seed soaking

MS height was significantly reduced by Terpal seed treatment by 18%, MS dry weight was not, however, significantly affected (Table 6.11). TIBA had no effect on MS size and neither of the seed treatments significantly affected the length or dry weight of the root system (Table 6.11).

Table 6.11 Effect of seed treatments on MS and root size 32 days after soaking uniculm wheat seeds ±SE.

Treatment	MS		Root system	
	Height	Dry weight	Length	Dry weight
	mm	mg	mm	mg
Control	156.2± 4.7	269.0±18.0	464.2±42.4	104.0±20.0
Terpal	128.2± 4.4**	316.0±26.0	465.8±17.4	95.0± 9.5
TIBA	176.0±11.5	325.0±32.0	358.6±34.2	101.0± 9.7

b) Uniculm barley.

In contrast to the above results for wheat the seed treatments on barley did not give rise to any significant differences in growth or tiller production and so this part of the experiment has not been presented.

Experiment 6.4 Foliar application of PGRs to uniculm barley plants.

Since seed application of PGRs proved unsuccessful in promoting tiller bud outgrowth in uniculm barley it was decided to investigate the effect of foliar application of PGRs at GS 13. A tillering genotype of barley was included for comparison.

MATERIALS AND METHODS

Seeds of uniculm and Triumph spring barley were sown on 15 April, 1983 in pots of John Innes No.1 compost and grown in the "old" glasshouse suite as described in Chapter 4. At GS 13 solutions of Terpal (equivalent to the recommended rate of application), BAP and TIBA (both at 10^{-4}M) were applied as a foliar spray until runoff. Tiller production and MS height were monitored 6 days after spraying and at weekly intervals thereafter.

RESULTS

All the treatments increased tiller production in the tillering genotype; Terpal and TIBA after only one week of application (Fig. 6.3a). The effects of Terpal and TIBA were significant at $p<0.01$ and $p<0.05$ respectively 5 weeks after spraying. Terpal increased tiller production by up to 52%. In contrast the treatments had no effect on tiller production by the uniculm barley plants; tillering was negligible in all these plants (Fig. 6.3a).

The MS height was reduced by Terpal and to a lesser extent by BAP in both the uniculm and tillering plants and these effects were evident after only one week from application (Fig. 6.3b and 6.3c). In the tillering barley only the effects of Terpal were significant ($p<0.01$) 5 weeks after spraying and in the uniculm barley both the effects of Terpal and BAP were significant ($p<0.01$ and $p<0.05$ respectively) by 5 weeks after spraying (Fig. 6.3b and Fig. 6.3c). Thus although the treatments influenced the growth of uniculm barley, that is, they reduced MS height, promotion of tiller bud outgrowth was not achieved.

Fig. 6.3

Effect of PGR treatments on:

a) tiller number of tillering (——)
and uniculm barley (-----) with time.

b) MS height of tillering barley with time.

c) MS height of uniculm barley with time.

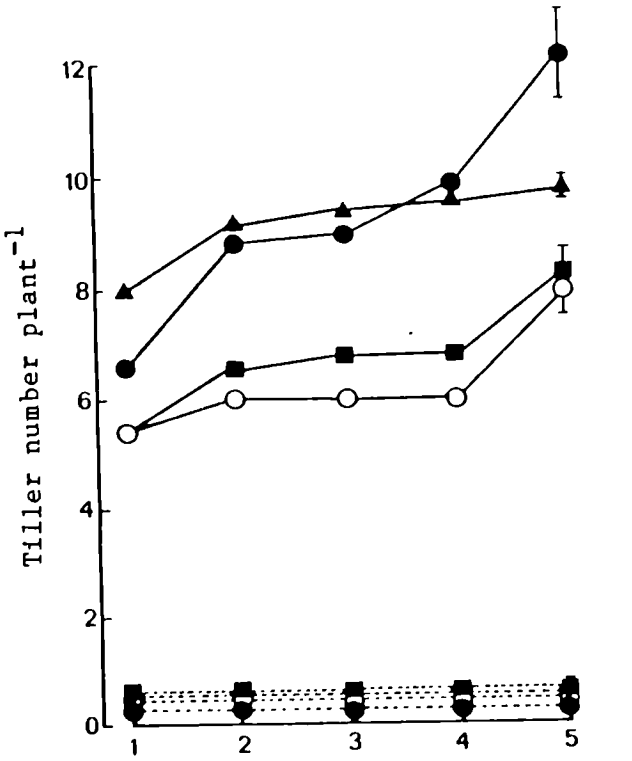
○ Control

● Terpal

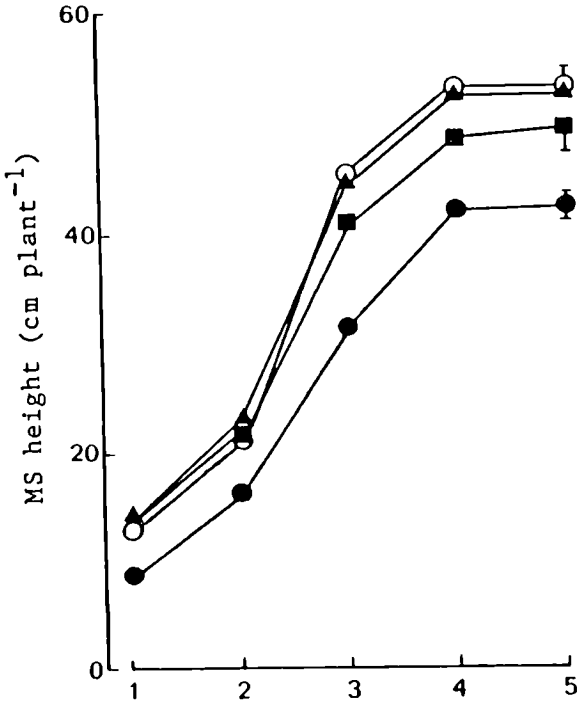
▲ TIBA

■ BAP

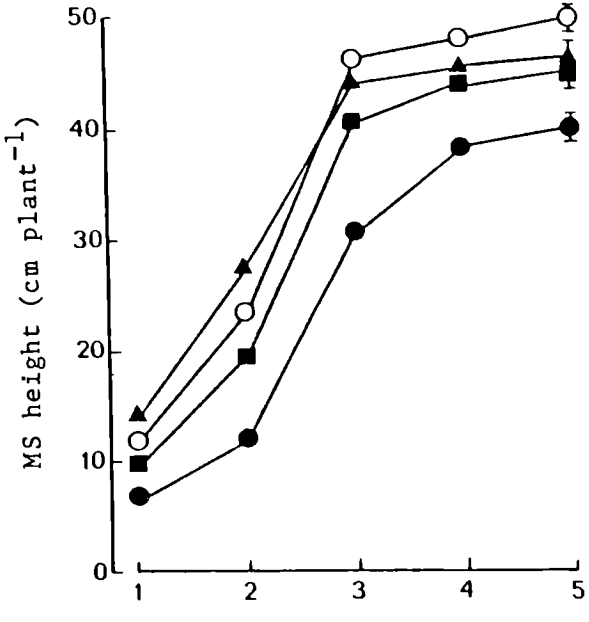
Vertical bars represent ±SE.


Tiller number plant^{-1}
0
2
4
6
8
10
12
1
2
3
4
5
Weeks after treatment application

(a)


MS height (cm plant^{-1})
0
20
40
60
1
2
3
4
5
Weeks after treatment application

(b)


MS height (cm plant^{-1})
0
10
20
30
40
50
1
2
3
4
5
Weeks after treatment application

(c)

Experiment 6.5 Foliar application of PGRs to uniculm wheat plants.

From the preceding experiments it was clear that the uniculm wheat was not strictly uniculm in that under certain conditions several tiller buds developed into tillers. The factors controlling this response were investigated further by applying a large range of PGR treatments to uniculm wheat plants at GS 13.

MATERIALS AND METHODS

Seeds of uniculm wheat were sown on 9 June, 1983 in pots containing John Innes No.1 compost and grown in the "old" glasshouse suite as described in Chapter 4. The treatments in Table 6.12 were applied at GS 13 and were applied twice in 3 days to increase their effectiveness. Unfortunately almost all of the plants had tillered by this time producing one or more tillers, T1 or T2, before the treatments were applied and after application no further tiller production could be stimulated. It was decided, therefore, to repeat this experiment at a different time of year. It was thought that although the same light and temperature regime would be used, the different photoperiod may encourage a stronger uniculm habit in control plants enabling any promotion of outgrowth of the T1 or T2 bud by the PGR treatments to be observed more clearly. Thus seeds of uniculm wheat were sown on 25 October, 1983 and treated at GS 13 on 9 and 11 November, 1983. This experiment was conducted in the "new" glasshouse suite as described in Chapter 4. Plants were harvested 2 and 4 weeks after treatment application and tiller buds were dissected out and counted. Tiller numbers and MS height of another set of plants were measured at 6 day intervals. Ears were counted and weighed at grain maturity.

Table 6.12 Treatments applied to uniculm wheat plants at GS 13.

Treatment	Application	Concentration
Control	Foliar spray	Distilled water + 0.05% v/v ethanol + 0.05% v/v Tween 20
Terpal	" "	Equivalent to recommended rate of application: 2.5 dm^3 ha^{-1}
10% Terpal	" "	10% of above, that is, the concentration applied in seed soaking experiments
Cerone	" "	Equivalent to recommended rate of application: 1.0 dm^3 ha^{-1}
Ancymidol	Root drench	2.5 μg per pot
BAP	Foliar spray	10^{-4}M + 0.05% v/v ethanol + 0.05% v/v Tween 20
TIBA	" "	" "
GA_3	" "	" "
NO_3	Root drench	12 mM $NaNO_3$

RESULTS

Tiller production by control plants was negligible in this experiment; initially (2 weeks after treatment application) they had growing tiller buds but these died before they could emerge as tillers since they were not present when plants were harvested 4 weeks after treatment application (Table 6.13). All the treatments except 10% Terpal increased the number of growing buds 2 weeks after treatment application. TIBA increased the number by 250%, Cerone by 200%, and Terpal, BAP and nitrogen by 150%. However by 4 weeks after treatment application many of these extra buds had died before they were able to emerge as tillers. Only Terpal, Cerone, TIBA, and to a lesser extent nitrogen resulted in a higher number of growing buds or emerged tillers than the control plants at 4 weeks after treatment application (Table 6.13).

Table 6.13 Effect of PGR treatments on number and identity of growing buds/tillers produced by 5 replicate plants at 2 and 4 weeks after application.

Treatment	Weeks after treatment application							
	2				4			
	Number of plants with a growing bud/tiller							
	T1	T2	T3	CT	T1	T2	T3	CT
Control	3	1	0	0	0	0	0	0
Terpal	4	4	2	0	5	1	0	0
10% Terpal	2	1	1	0	0	1	1	0
Cerone	5	3	2	2	4	0	0	0
Ancymidol	4	2	0	0	0	0	0	0
BAP	3	4	3	0	0	0	0	0
TIBA	5	5	4	0	4	0	0	0
GA_3	3	3	3	0	0	1	0	0
NO_3	4	4	2	0	2	0	1	0

The full Terpal concentration, Cerone, TIBA and nitrogen all markedly increased tiller production, with the Terpal and TIBA treatments resulting in 90% of plants having at least one tiller 32 days after treatment application (Fig. 6.4). This increased tiller production was observed after only 8 days of treatment application. All the other treatments had a negligible effect (Fig. 6.4). All the plants that tillered only produced one tiller, that is, T1, with the exception of the plants treated with Terpal or Cerone (Fig. 6.5a) which also produced other primary tillers, T2 and CT. Thirty percent of the Terpal treated plants and 10% of the Cerone treated plants also produced a T1P tiller.

The full Terpal, Cerone, TIBA and nitrogen treatments maintained their effect on tiller number until grain harvest (Fig. 6.5a). However only the plants treated with Terpal had a significantly ($p<0.05$) greater number of fertile ears, that is, a mean of 1.5 ± 0.2 ear-bearing shoots per plant compared to only one, that is, the MS in the control plants (Fig. 6.5a). MS ear weight was significantly ($p<0.05$) increased by the nitrogen treatment by 26% whereas Terpal, Cerone, TIBA, BAP and GA_3 all reduced MS ear weight by between 22 and 33%. The contribution of tiller ear weight by the treated plants, notably nitrate, Terpal, 10% Terpal and Cerone did not result in a greater ear weight per plant (Fig. 6.5b).

Main shoot height was significantly ($p<0.05$) reduced by the full Terpal treatment after only 8 days from application (Fig. 6.6a) and at ear emergence the height was significantly decreased by the full Terpal and Cerone treatments by about 33 and 14% respectively. Terpal delayed MS ear emergence by about one week and this illustrated in Plate 6.II. All the other treatments had a negligible effect on MS height (Fig. 6.6b). The number of MS leaves was unaffected by the treatments.

Fig. 6.4

Effect of treatments on the percentage of uniculm wheat plants producing at least one tiller with time.

a) ○ Control
   ● Terpal
   ▲ 10% Terpal
   ■ Cerone
   ◆ Ancymidol

b) ○ Control
   ● TIBA
   ▲ Nitrate
   ■ BAP
   ◆ GA_3

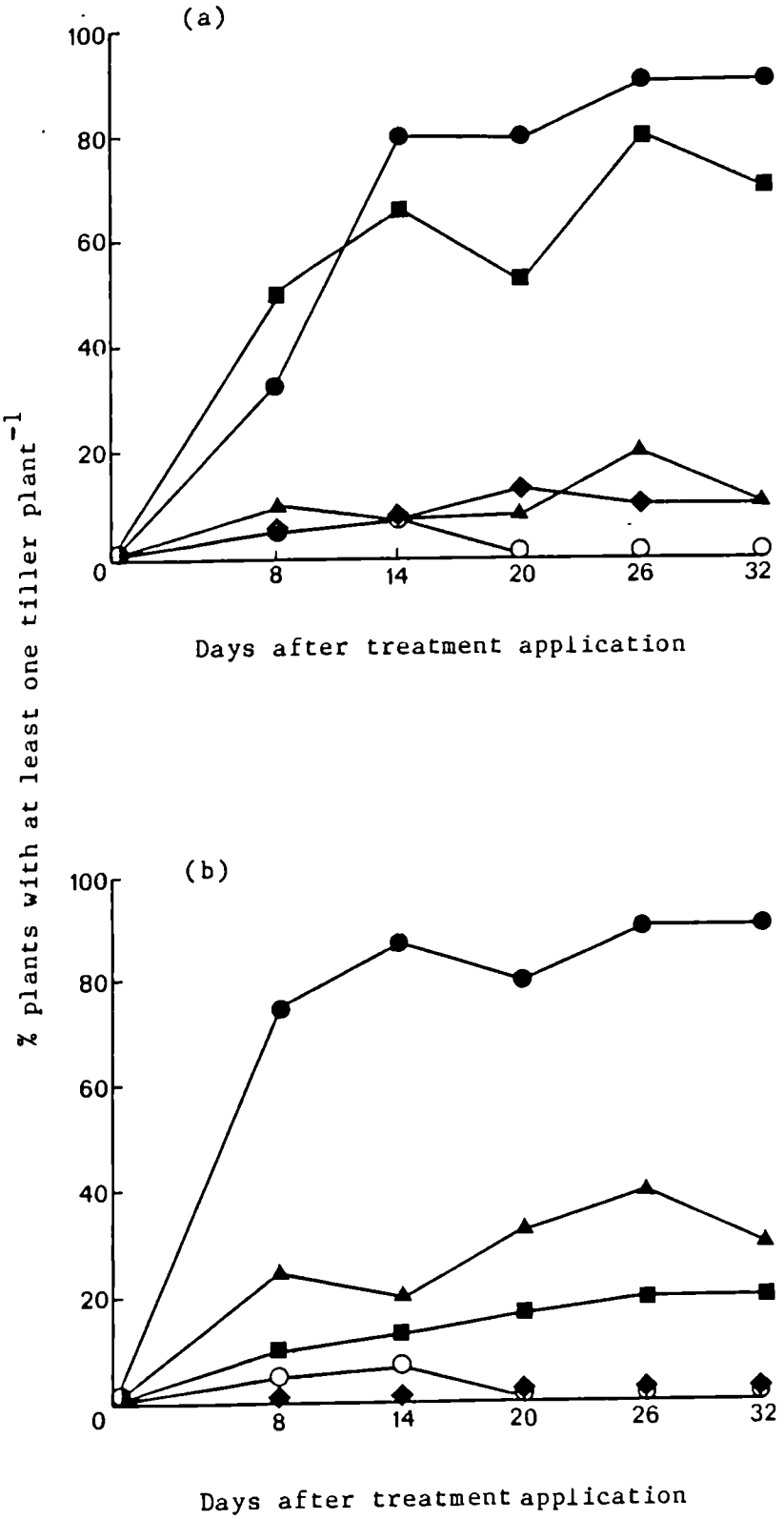
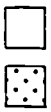

(a)
100
80
60
40
20
0
8
14
20
26
32
Days after treatment application
% plants with at least one tiller plant^{-1}
(b)
100
80
60
40
20
0
8
14
20
26
32
Days after treatment application

Fig. 6.5

Effect of treatments at grain harvest on:

a) tiller number (including MS)



ear-bearing shoots

non ear-bearing shoots

b) ear dry weight

MS ear weight

tiller ear weight

of uniculm wheat plants.

Vertical bars represent ±SE.

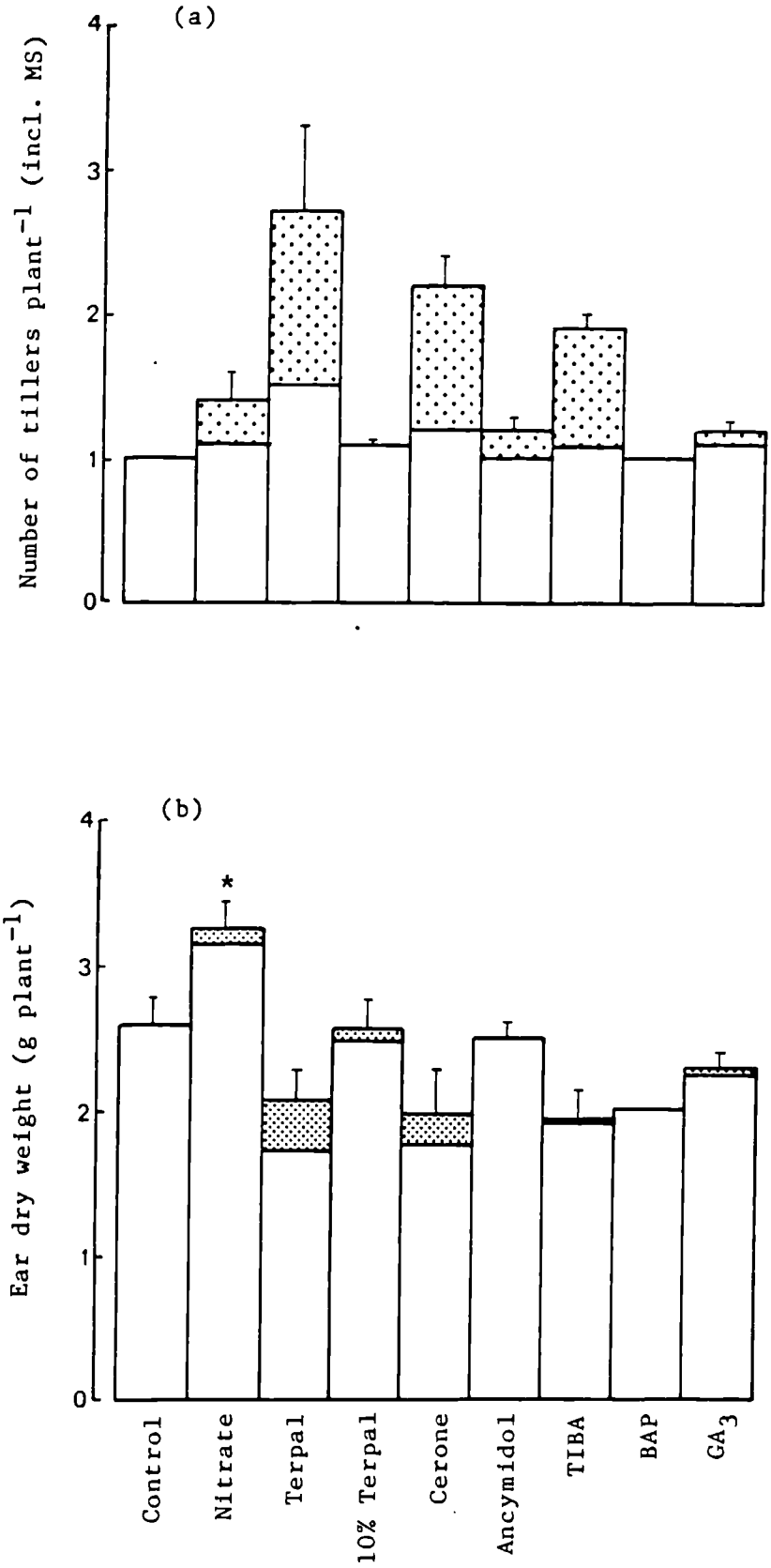

(a)
Number of tillers plant^{-1} (incl. MS)
0
1
2
3
4
(b)
Ear dry weight (g plant^{-1})
*
Control
Nitrate
Terpal
10% Terpal
Cerone
Ancymidol
TIBA
BAP
GA_3

Fig. 6.6

Effect of treatments on:

a) MS height with time

○ Control

● Nitrate

△ Terpal

▲ Cerone

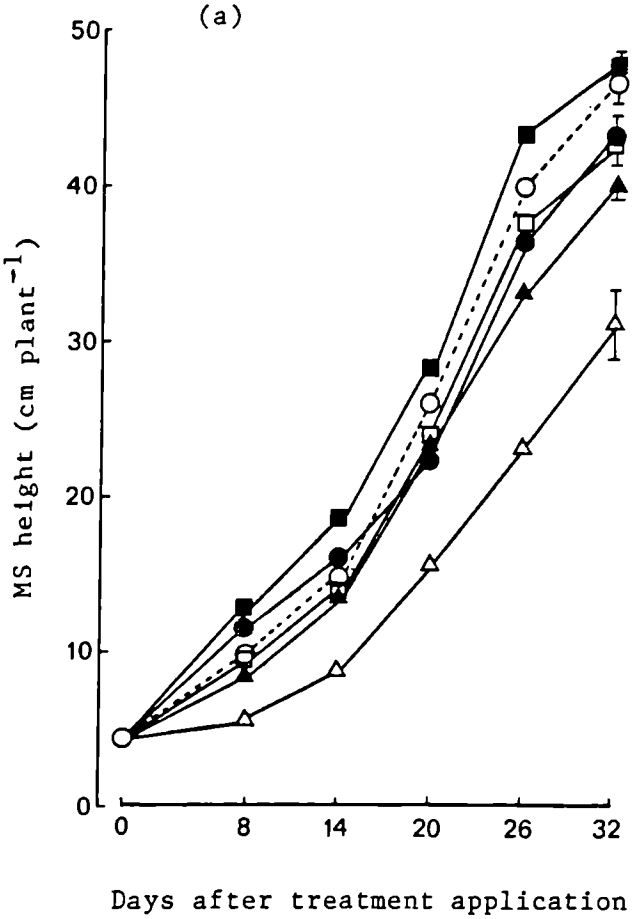
□ TIBA

■ GA_3

b) MS height at grain harvest.

Vertical bars represent ±SE.

(a)


MS height (cm plant^{-1})
50
40
30
20
10
0
0
8
14
20
26
32
Days after treatment application

(b)

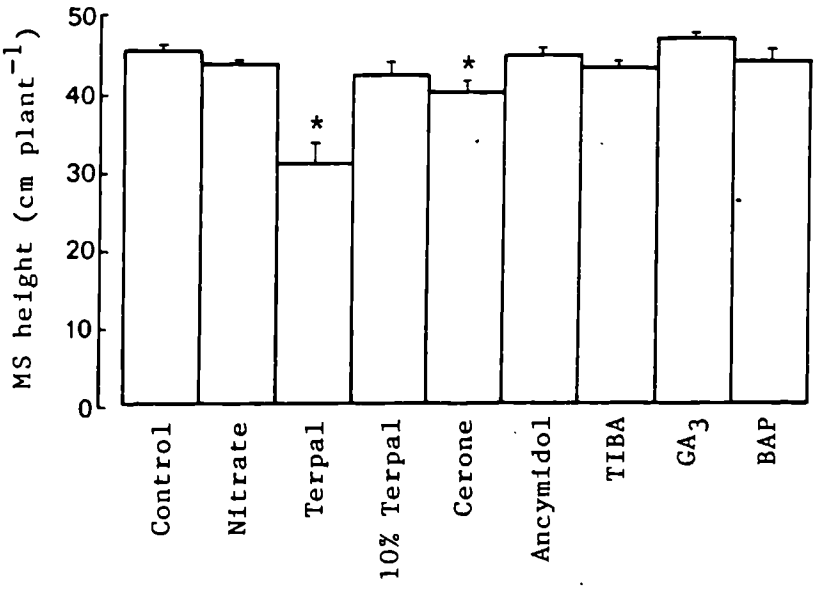

MS height (cm plant^{-1})
50
40
30
20
10
0
*
*
Control
Nitrate
Terpal
10% Terpal
Cerone
Ancymidol
TIBA
GA_3
BAP

Plate 6.II

Effect of Terpal application on the development of uniculm wheat. Full strength Terpal applied to leaves at GS 13; plants grown under glasshouse conditions. Photograph shows earlier emergence of MS ear in control plants (right) compared to Terpal treated plants (left). Both plants 7 weeks old.

:periment 6.6 Effect of PGRs on the distribution of ^{14}C-labelled
ssimilate in uniculm wheat plants.

ı order to ascertain whether the changes in tiller bud outgrowth
ollowing the application of Terpal, Cerone and TIBA to leaves were
elated to modifications in the supply of assimilate from the MS to the
illers, the pattern of distribution of ^{14}C-labelled assimilate was
ollowed in PGR treated plants.

ATERIALS AND METHODS

eeds of uniculm wheat were sown on 17 January, 1984 in pots containing
ohn Innes No.1 peatless compost and grown in the "new" glasshouse
uite as described in Chapter 4. PGR treatments were applied at GS 12
y foliar spray; it was decided to treat plants a little earlier than
sual since tiller bud death soon after commencement of growth was
bserved in the previous experiment. The treatments were, Terpal and
erone (both at concentrations equivalent to the recommended rate of
pplication), and TIBA (10^{-4}M + 0.05% v/v ethanol + 0.05% v/v Tween
.0). Distilled water + 0.05% v/v ethanol + 0.05% v/v Tween 20 was
.pplied to control plants. At 3 and 10 days after treatment
ıpplication, GS 13 and GS 14 respectively, plants were selected for
ınıformity and MS L1 was supplied with $^{14}CO_2$ as described in Experiment
ı.5. After 24 hours 4 replicate plants were harvested and separated
:nto component parts, that is, emerging tiller buds plus emerged
:illers, MS (stem plus unemerged leaves), MS leaves and roots; these
were oven-dried and weighed. Tiller buds and tillers were also counted
ınd measured. These samples were oxidised and counted as described in
Experiment 4.5.

SULTS

l the plants had a bud in the axil of L1 and some of these had mmenced growth by 30 days after sowing (10 days after spraying). out 25% of control plants had produced a T1 tiller by this time and us 75% of the plants were uniculms (Table 6.14). The Terpal, Cerone d TIBA treatments all increased the number of growing T1 buds by only days after spraying, Terpal and TIBA also promoted the emergence of tillers after 3 days of spraying. By 10 days after spraying only the BA treatment increased tiller production with 75% of plants producing T1 tiller; only 25% of the Terpal and Cerone treated plants produced tiller (Table 6.14). These responses to TIBA, Terpal and Cerone were a lower magnitude when compared to the previous experiment (Table .3). Elongation of the T2 bud had commenced in 25% of the Cerone and 3A treated plants after 10 days of spraying. Terpal and TIBA :reased the length of T1 by 131% and 38% respectively after 10 days spraying, the length of T1 in Cerone treated plants was unaffected ible 6.14). Although all of the treatments increased tiller bud :growth to some extent, only TIBA increased tiller dry weight gnificantly ($p<0.05$) at 10 days after application. The dry weight of : MS (stem plus unemerged leaves), MS leaves and roots was not fected by the treatments (Table 6.15).

ıble 6.14 Effect of PGR treatments on the number and length of :owing buds and tillers 3 and 10 days after spraying (n=4).

reatments	Days after treatment application	% plants with: growing bud		emerged tiller		Mean length (mm) ±SE of: growing bud		emerged tiller	
		T1	T2	T1	T2	T1	T2	T1	T2
ontrol	3	0	0	0	0	0	0	0	0
erpal	3	50	0	25	0	5±1.0	0	50± 0.0	0
erone	3	75	0	0	0	5±1.2	0	0	0
IBA	3	25	25	50	0	6±0.0	5±0.0	65±15.0	0
ontrol	10	0	0	25	0	0	0	35± 0.0	0
'erpal	10	25	0	25	0	6±0.0	0	81± 0.0	0
:erone	10	0	25	25	0	0	4±0.0	30± 0.0	0
'IBA	10	25	25	75	0	7±0.0	4±0.0	48± 9.3	0

Table 6.15 Effect of PGR treatments on the distribution of dry weight between component plant parts at 10 days after application ±SE.

Treatment	Dry weight (mg)				
	Tillers	MS (stem)	MS leaves	Roots	Total
Control	0.25±0.25	183.8±28.8	169.2± 9.5	157.7±21.8	510.9±59.3
Terpal	3.22±2.96	135.5±14.1	150.5±12.0	181.9±40.8	470.1±68.9
Cerone	0.27±0.27	173.4±24.0	159.7± 1.8	99.2±18.1	432.6±43.2
TIBA	1.12±0.19*	189.4±10.0	182.8±29.3	119.6±19.9	491.9±58.4

The amount of ^{14}C fixed per plant after 24 hours was similar in all treatments, with one exception, whether they had been applied 3 or 10 days previously. TIBA significantly ($p<0.05$) reduced the amount of ^{14}C fixed per plant 10 days after application (Table 6.16).

Table 6.16 Effect of PGR treatment on total ^{14}C fixed (DPM x 10^{-6}) per plant after 24 hours ±SE.

Days after	Treatment			
application	Control	Terpal	Cerone	TIBA
3	2.82±0.25	2.51±0.11	3.22±0.35	3.46±0.35
10	3.21±0.54	2.98±0.31	2.32±0.52	1.56±0.09*

Three days after treatment application about 44% of ^{14}C in the plant was recovered from the fed MS leaf (L1) irrespective of the treatments. Of the 56% of the ^{14}C translocated from the fed MS leaf, in control plants about 65% was translocated to the MS stem, about 13% to the MS leaves and about 21% to the roots; there were no tillers in these plants (Table 6.17). The treatments did not significantly modify the distribution of ^{14}C assimilate to the MS stem, MS leaves or roots except Cerone which significantly ($p<0.05$) increased the ^{14}C translocated to the roots (Table 6.17). Ten days after treatment application again about 44% of ^{14}C detected in the plant was recovered from the fed MS L1 in all treatments after the 24 hour period for translocation. Of the 56% of ^{14}C that was translocated from L1 in control plants only about 29% was translocated to the MS, again about 10% to the MS leaves and 60% to the roots; only 0.1% of the ^{14}C was translocated to tillers. Terpal and TIBA increased the amount of ^{14}C assimilate recovered from tillers but this was not statistically significant. Again Terpal had no effect on ^{14}C assimilate distribution

to the MS stem, MS leaves or roots whereas Cerone and TIBA significantly ($p<0.05$) increased the amount of ^{14}C recovered from the MS but not the MS leaves and Cerone reduced the ^{14}C translocated to the roots (Table 6.17).

Table 6.17 Effect of PGR treatments on the percentage distribution of ^{14}C-labelled assimilate exported from the fed MS leaf at 3 and 10 days after treatment application ±SE.

Treatment	Days after application	%^{14}C-assimilate exported from fed leaf			
		Tillers	MS	MS leaves	Roots
Control	3	0	65.4±3.9	13.2±2.2	21.4±3.8
Terpal	3	1.0±0.27	54.8±3.7	10.7±0.6	33.5±4.5
Cerone	3	0.8±0.23	54.1±3.5	10.5±0.2	34.6±4.2*
TIBA	3	13.5±6.90	56.6±4.9	7.8±1.9	22.1±1.8
Control	10	0.1±0.10	29.2±4.6	10.3±1.8	60.4±3.5
Terpal	10	3.6±3.40	20.2±4.9	11.6±2.1	64.6±3.7
Cerone	10	0.1±0.10	45.6±2.6*	14.5±6.8	39.8±5.8*
TIBA	10	1.6±0.90	46.7±5.9*	8.1±2.3	43.6±6.7

After 3 days of treatment application Terpal, Cerone and TIBA all increased the concentration of ^{14}C-labelled assimilate per mg of dry weight (DPM mg^{-1}) in the growing T1 and T2 tiller buds (Fig. 6.7a); no ^{14}C was recovered from buds of control plants as these were not elongating and were too small to dissect out from the plant. By 10 days after treatment application the concentration of ^{14}C was reduced since the plants had grown larger and the same amount of $^{14}CO_2$ was supplied. Terpal and TIBA increased ($p<0.05$) the concentration recovered from the tillers at this time; Cerone had no effect (Fig. 6.7b). At 3 days after treatment application none of the treatments modified the concentration

Fig. 6.7

Effect of treatments on the concentration of ^{14}C (DPM x 10^{-3} mg^{-1} of dry weight) in component plant parts at:

a) 3 days after treatment application

b) 10 " " " "

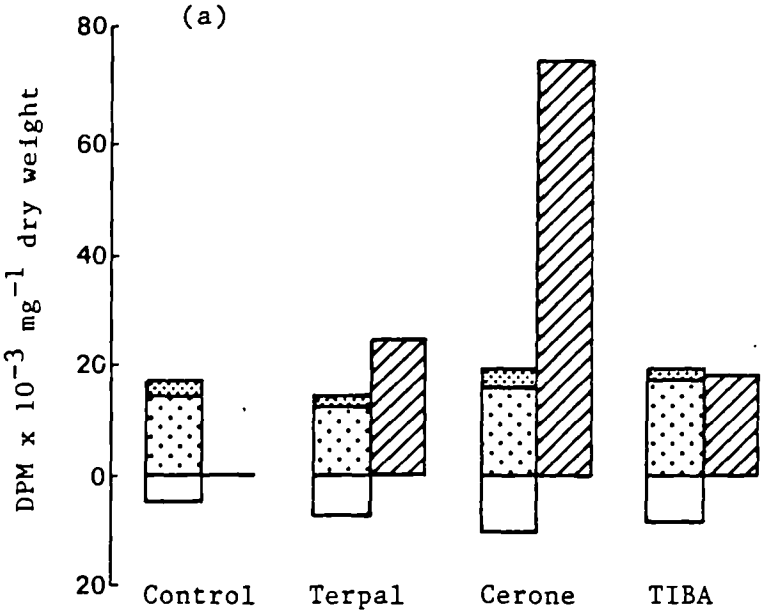

MS leaves

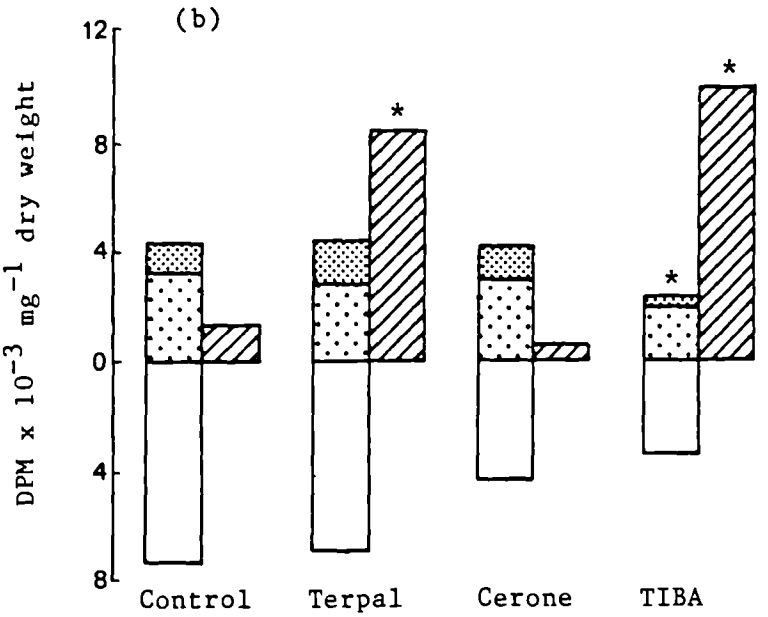

MS stem and unemerged leaves


roots


T1 and T2 buds/tillers

Vertical bars represent ±SE.


(a)
80
60
40
20
0
20
DPM x 10^{-3} mg^{-1} dry weight
Control
Terpal
Cerone
TIBA


(b)
12
8
4
0
4
8
DPM x 10^{-3} mg^{-1} dry weight
*
*
*
Control
Terpal
Cerone
TIBA

of ^{14}C in the roots, MS stem and MS leaves (Fig. 6.7a). By 10 days after application Terpal still had no effect on the concentration in the roots, MS stem and MS leaves but Cerone and TIBA appeared to reduce the concentration in the roots, MS stem and MS leaves respectively. However, only one of these effects was statistically significant ($p<0.05$), that was the reduction in the MS leaves by TIBA (Fig. 6.7b).

DISCUSSION

The barley and wheat uniculm lines responded quite differently to the various treatments, the barley retaining its restricted tillering habit and the wheat producing tillers in response to a range of experimental treatments. Thus it can be concluded that the mechanisms controlling tiller bud inhibition are distinctly different in the barley and wheat uniculms.

None of the treatments caused any significant tiller bud outgrowth in the barley, but seed applications of Terpal, BAP and TIBA and foliar applications of Terpal and BAP reduced MS height confirming the activity of these chemicals within the plant. Some of the PGR treatments when applied to the barley seeds either completely inhibited germination (50% Terpal and BAP in the growth cabinet) or inhibited the growth and development of the MS inflorescence (50% Terpal, BAP and TIBA in the glasshouse). Thus overall, the PGRs, whether applied to the seed or leaves, had an inhibitory effect on the growth and development of the uniculm barley plants. In the light of a preliminary anatomical study (Mrs A. Bell, pers. comm.) it seems possible that bud inhibition in barley is maintained by the absence of adequate vascular connections between the buds and the MS. Thus the supply of assimilate, nutrients and essential growth substances, for example cytokinins, to buds may be insufficient to support their outgrowth.

In contrast the uniculm wheat selection was found to be capable of tiller production. Tillering readily occurred when plants were grown in the growth cabinet and also when subjected to a range of PGR treatments, particularly Terpal, Cerone and TIBA. It is likely therefore, that the vascular connections in the wheat between the buds and the MS are adequate to allow some, if not free, movement of

substrates required for growth.

In the "old" glasshouse suite most of the wheat plants produced tillering phenotypes (Experiments 6.1, 6.2 and see Materials and Methods, Experiment 6.5) whereas in the "new" glasshouse suite plants were either all uniculm phenotypes or up to 40% produced tillers (Experiments 6.3, 6.5 and 6.6). The uniculm plants which tillered generally produced a single tiller. However, when the uniculm wheat plants were grown in the growth cabinet tillering was greatly increased, particularly when the plants were also grown in nutrient solution; 4 tillers per plant were produced in Experiment 6.1. The tillering cultivar, Broom, also produced significantly more tillers in the growth cabinet further indicating the more favourable conditions for tiller production of this environment. It is not clear which environmental factor leads to the stimulation of tillering. The temperature regimes were of a similar magnitude, except that the temperature did not fluctuate during the day in the growth cabinet. The light regimes were, however, more distinctly different; although the photoperiods were similar the irradiance in the glasshouse from natural daylight would be far higher than in the artificial environment and would be of a different spectral composition. The latter point may be particularly significant as illumination in the growth cabinet was by fluorescent tubes only. It was, therefore, deficient in light at the red end of the spectrum, and especially in far red light (Smith, 1975). There is some evidence that tiller bud outgrowth may be regulated by the ratio of red:far red light, tillering being favoured at high red:far red light ratios in Lolium spp. (Deregibus et al., 1983).

As in Triumph spring barley (Chapter 5) seed treatment with Terpal was found to produce profound and long lasting effects on plant growth and development. In glasshouse grown uniculm wheat, Terpal seed treatment

greatly accelerated the growth and development of tiller buds resulting in a greater proportion of elongating buds per plant and a greater emergence of tillers originating from the first leaf position, that is, T1. As tillering was increased in control plants grown in the growth cabinet this concealed any effect of Terpal seed treatment in this environment. MS leaf number was also increased by the Terpal seed treatment in glasshouse grown plants. These additional leaves and the greater number of growing tiller buds may have become alternate sinks for assimilates since the size of the MS stem and roots were diminished. It is unlikely that these effects were primarily due to a direct effect of Terpal as the amount of active ingredient taken up by the seed would be very small.

Where PGRs were applied to the leaves of uniculm wheat plants (Experiment 6.5), Terpal, Cerone and TIBA and to a lesser extent nitrogen, all promoted tiller bud elongation and emergence. There is some evidence that applications of Terpal, Cerone and TIBA also resulted in the increased distribution of ^{14}C-assimilate to the tillers from the MS fed leaf. These treatments have previously been shown to increase tiller production in tillering barley in the present thesis (Chapters 3 and 4). Without any PGR treatment most buds died soon after production and therefore no tillers were produced in control plants. Terpal and Cerone had the greatest effect resulting in the multiple emergence of tillers whilst TIBA, on the other hand, had a lesser effect generally promoting the production of only one tiller per plant. These results again suggest a more successful breaking down of apical dominance by ethylene since it is a component of both Terpal and Cerone. Ethylene is thought to interfere with auxin transport and thus the promoted bud outgrowth may be in response to a modification of auxin relations. This hypothesis is further supported by the effects of TIBA on bud outgrowth as this compound also inhibits auxin transport.

However, the Terpal and Cerone treatments significantly reduced MS height whilst TIBA had no effect (Experiment 6.5); these findings and the fact that TIBA had a smaller effect on tillering, suggest that the anti-gibberellin activity of these PGRs may have been responsible in part for the outgrowth of inhibited tiller buds. Anti-gibberellins have been previously implicated in causing tillering in a uniculm mutant. Applications of CCC to a uniculm mutant of barley reduced plant height and promoted tiller production which resulted in a greater grain yield due to a higher number of ears per plant (Bokhari and Youngner, 1971b). Further it has been suggested that the uniculm wheat line used in the present study (Atsmon and Jacobs, 1977) may have a greater capacity to produce gibberellins compared to tillering varieties and that this might increase the competitive ability of the MS which may in turn suppress tiller bud development (Marshall and Boyd, 1985).

CHAPTER 7

THE EFFECT OF TERPAL ON LEAF GROWTH AND PHOTOSYNTHESIS

INTRODUCTION

Most studies on leaf growth have been concerned with environmental factors such as the effects of temperature and water (Gallagher, 1979; Legg et al., 1979; Monteith and Elston, 1983) whereas relatively few have been concerned with the influence of PGRs. In the preceding chapters Terpal was found to have a marked effect on leaf size; lamina length of the MS leaves was reduced in both Triumph spring barley and the uniculm wheat selection when Terpal was applied to seeds at germination (Chapters 5 and 6). Other substances with anti-gibberellin activity have also been shown to retard leaf growth. For example, Foreman (1984) found that treatment of Lolium perenne with WL83801, an experimental growth retardant, significantly reduced both the rate and duration of leaf extension.

In the last few years, studies of leaf extension have been made with greater precision than previously possible due to the use of LVDTs (Linear Variable Differential Transducers) to continuously monitor growth (Gallagher et al., 1976b; Monteith et al., 1981). Thus accurate measurements of extension in slow growing (retardant-treated leaves) can now be obtained.

In the following experiments the effects of Terpal on leaf growth and photosynthesis were examined and the relevance of these results are discussed with respect to the modifications to tillering caused by Terpal application.

EXPERIMENTAL

Experiment 7.1 Effect of Terpal on leaf growth.

In this experiment an automated auxanometer system designed by Foreman (1984) and based on that originally described by Gallagher et al. (1976b) was used to obtain accurate profiles of MS and tiller leaf extension following the application of Terpal.

MATERIALS AND METHODS

Seeds of spring barley cv. Triumph, were sown individually in pots of John Innes No.1 potting compost and grown in the "new" glasshouse suite, as described in Chapter 4, between June and August, 1983. At the onset of tillering (GS 14) Terpal was applied to half of the plants by foliar spray at a rate equivalent to the normal agricultural rate (2.5 dm^3 ha^{-1}). After 4 days several plants were transferred to a growth room containing the auxanometer system. The plants were, from then onwards, illuminated by 400W mercury vapour lamps for a 16 hour photoperiod at 300 μE m^{-2} s^{-1} at canopy level. Temperature in the growth room was only poorly controlled and varied between 10 and 28°C. The plants were watered as required and placed in shallow dishes of water to reduce water deficit.

After one week (GS 16) in the growth room the emerging leaf tip of MS L7 and/or T1 L3 was carefully attached to the auxanometer. Monitoring of leaf extension commenced at the same point mid-way through the photoperiod in all replicate experiments and ceased when the leaf was fully expanded. Leaf extension was simultaneously measured on 3 plants using vertically mounted Linear Variable Differential Transducers (LVDTs) (RDP Electronics Ltd.). The output from the LVDTs, together

with that from 2 temperature sensors positioned close to the extending leaves, was interfaced with an Apple II Microcomputer via a 16 channel, 12 bit A/D converter (MC Computers). The software ran a clockcard (UCNW Electronics) which allowed readings to be taken at 30 minute intervals. Subroutines read the inputs, calculate the rates of extension and transfer this information to disk. At the end of an experiment (when leaf growth was completed) these data were transferred to a Dec 10 mainframe computer using software transfer programs, where data handling and graphic facilities produced the graphs presented in this chapter. This procedure followed that described by Foreman (1984) who established the auxanometer system and its associated software. At the end of an experiment the lengths of all fully expanded leaves were measured.

RESULTS

Leaf length increased with each successive leaf of both the MS and tillers of control plants (Table 7.1). Mean leaf length per shoot was reduced with each successive tiller, the MS having the longest mean leaf length. In Terpal treated plants, leaf length also increased with each successive leaf, except in the MS. When Terpal was applied, that is, at the emergence of L5 (GS 14) the lengths of subsequently emerging leaves (L6 and L7) were not significantly different from L5. MS leaves 5, 6 and 7 were all shorter than the corresponding leaves of control plants although only the effects of Terpal on L6 and L7 were statistically significant ($p<0.01$) (Table 7.1). Terpal also reduced the length of all tiller leaves, except T3 L1 which was little affected; only the effects of Terpal on T1 L2, T1 L3, T2 L1 and T1P L2 were significant ($p<0.01$) (Table 7.1). Although Terpal retarded leaf growth, tiller production was increased due to the enhanced emergence of secondary tillers, particularly T2P.

Table 7.1 Effect of Terpal on the length of fully expanded leaves at GS 17 ±SE. Terpal was applied as 5th leaf was emerging (GS 15).

Leaf	Length (mm)		Mean value (mm)	
	Control	Terpal	Control	Terpal
MS L1	102.8± 3.2	105.2± 3.8		
MS L2	215.7± 3.9	218.0± 5.6		
MS L3	288.7± 5.2	289.7±13.1		
MS L4	323.5± 3.5	301.7±12.0		
MS L5	336.5± 4.6	310.0±36.6		
MS L6	363.4± 5.3	268.4± 6.8 **		
MS L7	389.4±33.8	261.6±16.3 **	288.6±34.8	250.7±26.9
T1 L1	120.0± 7.1	112.7± 6.6		
T1 L2	306.2±19.7	201.2±11.5 **		
T1 L3	311.6± 8.6	219.0± 9.1 **	245.9±63.1	177.6±32.9
T2 L1	171.7±13.2	123.0± 7.2 **		
T2 L2	233.2± 9.4	214.5±10.7		
T2 L3	301.6±20.9	257.4±21.3	235.5±37.9	198.3±39.7
T3 L1	99.0±18.3	105.2±29.3		
T3 L2	231.4±46.0	158.0±19.1	165.2±66.4	131.6±26.5
T1P L1	78.0±10.0	40.2±16.3		
T1P L2	226.5± 7.4	109.0±31.1 **	152.2±74.5	74.6±34.5
T2P L1		50.7±14.6		
T2P L2		87.0±23.4		68.8+18.2

Of the data obtained from the auxanometer, the results presented are for a single leaf only. However, many replicates were measured and all showed similar patterns of growth to that described here; representative examples of the data obtained are presented. Leaf extension rate of the MS was always faster than that of tiller leaves especially during the light period (by between 10 and 60%) (Fig. 7.1a, 7.2a and 7.3a). Leaf extension usually showed a diurnal pattern (Fig. 7.1a) with the extension rate diminishing soon after the start of the dark period. This pattern of leaf extension occurred during only a slight change in diurnal temperature, (about a $3^{o}C$ reduction in the dark period) (Fig. 7.1b). It can be seen from Fig. 7.1a that the auxanometer system was very sensitive to changes in the rate of leaf extension. To simplify the presentation of subsequent results the extension rate was plotted using a 4 hour running mean (Fig. 7.2a and 7.3a). The pattern of extension over a 3 day period of growth is shown in Fig. 7.2a and it is clear that the rate of extension declines steadily with time as the leaf increases in length.

The effect of Terpal was to reduce the rate of leaf extension. MS leaf extension was reduced by about 40% (Fig. 7.2a) and since the duration of MS leaf extension in both control and Terpal treated plants was similar MS leaves were shorter in Terpal treated plants (Table 7.1). Compared to Fig. 7.1a, diurnal changes in leaf extension rate in Fig. 7.2a were less distinct although diurnal fluctuations in temperature in this case were much greater with a reduction of about $10^{o}C$ in the dark period (Fig. 7.2b). The extension rate of the tiller leaves was also reduced by the Terpal treatment, by about 40% (Fig. 7.3a) and also the duration of leaf extension by about 20 hours. This resulted in shorter tiller leaves in those plants treated with Terpal (Table 7.1). Again the diurnal pattern of leaf extension was poorly displayed particularly in Terpal treated plants (Fig. 7.3a). There were correspondingly small

Fig. 7.1

a) Extension rate of control plant leaves.

____ MS L7

----- T1 L3

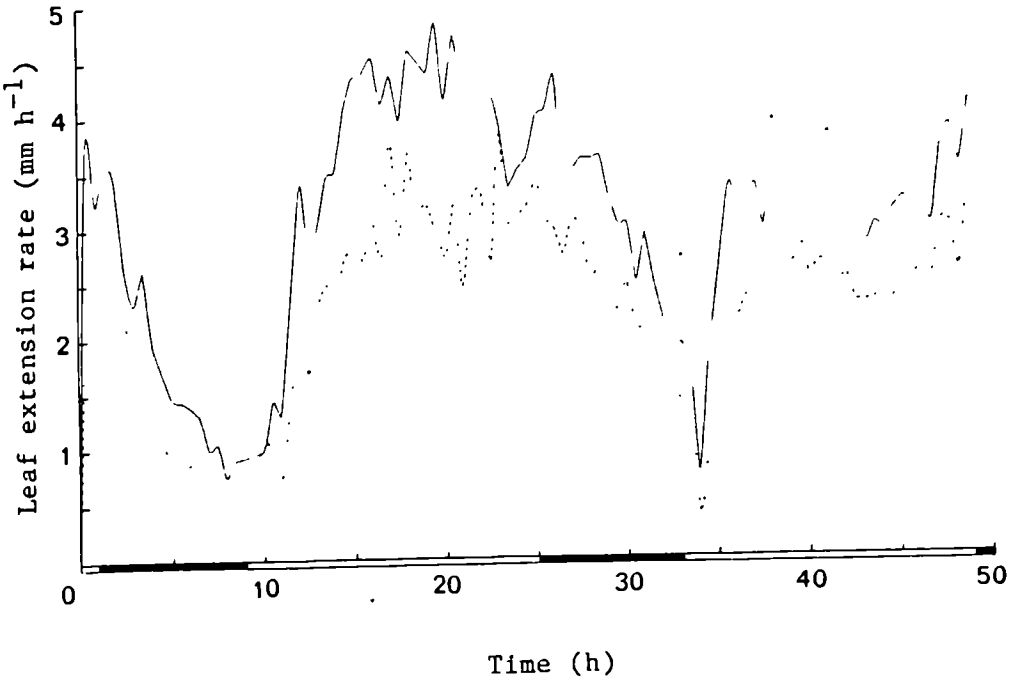
b) Temperature, sensors adjacent to:

____ MS L7

----- T1 L3

Open and solid bars indicate light and dark periods respectively.

(a)


Leaf extension rate (mm h^{-1})
5
4
3
2
1
0
10
20
30
40
50
Time (h)

(b)

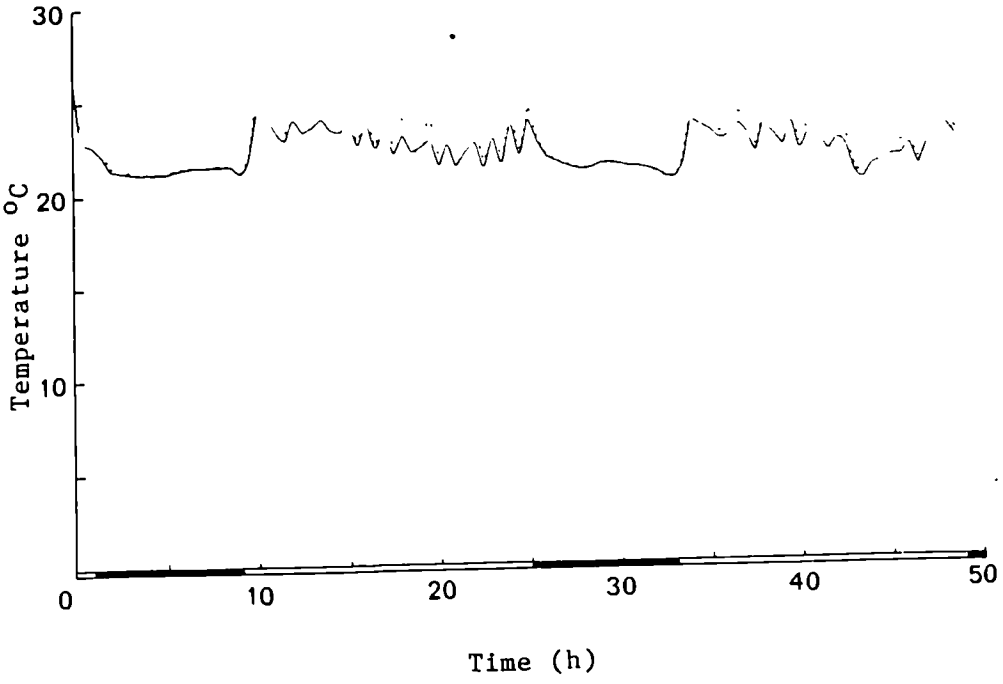

Temperature °C
30
20
10
0
10
20
30
40
50
Time (h)

Fig. 7.2

a) Effect of Terpal on the extension rate of MS L7.

—— Control

---- Terpal treated plants

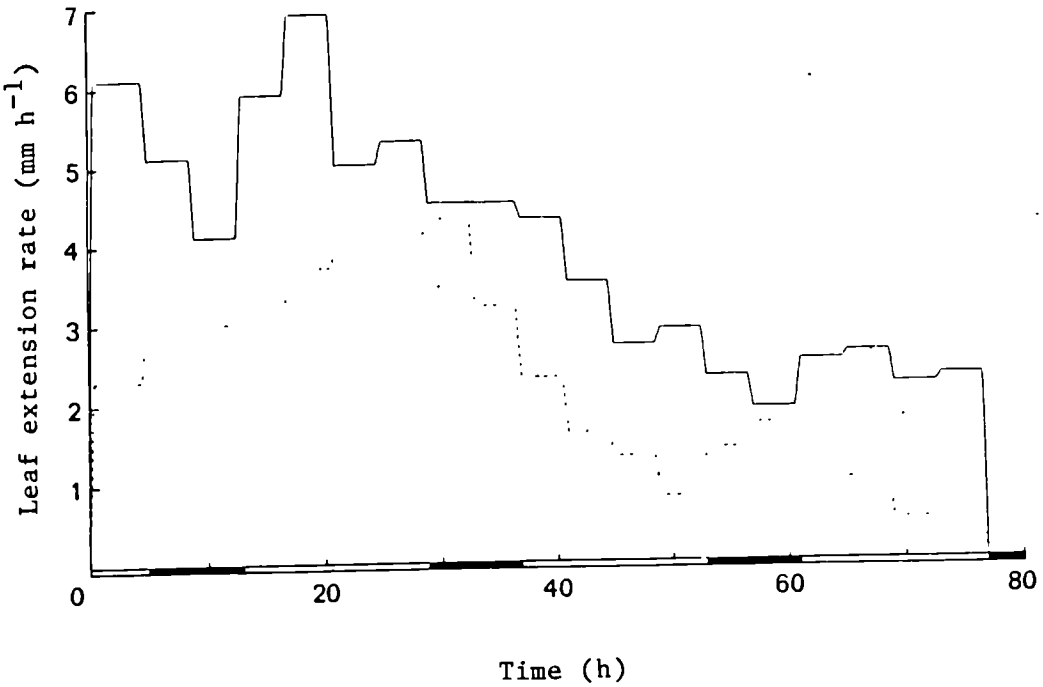
b) Temperature, sensors adjacent to:

—— Control leaf

---- Terpal treated leaf

Open and solid bars indicate light and dark periods respectively.

(a)


Leaf extension rate (mm h^{-1})
7
6
5
4
3
2
1
0
20
40
60
80
Time (h)

(b)

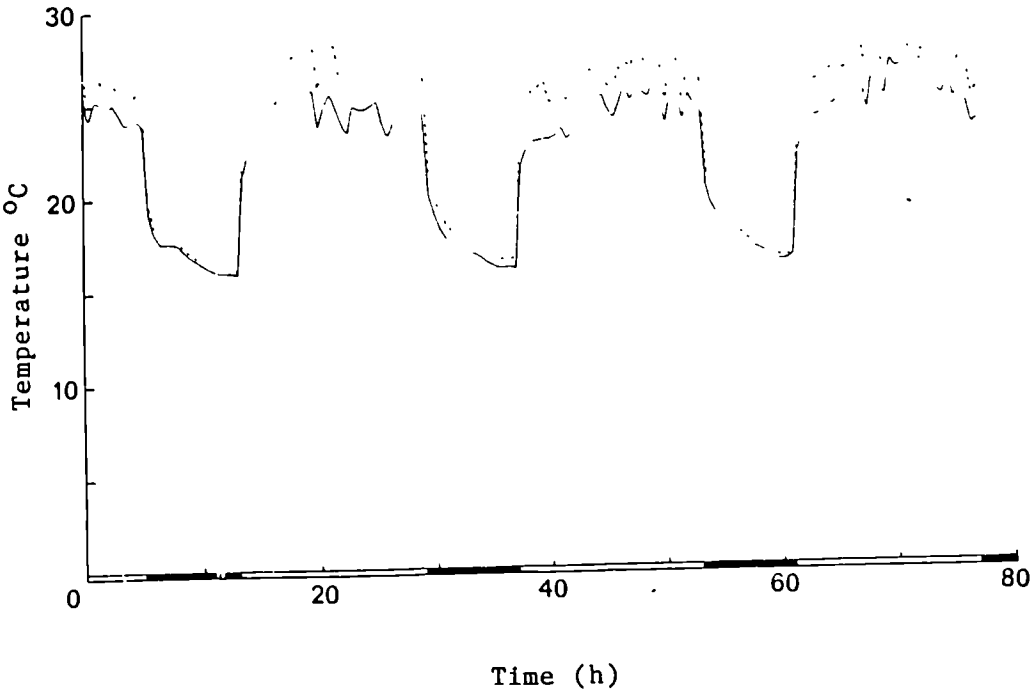

Temperature °C
30
20
10
0
20
40
60
80
Time (h)

Fig. 7.3

a) Effect of Terpal on the extension rate of T1 L3 with time.

—— Control

---- Terpal treated plants

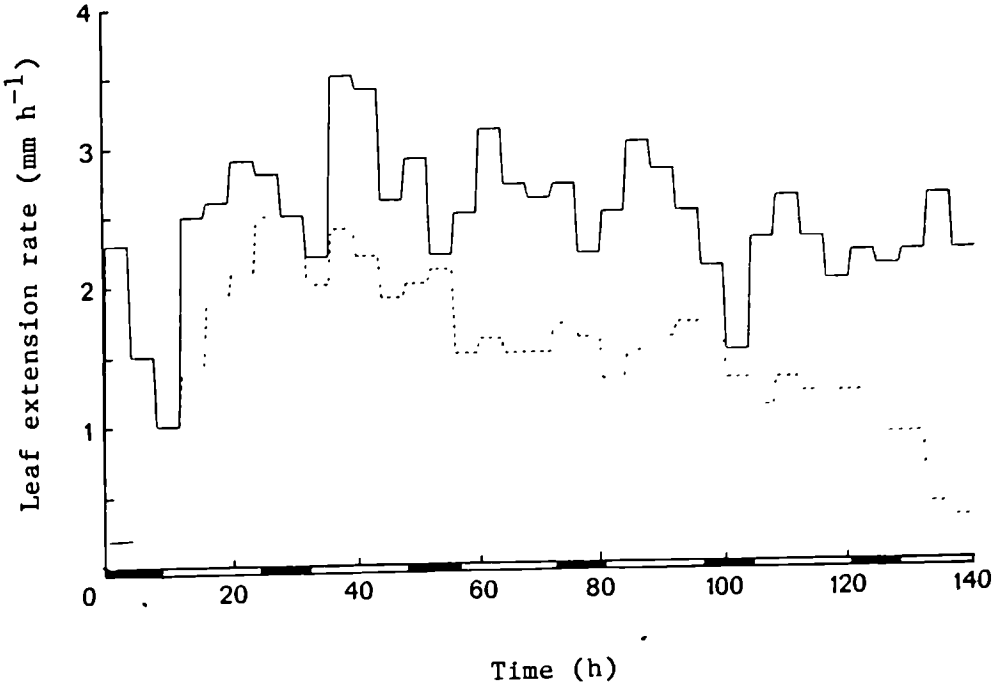
b) Temperature, sensors adjacent to:

—— Control leaf

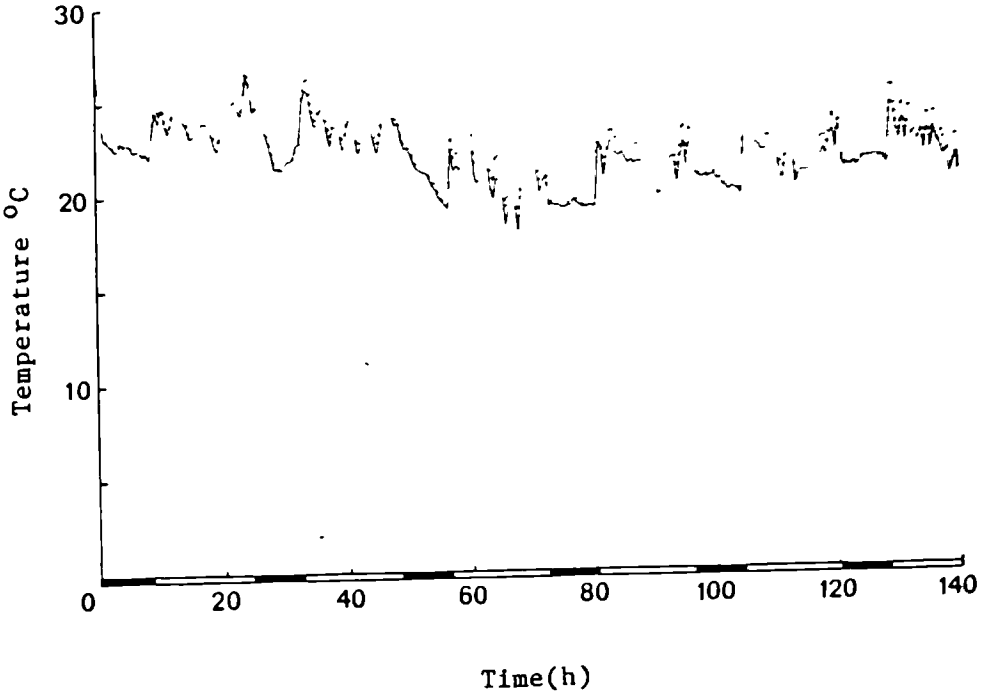
----Terpal treated leaf

Open and solid bars indicate light and dark periods respectively.

(a)


Leaf extension rate (mm h^{-1})
4
3
2
1
0
20
40
60
80
100
120
140
Time (h)

(b)


Temperature °C
30
20
10
0
20
40
60
80
100
120
140
Time(h)

fluctuations in temperature between day and night in this experiment (Fig. 7.3b).

Experiment 7.2 Effect of Terpal on leaf cell number.

In order to determine whether the reduction in leaf length following Terpal application was related to a reduction in leaf cell number or a reduction in cell enlargement, or to both, the number of cells in the lamina was determined. The technique employed was that of protoplast preparation and subsequent counting.

MATERIALS AND METHODS

Seeds of spring barley, cv. Triumph, were sown individually in pots of John Innes No.1 potting compost and grown in the "new" glasshouse suite, as described in Chapter 4, between January and February, 1984. Terpal was applied to half of the plants at GS 13 by foliar spray at a rate equivalent to the recommended agricultural rate of application. After 4 days plants were transferred to the controlled environment cabinet (as described in Chapter 3). Uniform plants were selected as MS L4 and T1 L1 reached full expansion. These leaves were then removed from the plant and immediately measured and weighed. Cells (protoplasts) were isolated from the central region of the lamina by the following enzyme digestion technique devised by J.D. Scholes (pers. comm.). The lower epidermis of the leaf was removed and a section of known area and weight was placed stripped side downwards in a Petri dish containing 10 cm^3 of buffer/enzyme cocktail (5 mM TRIS/MES buffer adjusted to pH 5.5 + 0.5 M Sorbitol, 1 mM $CaCl_2$, 0.3% v/v pectinase and 3.0% v/v cellulase). The leaf section was then incubated for 6 hours in the light at 30°C during which time the protoplasts were released into the medium. Protoplast counts from replicate sections were made using a

haemocytometer slide. The experiment was replicated 4 times.

RESULTS

In this experiment although Terpal reduced the length, area and fresh weight of the MS L4 the differences were not statistically significant (Table 7.2). Terpal also reduced the dimensions, area and fresh weight of the T1 L1; the effects on length, area and weight were significant ($p<0.05$). Terpal had no statistically significant effect on the number of cells per leaf blade, although they appear to have been reduced in T1 L1, or on the number of cells per mg fresh weight (Table 7.2).

Table 7.2 Effect of Terpal on lamina size and cell number of MS L4 and T1 L1 ±SE. Control (C), Terpal treated (T), fresh weight (FW).

Leaf	Length	Width	Area	Weight	Cell number $leaf^{-1}$	Cell number $mg\ FW^{-1}$
	mm	mm	cm^2	mg	$x10^{-6}$	$x10^{-6}$
C MS	264.7± 7.7	10.0±0.2	21.2±2.2	399.7±31.5	115.9±19.1	0.284±0.03
T MS	229.0±17.0	9.4±0.3	18.2±1.8	336.2±39.2	123.6±33.4	0.349±0.06
C T1	140.0±22.7	5.7±0.7	7.2±1.1	113.5±24.1	48.4±17.2	0.394±0.06
T T1	89.3±10.8	5.7±0.2	3.1±1.0	58.7± 4.8	26.1±12.0	0.411±0.16
	*		*	*		

Experiment 7.3 Effect of Terpal on net photosynthesis of leaves.

To determine if there was any effect of Terpal on the rate of net photosynthesis, the photosynthetic rates of MS and tiller leaves were measured using an Infra Red Gas Analyser (IRGA). The IRGA measures CO_2 depletion from ambient air by intact leaves and reflects the net chloroplast efficiency and resistances to gaseous exchange.

MATERIALS AND METHODS

Seeds of spring barley, cv. Triumph, were sown individually in pots of John Innes No.1 potting compost and grown in the "new" glasshouse suite, as described in Chapter 4, between November and December, 1983. Terpal was applied at GS 13 to half of the plants by foliar spray at a rate equivalent to the recommended agricultural rate of application. After 2 days the first sample of plants were transferred to the growth room containing the IRGA. The growth room had a 16 hour photoperiod, an irradiance of 300 $\mu E\ m^{-2}\ s^{-1}$ and a constant temperature of 21°C. Further samples of plants were transferred to this growth room when they had reached the following growth stages: 14,15,16 and 17 (about every 7 days). Uniform plants were selected and photosynthesis of all leaves measured. All measurements were made at a set time mid-way in the photoperiod. Photosynthesis of the attached leaves in air-sealed chambers was measured using a differential Infra Red Gas Analyser with a six channel automatic sampling unit (Analytical Development Co.) as described by Owera et al. (1981). At the end of an experiment tillers and leaves were counted, leaf areas were measured and plant parts were oven-dried and weighed. Six replicate plants were used.

RESULTS

As usual the effect of Terpal was to increase tiller production. This effect was observed immediately following Terpal application although it was not statistically significant until GS 15 when the Terpal treated plants had 42% more tillers than the control plants (Fig. 7.4a). MS leaf number was not modified by Terpal treatment; MS leaf senescence had commenced by GS 15 (Fig. 7.4b). The number of tiller leaves per plant was increased by the Terpal treatment but this was not statistically significant until GS 17 (Fig. 7.4c). This was entirely due to increased tiller production since the number of leaves per tiller remained constant. Although tiller number and number of tiller leaves were increased, total dry weight and total leaf area per plant were significantly reduced by Terpal treatment at GS 13,14 and 17 (Fig. 7.4d and Fig. 7.4e).

Leaf area, at full expansion, increased with each successive leaf of MS and tillers in both control and Terpal treated plants (Fig. 7.5a and 7.6a). At GS 14 Terpal reduced the area of all leaves; this effect was not statistically significant for MS L1 and L2 which were fully expanded at the time of Terpal application (Fig. 7.5a). Fig. 7.6a shows the maximum area attained, before senescence began, by each leaf during the course of the experiment and it can be seen that Terpal reduced the area of nearly all MS leaves (exceptions were L4, L7 and L8) and of every leaf of T1, T2, T1P and T3 although not all these reductions were statistically significant.

At GS 14 the rate of photosynthesis per leaf was closely related to leaf area (Fig. 7.5b) and correspondingly Terpal reduced the net photosynthetic rate per leaf of the majority of leaves monitored (Fig. 7.5b). At GS 17, and to a lesser extent at GS 14, highest rates of photosynthesis per unit area were monitored in expanding leaves (Fig.

Fig. 7.4

Effect of Terpal with time on:

a) tiller number

b) number of MS leaves plant^{-1}

c) total number of tiller leaves plant^{-1}

d) total plant dry weight

e) total plant leaf area

Terpal applied 2 days prior to first measurement at GS 13.

O Control

● Terpal treated plants

— live leaf number

--- senesced leaf number

Vertical bars represent ±SE.

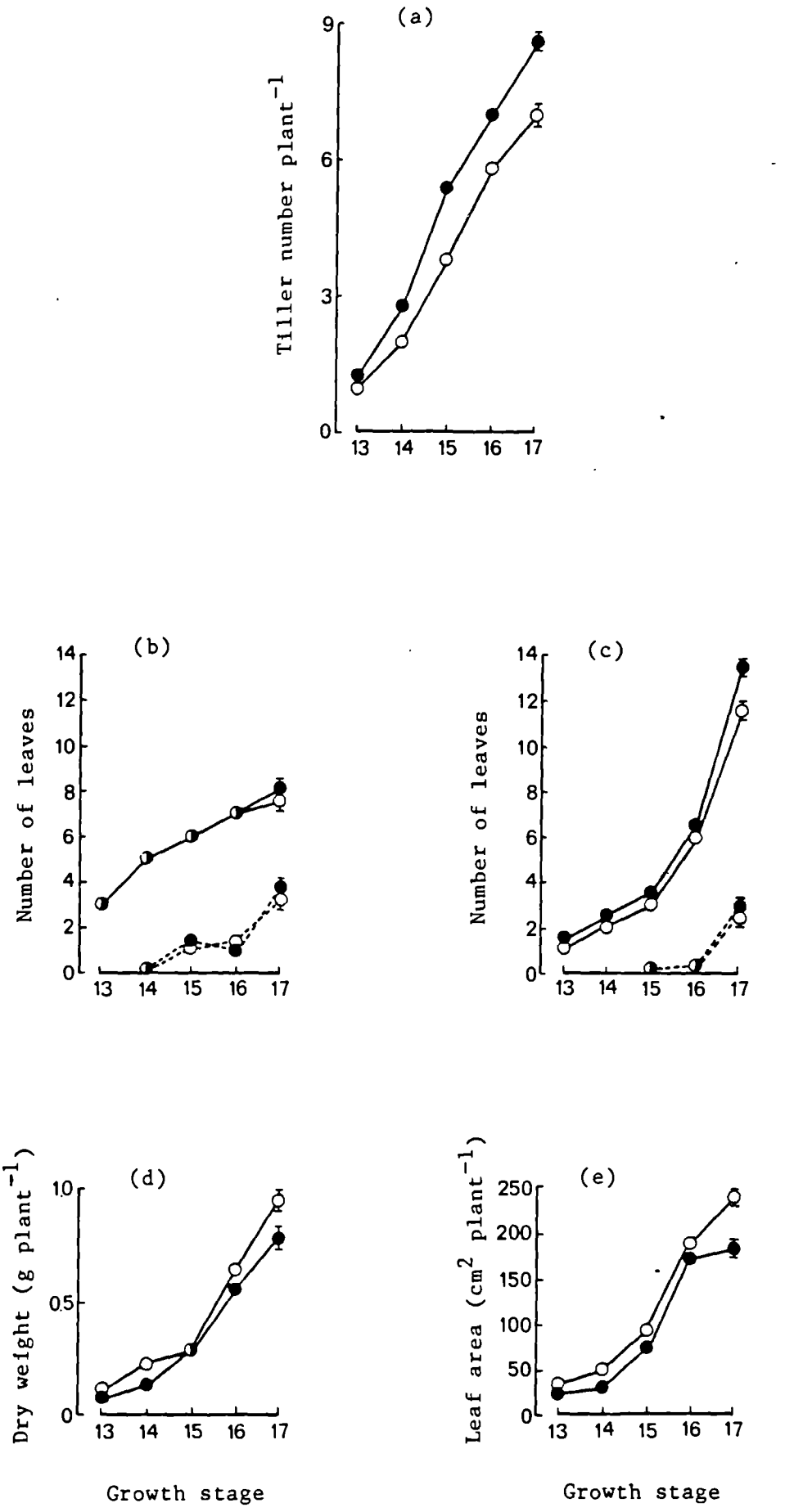

(a)
Tiller number plant^{-1}
9
6
3
0
13 14 15 16 17
(b)
Number of leaves
14
12
10
8
6
4
2
0
13 14 15 16 17
(c)
Number of leaves
14
12
10
8
6
4
2
0
13 14 15 16 17
(d)
Dry weight (g plant^{-1})
1.0
0.5
0
13 14 15 16 17
Growth stage
(e)
Leaf area (cm^2 plant^{-1})
250
200
150
100
50
0
13 14 15 16 17
Growth stage

Fig. 7.5

Effect of Terpal at GS 14 on:

a) individual leaf area

b) net photosynthetic rate $leaf^{-1}$

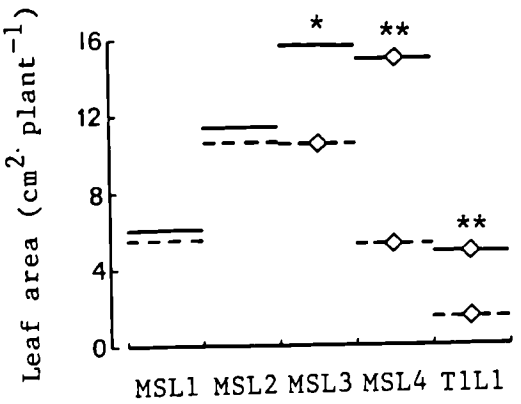
c) " " " " m^{-2} leaf area of individual leaves.

—— Control

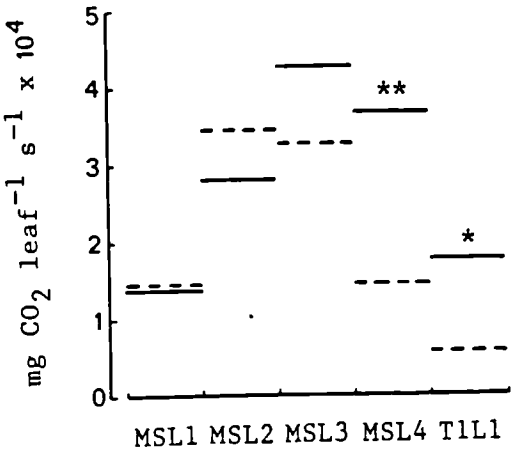
---- Terpal treated plants

◇ leaf not fully emerged

(a)


Leaf area (cm^2 plant^{-1})
16
12
8
4
0
*
**
**
MSL1 MSL2 MSL3 MSL4 T1L1

(b)


mg CO_2 leaf^{-1} s^{-1} x 10^4
5
4
3
2
1
0
**
*
MSL1 MSL2 MSL3 MSL4 T1L1

(c)

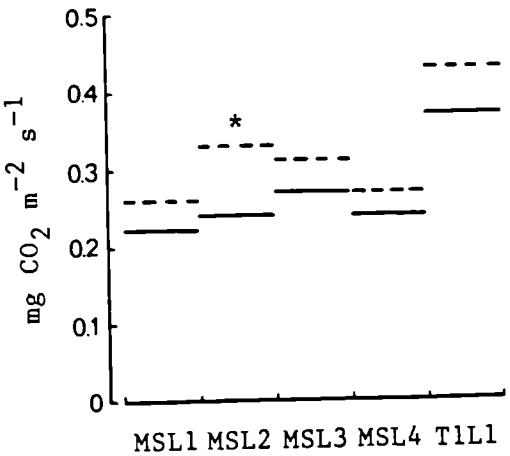

mg CO_2 m^{-2} s^{-1}
0.5
0.4
0.3
0.2
0.1
0
*
MSL1 MSL2 MSL3 MSL4 T1L1

Fig. 7.6

Effect of Terpal on:

a) maximum area attained by each leaf during development between GS 13 and GS 17

b) CO_2 evolution per unit leaf area at GS 17.

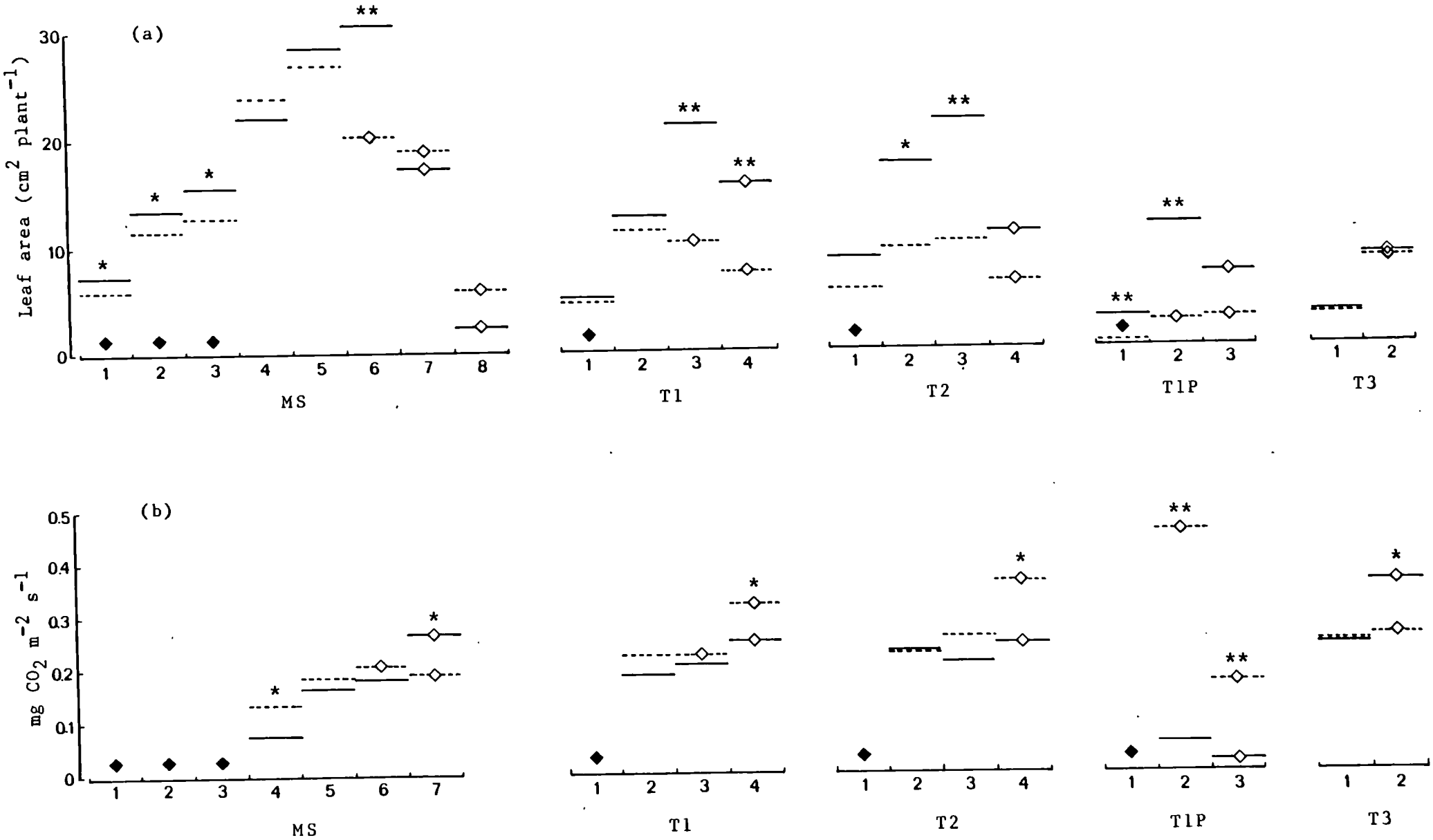
—— Control

---- Terpal treated plants

leaf number indicated on abscissa

◇ leaf not fully emerged

◆ leaf fully senesced at GS 17


(a)
Leaf area (cm^2 plant^{-1})
30
20
10
0
1 2 3 4 5 6 7 8
MS
1 2 3 4
T1
1 2 3 4
T2
1 2 3
T1P
1 2
T3
(b)
mg CO_2 m^{-2} s^{-1}
0.5
0.4
0.3
0.2
0.1
0
1 2 3 4 5 6 7
MS
1 2 3 4
T1
1 2 3 4
T2
1 2 3
T1P
1 2
T3

7.6b and 7.5c). Terpal increased the photosynthetic rate per unit area in every leaf at GS 14, this was only statistically significant for MS L2. At GS 17 Terpal also increased the net photosynthetic rate per unit area of most leaves (exceptions were MS L7, T2 L2 and T3 L2) although again this effect was not always statistically significant (Fig. 7.6b). At both GS 14 and 17 the increased photosynthetic rate was not sufficient to compensate for the reduced leaf area and overall the photosynthetic rate of the whole plant was reduced by Terpal (Fig. 7.7). The net rate of photosynthesis of the total plant was obtained by the addition of the rates of photosynthesis measured from individual leaves. The effect of Terpal was significant at all growth stages except GS 15. At GS 15 the rate of photosynthesis per plant was seen to decline, this was because of the onset of senescence and the emergence of several tillers too small to be monitored (Fig. 7.7).

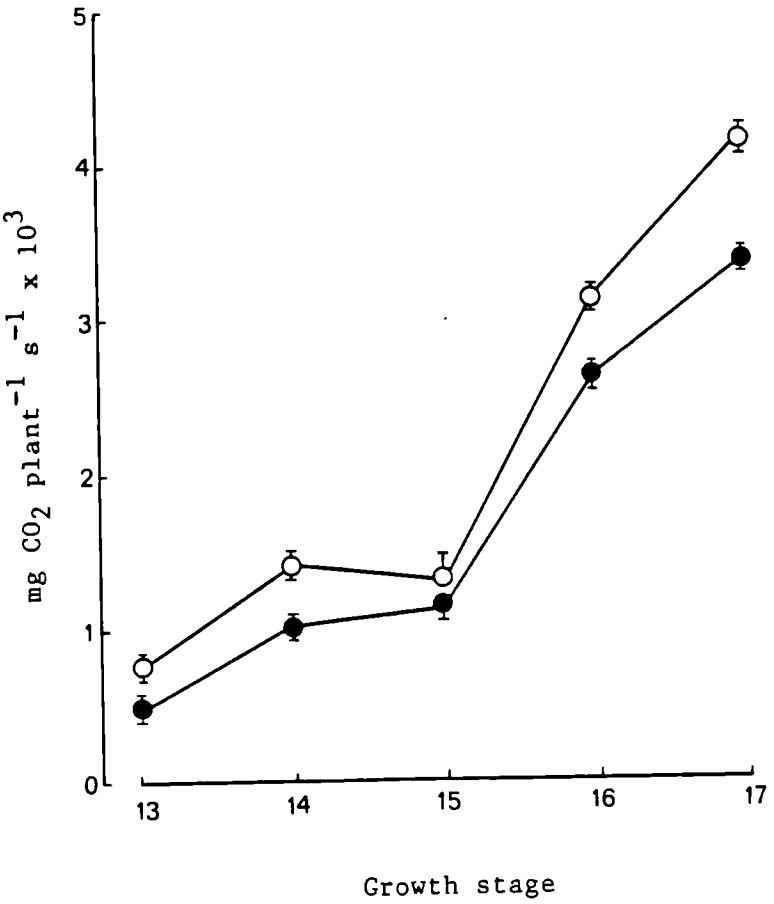
Fig. 7.7

Effect of Terpal on the net photosynthetic rate of all leaves added together between GS 13 and GS 17. Terpal applied 2 days prior to first measurement at GS 13.

○ Control

● Terpal treated plants

Vertical bars represent ±SE.


5
4
3
2
1
0
mg CO_2 $plant^{-1}$ s^{-1} x 10^3
13
14
15
16
17
Growth stage

DISCUSSION

It has been shown clearly that Terpal retards leaf extension of both the MS and tiller leaves when applied either to seeds (Chapter 5 and 6) or to leaves (present chapter). This response may be attributed to an inhibition of gibberellin activity via mepiquat chloride or to direct effects of ethylene, or to indirect effects of ethylene on endogenous gibberellin and auxin levels. There are numerous reports of high gibberellin-like activity in young leaves (Goodwin, 1978) and a correlation between leaf expansion and gibberellin levels has been shown (Humphries and Wheeler, 1963; Jurekova and Repka, 1973). In general it appears that leaf responses to gibberellin treatment are small although it has been reported to promote leaf extension (Gray, 1957; Goodwin, 1978) and alter leaf shape (Gray, 1957; Felippe and Dale, 1968). Substances with anti-gibberellin activity other than Terpal have been shown to retard leaf growth (Foreman, 1984). Ancymidol, a potent inhibitor of gibberellin biosynthesis (Coolbaugh and Hamilton, 1976), inhibits leaf expansion in cucumber (Cucumis sativus L.) and although this effect can be reversed by treatment with GA_3, GA_3 application to plants not treated with Ancymidol does not affect leaf area (Dicks and Abdel-Kawi, 1979). It has been suggested that growth retardants and gibberellins are only mutually antagonistic with respect to stem elongation and not to other aspects of growth (Sachs and Kofranek, 1963). Also Treharne et al. (1972) present data that indicates that the growth retardant, CCC, is not a specific inhibitor of GA_3 biosynthesis. Goodwin and Erwee (1983) conclude that endogenous gibberellins play only a modifying role in leaf growth.

Ethylene has been shown to be an effective inhibitor of leaf elongation (Goodwin, 1978; Van Andel and Verkerke, 1978). However, as ethylene can inhibit auxin synthesis and transport and promotes auxin metabolism

(Ernest and Valdovinos, 1971; Schneider and Wightman, 1978; Evans, 1984) part of the response to ethylene may be due to the inhibition of auxin activity. Although young expanding leaves are a major source of auxins (Humphries and Wheeler, 1963), auxins are thought to have only a small effect on leaf growth (Goodwin and Erwee, 1983). Thus far it does not seem possible to separate the effects of mepiquat chloride and ethephon on leaf growth.

The final length of the leaf depends on the number of cells produced by the basal meristems and the extent to which they enlarge. In the present study cell number was not significantly affected by the Terpal treatment, but since the effects of Terpal on leaf size were also small in this experiment it is not possible to come to any firm conclusion regarding the relative contributions of cell division and cell enlargement to final leaf size. There is evidence that GA_3 can promote cell expansion (Evans, 1984) indicating the possibility of GA_3 antagonism by Terpal in this respect. Ethylene, on the other hand, has been reported to inhibit plumular expansion by inhibiting cell division and DNA synthesis in pea (Apelbaum and Burg, 1972). Other growth retardants have been found to reduce leaf area via a reduction in both cell size and cell number, for example, Amo 1618, CCC and Phosphon in Chrysanthemum morifolium (Sachs and Kofranek, 1963) and Ancymidol in cucumber (Dicks and Abdel-Kawi, 1979).

In the present study Terpal significantly reduced the net photosynthetic rate of the whole plant which is thought to be directly related to the reduction in leaf area. Reductions in net CO_2 assimilation rate have been reported following applications of CCC to mustard (Sinapis alba) and it was suggested that this effect was either the result of mutual shading or the result of a reduced demand for assimilates because of stem shortening (Humphries, 1963). Applied

gibberellin on the other hand has been shown to increase the photosynthetic rate of wheat flag leaves by up to 17% (Gale et al., 1974). Pallaghy and Raschke (1972) reported no effect of ethylene on the photosynthetic rate or stomatal opening in Zea mays and this was supported by the experiments of Kays and Pallas (1980) where there were no effects of ethylene on the photosynthetic rate in Pisum sativum, Phaseolus vulgaris, or Zea mays but the photosynthetic rate was reduced in Arachis hypogaea and Helianthus annuus. There was some evidence that Terpal increased the photosynthetic rate per unit area, but since total dry weight was reduced it can be seen that this increase was insufficient to compensate for the diminished leaf size. Application of the growth retardant BTS44584 to soybeans (Glycine max) also increased net photosynthetic rate per unit area and this led to increased yields (Hewitt et al., 1982).

It is clear from the results in this chapter that the promotory effects of Terpal on the growth and development of secondary and tertiary tillers are at the expense of other plant organs. It has been shown that the size of all leaves (present chapter) and of the root system (Chapter 4, 5 and 6) are considerably diminished by Terpal treatment. It appears, therefore, that Terpal changes the direction of internal competition in favour of tiller buds. However, although tiller bud outgrowth and development are consistently promoted by Terpal treatment the coincident retardation of the leaves, MS stem and roots frequently results in the diminished growth of the plant as a whole.

GENERAL DISCUSSION

This investigation has attempted to provide an integrated study of the factors controlling tiller bud outgrowth, tiller development and survival; particular reference has been made to the relationship between tillering and events in the ontogeny of the MS. It was found that not all buds emerged as tillers, a proportion remained dormant and this varied between experiments and could be modified by nutrient and PGR treatments. There was a distinct hierarchical pattern of tiller development with respect to height, dry weight and ear size and this was dependent on the time of tiller appearance. Nutrient and PGR treatments diminished this pattern by causing the more rapid outgrowth and development of tillers leading to a more equal tiller and ear size. The commencement of tiller bud suppression and tiller death coincided with the onset of the reproductive phase of MS growth; the final stages of MS stem elongation are considered particularly relevant in this respect. The smallest and usually latest appearing tillers died first and such tillers have been considered wasteful of the plant's resources (Rawson and Donald, 1969; Gallagher and Biscoe, 1978) but there was no evidence that this was so in the present study. The proportion of tillers that survived to produce ears varied between 47 and 91% (Chapter 2, 4 and 5), and there appeared to be no relation between the number of dying tillers and total plant ear weight.

It has been proposed that the difference in size between the MS, tillers and roots is caused by competition between them for assimilate or other resources (Chapter 3). The MS is considered to be a strong sink with a high demand and so may suppress the growth of other organs which are weaker sinks. It is not clear how the sink potential and therefore the dominance of the MS is achieved (Chapter 1). Resource competition, which is manifested in the partitioning of dry matter, can be manipulated, for example, by defoliation (Richards, 1983), by nitrogen fertilization (Aspinall, 1961; Chapter 4), or by PGR

application (Koranteng and Matthews, 1982; Chapter 4). Modern cereal varieties have higher yields because of a greater harvest index rather than a greater production of total dry matter (Thorne, 1971; Wareing, 1978; Austin et al., 1980a; Islam and Sedgley, 1981). It is considered that reduced competition from non-productive organs has resulted in the formation of larger ears (Kirby, 1973a; Rogan and Smith, 1975). Perhaps the selection of the uniculm plant is the most direct way of incorporating the most dry matter into the yield bearing fraction, but so far there is no evidence to support this (Chapter 6).

Of the PGRs applied, early applications of Terpal had the most pronounced effect on tillering, greatly promoting the emergence, growth, development and survival of secondary and tertiary tillers; similar effects were apparent even in the uniculm wheat selection where the emergence of up to 3 tillers was stimulated (Chapter 6). However, these effects rarely resulted in an increased dry matter yield as the growth of the MS, leaves, roots and individual ears was retarded, indeed total plant dry weight was often reduced (Chapter 4, 5, 6 and 7). The harvest index of the Terpal treated plants was little affected since although the number of ear-bearing shoots was increased mean ear weight was reduced.

The responses to Terpal application, with respect to tillering, were consistent in all experiments except those conducted under field conditions (Chapter 2). In the first field experiment, Experiment 2.1, Terpal had a very small effect, with no modification of tiller number, whereas tillering was greatly enhanced in the second field experiment in the following year, Experiment 2.2, as in all other experiments with Terpal. Such variability, particularly between years and sites, is frequently encountered in the field (Gales, 1983) since climatic and soil conditions are difficult if not impossible to control. Other possible causes of these inconsistent responses to Terpal application

in the field have already been discussed (Chapter 2). Another inconsistent finding of the field studies was that as well as increasing tillering in Experiment 2.2, Terpal also significantly increased total plant dry weight whereas in all other experiments it was either reduced or not affected. Although grain yield was not significantly increased, it is possible that Terpal may potentially increase yield under certain conditions, for example, conditions of high nutrition or low plant density.

To obtain yield improvements by manipulating dry matter distribution by using PGRs requires an understanding of the processes controlling the partition of assimilates and the modes of action of the PGRs concerned. However, it seems that the mechanisms involved are extremely complex and that there are many problems associated with the investigation of this subject. Each type of growth substance has a wide range of physiological effects and these may vary in different species or even genotypes, in different parts of the same plant or at different growth stages. An individual response may be mediated by more than one type of growth substance (Leopold and Nooden, 1984), for example, internode extension is regulated by both auxin and gibberellins. Furthermore, where interactions of growth substances are involved the precise ratio or balance of these may be vital, for example, the ratio between auxin and cytokinins is thought to be involved in bud inhibition/outgrowth. Such a hormonal balance may be influenced by environmental factors, for example, irradiance or nutrient status (Blake et al., 1983). Applications of PGRs to this complex system will undoubtedly result in a wide spectrum of growth responses (Wareing, 1976). Furthermore, reports of PGR action in the literature are often inconsistent and this may be because of the large number of species studied, the difference in concentrations and times of application used or because of differences in the amount of uptake.

From the findings of the present study it is not possible to firmly identify the growth substance that is central to the tillering response evoked by Terpal application, although speculations about its mode of action have been made. There are several hypotheses; one is that the promoted tillering is a secondary effect of Terpal, following stem shortening, due to changes in the distribution and partitioning of assimilates within the plant. A second is that Terpal is thought to block the action of endogenous gibberellins (Jensen and Andersen, 1981) which may diminish apical dominance and enhance lateral bud outgrowth. However, there is some evidence that growth retardants with supposed anti-gibberellin action are not specific inhibitors of gibberellin biosynthesis or may only antagonize the effects of gibberellin on stem elongation (Halevy, 1963; Sachs and Kofranek, 1963; Treharne et al., 1972). Indeed it has been reported that CCC may even increase levels of endogenous gibberellins in some species (Reid and Crozier, 1970; Wareing, 1976; Smith et al., 1982).

GA_3 and ABA arise from the same pathway and share mevalonic acid as a common precursor (Dicks, 1976; Norman et al., 1983) and so it is pertinent to know whether or not growth retardants with supposed anti-gibberellin action also affect ABA levels. Levels of endogenous ABA have been found to increase on application of growth retardants, a likely explanation is that the blocking of the GA_3 biosynthetic pathway leads to enhancement of the ABA biosynthetic pathway (Luckwill, 1981). However, in the fungus, Cercospora rosicolor, Norman et al. (1983) found that several growth retardants including CCC, Ancymidol, AMO 1618 and mepiquat chloride inhibited ABA biosynthesis. These findings may help to explain some of the diverse responses described following the application of growth retardants and also confirms the need for further studies on the mode of action of such compounds. Applications of ABA to

the lateral buds of tomato strongly inhibited their outgrowth (Tucker, 1977a) and also studies using oat stem segments have indicated that ABA may be involved in inhibiting tiller bud release and elongation (Harrison and Kaufman, 1980). Therefore simple GA_3 suppression alone cannot explain all of the growth responses observed.

On the other hand, the effects of Terpal could arise from the ethephon component. However, responses to ethephon application should be viewed with some caution since it yields not only ethylene but phosphate and chloride (Zeroni and Hall, 1980) which may also influence growth. Applications of ethylene (both via ethephon and as ethylene gas) have produced conflicting results with respect to lateral bud outgrowth (Chapter 3). Such variability may be related to differences in the relative levels of auxin and ethylene since it is well known that auxin increases ethylene concentrations (Abeles, 1973; Evans, 1984) whereas ethylene reduces auxin transport and synthesis (Burg and Burg, 1966; Morgan and Gausman, 1966; Beyer and Morgan, 1970). It has been suggested that it is auxin-induced ethylene production that inhibits lateral bud outgrowth in dicotyledons (Blake et al., 1983). Also the same authors demonstrated that 1-aminocyclopropane-1-carboxylic acid (ACC) may be the agent involved in lateral bud inhibition since application of ACC to decapitated pea plants inhibited bud outgrowth. However, the role of ACC as an ethylene precursor has recently been confirmed (Lürssen and Konze, 1985). It is speculated that in cases where ethylene application promotes bud outgrowth, as in the present study (Chapter 3), the effect of ethylene may be a secondary one via a reduction of inhibitory auxin levels. This conclusion is supported by the response to TIBA (anti-auxin) application (Chapter 3, 4 and 6), although the stimulation of tiller bud outgrowth was not as great as that produced by Terpal application when MS size was also retarded. It is also known that auxin maintains high levels of ABA (Tucker, 1978)

and furthermore that GA_3 is involved in the regulation of auxin (Evans, 1984). It appears, therefore, that Terpal may interfere with the balance of all these endogenous growth substances in such a way as to favour tillering.

The range of PGRs is increasing and they have a wide spectrum of uses in world agriculture but at present most of these are small and specialist. The growth retardants, particularly for use on cereals, for example, CCC, are the exception. The use of growth retardants to control lodging is well established, but benefits may also be gained from using these same PGRs on sites where lodging is not a problem or on varieties that are not susceptible to lodging as in the current investigation. Favourable modifications to crop development may be achieved if the PGRs are applied early, for example, to the seed on germination (Chapter 5). Seed application of chemicals provides a relatively inexpensive and easy technique of application which may be especially useful in arid regions as it economises on water use. There are many targets for growth retardant action other than the promotion of tillering or increase in the synchrony of tillering or increased tiller survival as described in the present thesis; examples of these include increasing leaf area duration, prevention of spikelet abortion and rooting of later produced tillers. There is therefore much scope for research into the influence of PGRs on various plant parts. How PGRs, such as CCC and Terpal, interact with N fertilizer has been the subject of certain trials for several years (Herbert, 1983) and knowledge of this subject is essential if the grower is to obtain optimum performance from growth retardants.

In some respects however, the genetic approach to improvement of crop characteristics may be superior to the use of PGRs (Austin et al., 1980b; Lürssen, 1981). The selection of genotypes with sychronous

tiller ear emergence (Paroda, 1971; Stoskopf and Fairey, 1975) or of genotypes with tillers that root freely at their basal nodes thus allowing a more direct supply of nutrients to tillers and thereby possibly improving their survival and productivity (Anderson-Taylor and Marshall, 1983) are examples of potential selection criteria for realising greater tiller productivity. Nevertheless the possibility remains that such manipulations may in the future be gained via applications of PGRs.

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APPENDIX

Rainfall and temperature data obtained from UCNW farm weather station in 1983 indicating "good" rainfall and no unusual extremes of temperature during the growing season. (Sowing date: 18/4/83, harvest date: 10/8/83).

a) Rainfall

b) Temperature at 10 (-----) and 30 cm (——) above ground level.