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The Effects of Established Trees on Woody Regeneration during Secondary Succession in Tropical Dry Forests

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ABSTRACT

Understanding the mechanisms controlling secondary succession in tropical dry forests is important for the conservation and restoration of this highly threatened biome. Canopy-forming trees in tropical forests strongly influence later stages of succession through their effect on woody plant regeneration. In dry forests, this may be complex given the seasonal interplay of water and light limitations. We reviewed observational and experimental studies to assess (1) the relative importance of positive and negative effects of established trees on regeneration, (2) the mechanisms underlying these effects, and (3) to test the "stress gradient hypothesis" in successional tropical dry forests. The effects of established trees on seed dispersal, seed survival and seed germination—either through direct changes to moisture and temperature regimes or mediated by seed dispersers and predators—are mainly positive. The balance between positive and negative effects on seedling establishment is more complex and depends on the season and leaf phenology of both trees and seedlings. Seedling survival is generally enhanced by established trees mitigating dry conditions. Established trees have counteracting effects on water and light availability that influence seedling growth. The probability of a positive effect of established trees on seedling survival decreases with increased rainfall, which supports the stress gradient hypothesis. Priorities for future research are experiments to test for facilitation and competition and their underlying mechanisms, long-term studies evaluating how these effects change with ontogeny, and studies focussing on the species-specificity of interactions.

Key words: competition; facilitation; germination; seed dispersal; seedling establishment; shade effects; stress gradient hypothesis; water limitation.

PLANT-PLANT INTERACTIONS ARE IMPORTANT FOR STRUCTURING PLANT POPULATIONS AND COMMUNITIES (Bertness & Callaway 1994) and can influence ecological processes and patterns up to the landscape scale (Bruno *et al.* 2003). These interactions are influenced by the direct or indirect ways that one plant makes the abiotic and biotic environment more favourable (*i.e.*, facilitation) or unfavourable (*i.e.*, competition) for another (Callaway 2007, Brooker *et al.* 2008). Following major disturbance the interactions between the first established plants and subsequent ones are critical for understanding of succession (Connell & Slatyer 1977, Brooker *et al.* 2008), but succession is a complex process also involving other factors that act across scales, such as land use and disturbance history, seed dispersal limitation, soil properties, plant-animal interactions (Chazdon 2003, Hobbs *et al.* 2007, Holl 2012), and stochastic events (Young *et al.* 2005).

Tropical dry forests (TDF) have undergone widespread conversion to agriculture (Sanchez-Azofeifa & Portillo-Quintero 2011) and are one of the Earth's most threatened ecosystems (Janzen 1988, Miles *et al.* 2006). However, they have been far less studied than tropical moist and temperate forests (Quesada *et al.* 2009). Many TDF have regrown after the abandonment of agriculture and are undergoing secondary succession driven by remnant organisms or their propagules (Chazdon 2003). A better understanding of the ecology of TDF secondary succession is needed to inform the design of science-based restoration practices (Vieira & Scariot 2006b), as well as to test ecological theories and models.

The stress gradient hypothesis predicts that facilitation is more important when environmental conditions are particularly harsh (Bertness & Callaway 1994, Callaway 1995, Callaway & Walker 1997). Tropical dry forests are highly seasonal environments, meaning they are also seasonally stressful ones. During the rainy season water is rarely limiting and instead light becomes the main factor limiting regeneration. Moreover, micro-climatic conditions change during early secondary succession in TDF because of the rapid increase in stem density, cover and above-ground biomass (Kennard 2002, Lebrija-Trejos *et al.* 2010, Maza-Villalobos *et al.* 2011, Becknell *et al.* 2012). Shade of established trees can increase soil moisture by reducing air and soil temperature and increasing relative humidity (Lebrija-Trejos *et al.* 2011), which lowers transpiration from tree seedlings and other sub-canopy plants. Litter from established trees also reduces evaporation from the soil surface, and its decomposition enhances soil organic matter that increases water retention in the soil (Sayer 2006, Xiong *et al.* 2008). However, these effects are strongly counteracted by the transpiration of canopy trees, which acts as the major sink for soil moisture in forests (Lebrija-Trejos *et al.* 2011). In contrast, if the roots of canopy trees take up water from deeper in the soil (hydraulic lift), this can increase water availability to shallower-rooted seedlings (Callaway 2007). The balance between positive and negative interactions in successional TDF is therefore complex and dependant on the life stage of the individuals involved, their physiology, indirect interactions via other organisms, and the intensity of abiotic constraints (Callaway & Walker 1997).

Our objective is to understand the mechanisms by which the first generation of trees regenerating in successional TDF (referred to hereafter as "established trees") influences the regeneration of woody plants from the local species pool, and therefore secondary succession. We focus on the early and critical stages of the process of regeneration (*sensu* Grubb 1977)—seed dispersal, survival of seeds, germination and seedling establishment (Poorter 2007) to answer the following questions. (1) What is the relative importance of positive and negative effects of established trees on woody plant regeneration? We expect that overall the effects of established trees are positive, *i.e.*, they ameliorate the stressful environmental conditions in TDF. We also expect that the effects of established trees vary across the stages of regeneration because of the changing requirements of young plants. (2) What are the mechanisms by which established trees influence regeneration? We expect that the primary direct mechanism by which established trees influence regeneration is by providing cover that mitigates harsh micro-climatic conditions. However, we predict that this positive effect is less important for seedling growth because growth occurs mainly during the wet season when availability of water is generally not limited (Rincón & Huante 1993). We also expect indirect effects of established trees mediated by animals, especially for the seed dispersal stage. (3) Finally, do previously published studies of regeneration in TDF support the stress gradient hypothesis? We expected the positive effect of established trees to be more important in sites with a low mean annual rainfall (MAR) where water availability is more limited.

METHODS

SELECTION OF STUDIES FOR REVIEW.—In April 2012, we searched the *Web of Science* and *Science Direct* databases using the following combination of keywords (succession* OR secondary) AND tropical AND dry AND forest* AND (competition OR facilitation OR nurse* OR restoration). We supplemented this search with a small number of additional studies found via the references cited in the included studies. The search was updated regularly until June 2015 using the same search strategy.

SELECTION CRITERIA.—We selected for inclusion in our review all studies meeting the following two criteria. First, studies had to be conducted in TDF, defined as forests with a mean annual rainfall (MAR) of 500-2000 mm and mean annual temperature (MAT) >17 °C (Holdridge 1967, Becknell *et al.* 2012) with at least three months of severe drought (rainfall <100 mm) (Sanchez-Azofeifa *et al.* 2005). This includes forests with varying degrees of deciduousness (Vieira &

Scariot 2006b). Second, studies had to focus on forests undergoing secondary succession. We excluded from our review studies of succession on sites where the disturbance was such that soil was initially lacking (*e.g.*, due to mining or volcanic eruption), because processes occurring during primary succession differ from those occurring during secondary succession (Chazdon 2003). Moreover, secondary succession is far more common than primary succession in the TDF biome because of the attractiveness of TDF for human activities and particularly agriculture (Aronson *et al.* 2005). Alternatively, studies were selected for inclusion that tested the effect of established trees by comparing them with open areas or by comparing different types of tree cover, or manipulated environmental conditions (*e.g.*, by shading or additional watering) in a natural or controlled environment (*e.g.*, shadehouse).

DATA COLLECTION.—We sorted the selected studies by the regeneration stage they investigated: seed dispersal, seed survival, seed germination and seedling establishment. We use the term seed to refer to the dispersal unit, sometimes called a propagule or dispersule, because for the majority of species considered the unit is a seed. However, in some species the unit also included part or all of the fruit. In addition, while the seedling establishment phase starts with seed germination, definitions of the end of this phase are often quite arbitrary (Grubb 1977). Some definitions, mainly for forest vegetation surveys, propose a maximum seedling size, generally 1 or 1.3 m (Newton 2007). However, the time needed to reach this size can vary greatly depending on the species and environmental conditions, which is why most studies of seedling establishment are carried out for a fixed time period after germination. For the studies we reviewed that reported this time period the average was 20 months (range: 2-50 months). We therefore consider the seedling establishment phase as approximately the first two years of the life of a tree, recognizing it can extend up to four years. Throughout the text we report seedling survival and growth for the duration of the seedling establishment phase considered by the original studies.

To evaluate the relative importance of positive and negative effects of established trees on each woody plant regeneration stage, we searched the selected studies for results comparing each regeneration stage at (1) different stages of succession or (2) between areas with established trees and open areas. These comparisons summarize the net outcome of positive and negative effects of established trees on subsequently establishing ones; for this reason, we favour the use of the terms “net positive effects” or “net negative effects” rather than facilitation or competition.

To understand which mechanisms underlie the effect of established trees on woody plant regeneration we used studies testing the correlation between the outcome of the regeneration stage under consideration and the environmental factors being manipulated or compared. For example, to test the effect of shade provided by established trees on seedling growth, we used studies testing for correlations between seedling growth and the amount of shade. When we found no such studies, we searched the discussion of the selected studies for possible hypotheses regarding the mechanisms.

Finally, data on MAR reported in studies was used to test if the net effect of established trees depends on MAR.

DATA ANALYSIS.—Although we initially hoped to conduct a meta-analysis of effect sizes for each of the research questions (Koricheva & Gurevitch 2014), we were unable to because of the low number of studies for some questions, the heterogeneous measures of plant responses and treatments applied, and because few of the studies reported any measure of variance in their results. To test the stress gradient hypothesis in the context of regeneration in TDF secondary succession, we analysed the net outcome of the effect of established trees on seedlings with logistic regressions (binomial generalized linear models with logit link function), using both survival and growth as dependent variables. To test for net positive effects, we scored as '1' studies that show a net positive effect and '0' studies that show a non-significant or negative effect. In contrast, to test for net negative effects, we scored '1' for studies that show a net negative effect and '0' those that report a non-significant or positive effect. We then used these values to fit four models (for net positive and negative effects, and for survival and growth) against the MAR using the R statistical programming language (R core team 2013). The low number of studies found for the other stages of regeneration did not allow such analysis.

RESULTS

SELECTED STUDIES.—The first search yielded 206 studies, of which 29 met our criteria (Table 1). The numbers of studies for each methodological approach were quite similar (Table 1). For the studies of forests that were undergoing secondary succession, the previous land-use was generally agriculture (cultivation or pasture) and the timing varied from immediately after abandonment to several decades later (Table 2). Of studies meeting our criteria, 20 were carried out in the Neotropics (69% of all included studies), mainly in Mexico, Brazil and Costa Rica. Four studies were carried out in Asia (14%), three in the Pacific (Hawaii, 10%), and two in Africa (Ethiopia, 7%).

EVIDENCE OF POSITIVE AND NEGATIVE INTERACTIONS AND THE UNDERLYING MECHANISMS.—The numbers of studies on seed dispersal, seed survival and seed germination were very low (five, three and four, respectively). There were 21 studies on the seedling establishment stage (Table 1). Ten studies reported the overall net outcome of established trees on seedlings (Table 3). Eight experimental studies artificially controlled light and water availability (Table 4). A summary of the positive and negative effects of established trees on regeneration and the mechanisms influencing each stage of regeneration is presented in Fig. 1.

STRESS GRADIENT HYPOTHESIS.—Due to low number of studies, we were only able to test the stress gradient hypothesis with studies of seedling establishment. We found that the probability of a net positive effect of established trees on survival of seedlings decreased with increasing rainfall (χ^2 test $P = 0.008$, $R^2 = 0.43$), whereas the probability of a net negative effect increases with rainfall ($P = 0.009$, $R^2 = 0.56$) (Fig. 2). In contrast, there was no evidence of a correlation between net positive effect ($P = 0.853$) or net negative effect ($P = 0.862$) on seedling growth and MAR.

DISCUSSION

EFFECTS OF ESTABLISHED TREES ON SEED DISPERSAL.— Areas with established trees have been shown to have enhanced seed rain when compared with open areas (Callaway 2007), and the results of studies conducted in TDF are consistent with this observation. However, we also found that this is highly dependent on the seed dispersal agent. For zoochorous seeds this effect is mediated by animal dispersers, mainly birds and bats, which are attracted by established trees that can provide perches or food (Vieira & Scariot 2006b) (Fig. 1). Studies of seedlings often show a high percentage of zoochorous species under tree canopies (Wydhayagarn *et al.* 2009), and chronosequence studies show an increase in the proportion of zoochorous species during secondary succession (Opler *et al.* 1980). Ferguson *et al.* (2003) also observed that the recruitment of fleshy-fruited individuals was higher when trees were present in the previous land-use (agroforestry and swidden cultivation), and that it was positively correlated with the basal area of trees present at the start of succession. Features of trees responsible for attraction of dispersers are not well understood, however. It is probable that animal dispersers are attracted to particular tree species because of their flowers and fruits, branching structures, or sizes (Wydhayagarn *et al.* 2009). Zelikova and Breed (2008) also suggested that established trees can affect the dispersal of seeds by ants; they found that seeds of two fleshy-fruited species were removed less often (~20% vs. ~65%) in successional forests compared with open sites, but that they were dispersed longer distances (1.1 m vs. 0.5 m). However, more studies are needed to see if this is generally true.

In contrast, we found that the input rate of seeds of anemochorous woody plant species was mainly influenced by the distance to the source of seeds (Teegalapalli *et al.* 2010). Because they create turbulence in the laminar flow of wind, it has been argued that the crowns of trees can act as a seed trap for anemochorous species in many systems (Callaway 2007). To the best of our knowledge, however, this possibility has not been studied in successional TDF.

EFFECTS OF ESTABLISHED TREES ON POST-DISPERSAL SURVIVAL OF SEEDS.—Vieira and Scariot (2006a) found that seed desiccation appears to be more important in open areas than under tree canopies. This suggests a positive effect of tree canopy cover on seed survival via mitigation of conditions that desiccate seeds. However, species differ in the susceptibility of their seeds to desiccation under the dry conditions of early-successional environments; Vieira and Scariot (2006a) showed that species with thin seed coats and high water-content had a higher sensitivity to desiccation in open pasture than did other species.

The changes in seed predation and removal by animals in different successional stages are more complex (Fig. 1). Hammond (1995) found that seeds in old successional (> 30 yr) and mature forest were less prone to predation, which he attributed to the thickness of the litter layer that protects seeds from rodents and other predators. However, Wassie *et al.* (2010) found some evidence of higher rates of seed predation by rodents under a closed canopy (~93%) than gaps (~87%), which they attributed to gap-avoidance by rodents. Vieira and Scariot (2006a) showed that differences in the patterns of seed predation during secondary succession depended on the type of seed. They attributed this to variation in the activity of different seed predators ranging from insects to large mammals in forests at different successional stages. More studies, especially if they measure micro-scale climatic conditions, are needed to disentangle these complex effects of established trees on seed desiccation and predation that depend on the interaction of type of seed, type of consumer and successional stage.

EFFECTS OF ESTABLISHED TREES ON SEED GERMINATION.—Through the measurement of seed germination relative to natural seed rain, Hardwick *et al.* (1997) showed a higher germination rate under forest cover than under the cover of herbs and shrubs in post-agricultural successional vegetation in Thailand. For one species they documented 96 percent of germination in forest vs. 1 percent at the edge of a clearing and 54 percent at the centre of a clearing; for another species germination in these habitats was 11, 8, and 7 percent (respectively). The values for the first species suggest that canopy cover might have a positive effect on seed germination (Fig. 1), which is consistent with the results of two of three studies carried out in controlled environments (Hardwick *et al.* 1997, McLaren & McDonald 2003a, but see Ray & Brown 1995). Supplementary watering also had a positive effect on germination in the experiment of McLaren and McDonald (2003a), but the results of Hardwick *et al.* (1997) were species-specific. Both studies also found an interaction of shading and watering treatments, at least for some of the tested species. McLaren and McDonald (2003a) observed that watering increased germination rate only for the unshaded treatments, which suggests that supplementary water is needed only under the desiccating environment of full sunlight. Moisture conditions therefore seem to be important in explaining the positive effect of established trees on seed germination of TDF species. However, more field studies are required to substantiate these effects, especially those monitoring seasonal variation in soil moisture under different forms of vegetation cover.

The response of seed germination to established trees is likely to differ between species. Of the three species that they tested, Hardwick *et al.* (1997) found that germination was most strongly promoted by shade or by additional watering in the largest-seeded species. Shading also promoted germination of the two smaller-seeded species, but additional watering benefited germination only for one of the two. Tests of a greater number of species are needed to establish relationships with seed traits such as seed moisture content, seed size and presence of a hard coat.

EFFECTS OF ESTABLISHED TREES ON SEEDLING ESTABLISHMENT.—A majority of studies reported a positive net effect of established trees on seedling survival for at least some of the seedling species studied (Teketay 1997, Hoffmann 2000, Cabin *et al.* 2002a, McLaren & McDonald 2003b, Vieira *et al.* 2006, Santiago-Garcia *et al.* 2008, Wolfe & Van Bloem 2012). However, some studies did report a net negative effect (Marod *et al.* 2004, González-Rivas *et al.* 2009, Castro-Marin *et al.* 2011). In contrast, for seedling growth the majority of studies reported a negative effect of established trees (but see Hoffmann 2000, Santiago-Garcia *et al.* 2008).

Established trees appear to influence seedling mortality by changing water availability (Fig. 1). Six experimental studies reported a positive effect of shading on TDF seedling survival (Ray & Brown 1995, Cabin *et al.* 2002b, McLaren & McDonald 2003a, Vieira *et al.* 2008, Badano *et al.* 2011, Thaxton *et al.* 2012), which Cabin *et al.* (2002b) attributed to mitigation of desiccating conditions. Moreover, the three studies that experimentally altered water availability all showed a positive impact of additional watering on seedling survival (McLaren & McDonald 2003a, Marod *et al.* 2004, Thaxton *et al.* 2012). Water shortage was put forward as the main cause of mortality during the TDF dry season (Lieberman & Li 1992, Gerhardt 1996, Cabin *et al.* 2002a, Marod *et al.* 2002, Vieira & Scariot 2006b). However, the effect of established trees on seedling survival mediated via water balance is relatively small in early stages of succession, when the canopy cover is still predominantly open (Hammond 1995). Regarding seedling growth, the effect of water availability differs amongst studies (Table 4). This effect may depend on the soil type, in particular its texture and plant-available water capacity (Marod *et al.* 2004, McLaren & McDonald 2003a). An experiment in which root competition was eliminated with trenches showed a negative effect of established trees below-ground, both on survival and growth of seedlings (Gerhardt 1996). Changes in water availability can affect seedling resource allocation (Blain & Kellman 1991), which can subsequently affect rates of water uptake (through allocation to root growth) and photosynthesis (through shoot allocation) and therefore modify the drought tolerance and growth of seedlings.

Reduction of light availability by established trees can have a negative effect on seedling growth (Rincón & Huante 1993, McLaren & McDonald 2003a; Fig. 1). However, Badano *et al.* (2011) found that shading improved the physiological performance of seedlings, associated with reduction in leaf temperature. Moreover, shade can have a different effect on the growth of different parts of the plant: McLaren and McDonald (2003a) found that heavy shading enhanced growth in height while reducing growth in diameter and Rincón and Huante (1993) found that shading induced a higher allocation of biomass to leaves. These results suggest that shade causes an allocation of resources towards growth that can increase photosynthesis in the sub-canopy environment.

Our review suggests that the positive effect of established trees on seedling survival is predominantly mediated by moisture regime during the dry season and that the negative effect of trees on seedling growth is via limitation of light during the wet season (Cabin *et al.* 2002a, McLaren & McDonald 2003b, Vieira & Scariot 2006b, Wolfe & Van Bloem 2012). However, these effects are not independent, and physiological response of seedlings to one environmental condition may alter the effect of another. Rincón and Huante (1993) found that a higher light level induced a higher allocation of biomass to roots, which could enable a higher rate of water uptake and thus a reduction in mortality rate during the subsequent dry season.

The capacity of established trees to cast shade during the dry season depends on their leaf phenology (evergreen or deciduous). Because deciduous trees cast little shade during the dry season, the local openness of the canopy, and hence microclimatic stress, increases with the proportion of deciduous trees. We hypothesize that the established trees in these forests would have too little or no positive effect on seedlings during the dry season to counterbalance a negative effect during the wet season (Vieira *et al*. 2006). Of the four field studies carried out in deciduous forests, three showed an overall negative effect of established trees on seedling survival (Table 3). Moreover, experimental manipulation of above-ground effects by thinning trees (Gerhardt 1996) showed that in deciduous forest the dominant above-ground effect is negative. In contrast, in semi-evergreen forest that retains some foliage during the dry season the net above-ground effect varied amongst the regenerating species. Leaf phenology of seedlings is likely to explain their species-specific response to the effect of established trees; deciduous species, for which growth is limited to the wet season, may be more sensitive than evergreen species to the negative effect of shading during this season (Ray & Brown 1995). In contrast, evergreen and semi-deciduous species may be more sensitive to water loss by transpiration during the dry season than deciduous species, as supported by Marod *et al.* (2004).

While research in TDF mainly focuses on effects mediated by light and moisture, there is also the potential for established trees to influence seedlings via competition for soil nutrients (Casper & Jackson 1997, Coomes & Grubb 2000) or increased nutrient availability to seedlings from litter decomposition (Callaway 2007, Berg & McClaugherty 2008, Cornwell *et al.* 2008; Fig. 1). Established trees could also have indirect effects on seedlings via insect herbivores (Fig. 1). Using a factorial experimental design that controlled above- and below-ground interactions, Gerhardt (1998) found that the effects on seedlings of both were positive. She attributed the below-ground effect to root competition, which could decrease the nutritional value of seedling leaves and therefore their palatability and susceptibility to herbivory. She attributed the above-ground effect to reduced light levels impeding insect activity (see also Badano *et al.* 2011). Nevertheless, the effects of herbivory on seedlings under canopy shade may be greater than in higher light levels; the consequences of reduced photosynthetic activity from lost leaf area are greater when photosynthesis is already limited at low light levels (Gerhardt 1998).

STRESS GRADIENT HYPOTHESIS.—We found that there is evidence in support of the stress gradient hypothesis for seedling survival but not for seedling growth. For survival, the switching point from a higher probability of positive to negative effects of established trees with increasing MAR appears to occur at around 1400 mm (Fig. 2). This MAR threshold is similar to that found by McDonald *et al.* (2010) for a shift in TDF to dominance by sexual instead of vegetative reproduction.

METHODOLOGICAL LIMITATIONS AND PRIORITIES FOR FUTURE RESEARCH.—The studies reviewed used a wide range of approaches. However, this diversity of methodological approaches can make it difficult to draw generalizations across studies. This issue, together with the low number of studies and the rarity with which they reported any measure of the variance of their results, prevents the use of meta-analytical techniques (Koricheva & Gurevitch 2014). Nevertheless, our review does elucidate trends, identify gaps in current knowledge, and suggest future research directions. We identified five components of the interactions between established trees and subsequent regeneration during secondary succession that we suggest are the main priorities for future research. (1) There is a need for more studies of root interactions and other below-ground processes—either direct or mediated by mycorrhizal symbionts—and their impact on seedlings' capacity to acquire water and nutrients (Coomes & Grubb 2000). (2) More research should focus on indirect interactions mediated by biotic agents such as seed dispersers/predators, herbivorous insects, symbionts or shared competitors, especially for the seedling establishment phase (Callaway 2007). (3) Factorial experiments in the field as well as controlled environments are needed to distinguish between the effect of shading on photosynthesis through modification of irradiance and the effect on desiccation through modification of temperature and moisture of air and soil. (4) There is a need for long-term studies in a broader diversity of sites—most of the studies reviewed were conducted in the Neotropics—on how the interactions between established trees and seedlings change as the latter develop into saplings and adults (Gomez-Aparicio *et al.* 2004, Young *et al.* 2005, Callaway 2007). (5) Research on plant functional traits may help understanding of the species-specificity of the reviewed interactions. A focus on leaf phenological traits in both established trees and seedlings is particularly needed since leaf phenology influences above-ground microclimate and soil conditions through its effect on timing of water uptake and litter input (Hasselquist *et al.* 2010). Seed traits, especially seed size, moisture and nutrient content, and presence of a hard coat, as well as traits related to the acquisition and use of resources, *e.g.*, allocation of biomass, dry matter content, and shoot and root architecture, should also be considered. Using a functional trait approach would be especially interesting to determine if there is a trade-off in drought and shade tolerance of seedlings amongst species, or if there is a dichotomy between resource conservative strategies (of species able to tolerate low availability of both light and water) and resource acquisitive strategies (for species that show higher growth rate but require greater availability of both light and water resources) (Wright *et al.* 2004). While some of the reviewed studies that compared evergreen and deciduous species in TDF support the trade-off hypothesis (Ray & Brown 1995, Marod *et al.* 2004), they studied too few species to allow extrapolation of this finding.

In seasonal TDF, direct or indirect interactions between established trees and woody plants regenerating below their canopy are important at every stage of the regeneration process. The positive effects of established trees at early stages of regeneration support the importance of facilitation during secondary succession. However, during subsequent stages of regeneration as seedlings establish and grow, the effects become more complex and dependent on seasonality of rainfall and on species. Nevertheless, the effect of established trees on seedling survival shifts from positive to negative when MAR increases, in accord with the stress gradient hypothesis. Overall, the effect of established trees on regeneration during secondary succession in TDF remains poorly understood and a fruitful area for further research.

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TABLE 1. *Selected studies. The total number of studies is 29 and the number of studies per regeneration stage and/or methodological approach is indicated in bold in the table. Some studies considered more than one regeneration stage and/or used more than one approach.*

	Regeneration stage			
Methodological approach	Seed dispersal **5 studies**	Seed survival **3 studies**	Germination **4 studies**	Seedling establishment **21 studies**
In secondary successional forests **13 studies**	Ferguson *et al*.(2003) Opler *et al.* (1980) Teegalapalli *et al.* (2010) Wydhayagarn *et al.* (2009) **4 studies**	Hammond (1995) **1 study**	Ray and Brown (1995) **1 study**	Cabin *et al*. (2002a) Cabin *et al*. (2002b) Gerhardt (1996) Gerhardt (1998) González-Rivas *et al.* (2009) Hammond (1995) Ray and Brown (1995) Santiago-Garcia *et al*. (2008) Thaxton *et al.* (2012) **9 studies**
Comparison of open areas and established tree cover or of different tree cover **16 studies**	Teegalapalli *et al.* (2010) Wydhayagarn *et al.* (2009) Zelikova and Breed (2008) **3 studies**	Vieira and Scariot (2006a) Wassie *et al.* (2010) **2 studies**	Hardwick *et al.* (1997) **1 study**	Cabin *et al.* (2002a) Castro-Marin *et al.* (2011) González-Rivas *et al.* (2009) Hoffmann (2000) Marod *et al.* (2004) McLaren and McDonald (2003b)

				Santiago-Garcia *et al.* (2008) Teketay (1997) Vieira *et al.* (2006) Wolfe and Van Bloem (2012) **10 studies**
Experimental manipulation of environmental conditions **12 studies**	**0 study**	**0 study**	Blain and Kellman (1991) Hardwick *et al.* (1997) McLaren and McDonald (2003a) Ray and Brown (1995) **4 studies**	Badano *et al.* (2011) Blain and Kellman (1991) Cabin *et al.* (2002b) Gerhardt (1996) Gerhardt (1998) Marod *et al.* (2004) McLaren and McDonald (2003a) Ray and Brown (1995) Rincón and Huante (1993) Thaxton *et al.* (2012) Vieira *et al.* (2008) **11 studies**

TABLE 2. *Location and site history of the reviewed studies of forests that were undergoing secondary succession. Studies that just compared open areas and areas with established trees, and experimental studies carried out in controlled environments are not included in this table.*

Reference	Country	Past land-use	Time since the beginning of secondary succession (abandonment of past land-use) (yr)
Cabin *et al.* (2002a)	Hawaii	Degradation by cattle and feral goats	42
Cabin *et al.* (2002b)	Hawaii	Human disturbance	1-2
Ferguson *et al.* (2003)	Guatemala	Agriculture (agroforestry, swidden cultivation, pasture, intensive monoculture)	0-4
Gerhardt (1996)	Costa Rica	Pasture	25
Gerhardt (1998)	Costa Rica	Pasture	25
González-Rivas *et al.* (2009)	Nicaragua	Agricultural crops	4, 9, 14
Hammond (1995)	Mexico	Shifting agriculture	2, 4, 10, 30
Ray and Brown (1995)	Virgin Islands	Grazing	35
Santiago-Garcia *et al.* (2008)	Puerto Rico	Pasture	0
Teegalapalli *et al.* (2010)	India	Rice cultivation	4
Thaxton *et al.* (2012)	Hawaii	Degradation by ungulates and fire	>10
Wydhayagarn *et al.* (2009)	Thailand	Agricultural crops	8 (active restoration)

TABLE 3. *Main results of studies on effects of established trees on seedlings in tropical dry forests. + indicates a positive effect of established trees on seedlings, - indicates a negative effect and 0 indicates an absence of significant effect. Several types of effect are indicated as +/0 or 0/-, meaning that the effect differs between seedling species. Mean annual rainfalls are those given in the source papers. When shown, the standard error reflects the variation between years. The number of dry months can be given as a range (*e.g.*, 4 to 5). When there are two dry seasons, the length of both is given (*e.g.*, *5 and 3). The number of studied seedling species distinguishes those that are experimentally seeded or planted, or naturally regenerated ("natural").*

Reference	Community leaf phenology	Mean annual rainfall (mm)	Number of dry months	Number of studied seedling species	Treatments	Net effect of established tree on survival	Net effect of established tree on growth
Cabin *et al.* (2002a)	no data	500	irregular	6 (seeded)	closed canopy open area	+	no data
McLaren and McDonald (2003b)	no data	780	4 to 5	64 (natural)	clear cut 50% cut uncut	+	-
Santiago-Garcia *et al.* (2008)	no data	860	4 and 2	24 (planted)	closed canopy open area	+	+
Wolfe and Van Bloem (2012)	no data	860	4 and 2	14 (planted)	forest un-burnt and burnt grass area	+	-

Teketay (1997)	evergreen	1200	5 and 1	2 (natural) 3 (planted)	closed canopy open area	+/0	0/-
Vieira *et al.* (2006)	deciduous	1236 ± 50	6	7 (planted)	closed canopy open area	+	-
González-Rivas *et al.* (2009)	deciduous	1431 ± 369	5	2 (survival) 1 (growth) (all planted)	closed canopy partially open open area	-	-
Castro-Marin *et al.* (2011)	deciduous	1431 ± 369	5	3 (survival) 1 (growth) (all planted)	closed canopy partially open open area	-	-
Hoffmann (2000)	no data	1480	5	3 (forest species, planted)	dense canopy intermediate open area	+/0	+
Marod *et al.* (2004)	deciduous	1546	5	6 (planted)	closed canopy open area	-	-

TABLE 4. *Main results of studies on the effects of light and water factors on seedling establishment in tropical dry forests. + indicates a positive effect of shading/watering on seedlings, - a negative effect and 0 an absence of significant effect. +/0, +/- and 0/- indicate that results vary between seedling species. N stands for nursery, GC for growth chamber, GH for greenhouse, F for field, Natural for naturally regenerating, NT for not tested, S for shading, NS for no shading, W for watering, and NW for no watering.*

	Cabin *et al.* (2002b)	Thaxton *et al.* (2012)	Rincón and Huante (1993)	Badano *et al.* (2011)	McLaren and McDonald (2003a)	Ray and Brown (1995)	Vieira *et al.* (2008)	Marod *et al.* (2004)
Experiment	F	F	GC	F	N	F	GH	F
Location	Hawaii	Hawaii	Mexico	Mexico	Jamaica	Virgin Islands	Brazil	Thailand
Mean annual rainfall (mm)	500	500-750	748	750-900	780	1140	1236	1546
Number of dry months	highly variable	not distinctly seasonal	8	8	4-5	4	6	5
Number of studied species	12 and natural	11	5	2	4	10	8	6
Water treatment	NT	additional ambient	NT	NT	regular W NW	NT	NT	W during dry season NW

Artificial shading (% of full sunlight)	NS S (50%)	NS S (60%)	as in medium size gap as under canopy	NS S (20%)	NS (86%) partial S (37%) heavy S (6%)	NS S (25%)	NS (72%) partial S (40%) heavy S (10 %)	NT
Effect of supplementary water								
Survival	NT	+	NT	NT	+	NT	NT	+/0
Growth								
diameter	NT	NT	NT	NT	+	NT	NT	+/0
height	NT	0	NT	NT	+	NT	NT	0
Effect of shading								
Survival	+/0	+	NT	+	+	+	+	NT
Growth								
diameter	NT	NT	NT	NT	+ (partial S) - (heavy S)	NT	+/-	NT
height	NT	+	NT	NT	+	0	NT	NT
biomass	NT	NT	-	NT	NT	0/-	+/-	NT
Effect of interaction between supplementary water and shading								
Survival	NT	0	NT	NT	+	NT	NT	NT
Growth								
diameter	NT	NT	NT	NT	0	NT	NT	NT
height	NT	0	NT	NT	0	NT	NT	NT

FIGURE LEGENDS

FIGURE 1. Mechanisms underlying the effect of trees that establish in the early stages of secondary succession on subsequent regeneration of woody plants in seasonally dry tropical forests. Each mechanism is shown by two arrows: one from the established trees' box to either the box of abiotic factors or the box of biotic factors and the other from the factors' box to the regeneration box. This figure synthesises the main trends discussed in the review. The plus, minus and zero symbols indicate positive, negative and absence of effect, respectively. The different types of arrow are only used for the visual clarity of the figure. The letters on the arrows refer to the factors influencing the effect considered: a successional stage, b predator type, c leaf phenology of the established tree species, d density of canopy cover, e seed type, f regenerating species and g intensity of shading.

FIGURE 2. Probability of observing a net positive effect or a net negative effect of established trees on seedling survival in seasonally dry tropical forests as a function of the mean annual rainfall. Models fitted with logistic regressions: positive effect (P = 0.008, R^2 = 0.43), negative effect (P = 0.009, R^2 = 0.56)