

## CHAPTER TEN

# Drought as a driver of tropical tree species regeneration dynamics and distribution patterns

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### 10.1 Introduction

Tropical forests harbour the most diverse plant communities on Earth. This high diversity makes it particularly challenging to understand and predict how these communities will be altered by changing climatic conditions. However, doing so is imperative since, like other systems, tropical forests have experienced and are predicted to experience increases in CO<sub>2</sub> and temperature, as well as large shifts in precipitation patterns (Bawa & Markham 1995; IPCC 2007; Malhi & Phillips 2004). Nonetheless, studies of how tropical species will respond to climate change are scarce (e.g. Colwell *et al.* 2008; Miles, Grainger & Phillips 2004).

One of the main consequences of global climate change projected for the tropics is shifts in rainfall patterns (Hulme & Viner 1998). Models have predicted changes in annual rainfall up to 3000 mm per year, and changes in dry season length of up to several months in the tropics (Cox *et al.* 2000; Hulme & Viner 1998; Neelin *et al.* 2006). Projections differ hugely among tropical regions, and both increases and decreases are expected (Hulme & Viner 1998; IPCC 2007; Neelin *et al.* 2006). Global climate models are converging on projecting significant decreases in mean rainfall in Central and South America, while increases are expected in tropical Africa and Southeast Asia, although considerable uncertainty in rainfall projections still exists (IPCC 2007). Increases in extreme weather events (e.g. droughts, intense precipitation) are also expected in tropical regions (IPCC 2007). Increased frequency of

El Niño events (Timmermann *et al.* 1999) would also affect rainfall patterns in the tropics, since El Niño is associated with extreme climatic events including drought and flooding. At regional scales, changes in climate are also likely to result from land-use change, with large-scale deforestation and habitat fragmentation leading to drier conditions (Costa & Foley 2000; Hoffmann, Schroeder & Jackson 2003; Malhi *et al.* 2008).

Predicting how changing precipitation patterns will affect tropical forests depends on a clear understanding of how tree species are affected by water availability. Tree species' responses to water availability play a significant role in influencing their distribution patterns and abundance (Baltzer *et al.* 2008; Comita & Engelbrecht 2009; Engelbrecht *et al.* 2007). This in turn shapes patterns of community composition and diversity across landscapes (Pyke *et al.* 2001; ter Steege *et al.* 2006; Toledo *et al.* 2011) and ultimately influences ecosystem functioning (Bunker *et al.* 2005; Hooper & Vitousek 1997). Thus, shifts in water availability are likely to have significant consequences for tropical forests.

Adult trees have exhibited increased mortality rates in response to severe experimental and natural droughts in tropical forests (e.g. Allen *et al.* 2010; Ashton 1993; Becker & Wong 1993; Condit, Hubbell & Foster 1995; da Costa *et al.* 2010; Nakagawa *et al.* 2000; Nepstad *et al.* 2007; Phillips *et al.* 2010; Williamson *et al.* 2000; Potts 2003; Slik 2004), suggesting that substantial changes in rainfall patterns will influence tropical forests through alterations to current tree composition. However, even small changes in climate may alter tropical forest communities through effects on juvenile plants. Most tropical tree species spend tens to potentially hundreds of years in the forest understorey as seedlings or small saplings (Delissio *et al.* 2002; Hubbell 1998) whose ability to persist in the face of multiple stresses (e.g. pest pressure, light, water and nutrient limitation) determines their chances of reaching the reproductive stage. Seedlings and small saplings are thought to be more susceptible to changes in water availability than larger individuals, owing to their relatively shallow roots which do not reach deep, moist soil layers (Cao 2000; Engelbrecht & Kursar 2003; Gibbons & Newbery 2003) and to asymmetric competition with adults for soil moisture (Lewis & Tanner 2000). Impacts of changing precipitation patterns on juvenile plants are likely to alter future forest composition, since early life stages are considered a bottleneck in the life cycle of trees (Harper 1977) and since processes affecting seedling recruitment and survival are hypothesised to play a major role in the maintenance of high levels of diversity in tropical tree communities (Chesson & Warner 1981; Connell 1971; Grubb 1977; Janzen 1970).

In order to gain a better understanding of how shifts in precipitation patterns due to climate change will alter tropical forests, we examine how

tropical tree species respond to variation in water availability and how that translates into species distributions and patterns of diversity. Here we focus specifically on how regeneration dynamics are affected by low water availability (i.e. drought). We review recent experimental and observational studies from tropical forests, and present new data from our own ongoing studies in the forests of central Panama. We largely restrict our review to studies assessing effects of water availability on seedlings in the field, because of the limitations of greenhouse and laboratory experiments (see Box 10.1).

### **BOX 10.1 Field versus pot experiments on seedling responses to drought**

Field experiments are best suited for examining the ecological importance of variation in water availability in natural habitats, whereas isolated effects of individual factors and how they specifically influence plants are generally best explored under controlled conditions in the laboratory or in the greenhouse. Field experiments allow for the evaluation of the effects of individual factors in the context of all other processes influencing species performance in the natural habitat, thus giving a more realistic picture of the ecological importance of a factor. For example, low light levels in the understorey may limit seedling performance in the field so that plants cannot take advantage of added moisture. Additionally, working under field conditions assures that environmental variations are within the ranges relevant in the habitat. With adequate experimental design and interpretation, these aspects outweigh the problem of limited experimental control of water availability in field experiments, especially in the light of a number of substantial problems associated specifically with drought experiments in potted plants, many of which are avoided in field experiments:

- The rate of drying in pots is mainly given by water depletion by the plants, which in turn is proportional to the transpiration rates of the plants (Jarvis & Jarvis 1963). Larger individuals and/or species with high transpiration rates deplete the available water faster and are therefore subjected to drought stress earlier than smaller/less transpiring plants – potentially leading to the erroneous conclusion that they are more drought-sensitive. This may be especially pronounced when comparing deciduous and evergreen plants with vastly different leaf areas. In contrast to pot experiments, in the field, asymmetric competition for water from the surrounding trees overrides water depletion from any target seedling, so that drying rates are independent of seedling size and transpirational behaviour.

**BOX 10.1 (cont.)**

- Maintaining low, relevant and constant water availability treatments across species (and potential additional treatments, such as light) is rather complicated in pot experiments owing to the interaction of plant size/behaviour (which are in turn influenced by many treatments) and soil water content, i.e. drought intensity.
- It is well known that root restriction in containers can change allocation patterns and limit growth. Since root allocation and extension influence plant access to water and water uptake, this may significantly affect plant water relations.
- The limited soil volume available to plants in pots additionally implies that they cannot evade drought by developing deeper/more extended root systems, and thus gaining access to additional water.
- The rate and direction of drying in pots are usually substantially different from field conditions (e.g. faster drying and no progressive drying from the top to lower soil layers). Gradual acclimation to drought conditions over time is known to be important for plant performance under drought. Given the substantially different drying dynamics, drought responses in pots may not reflect processes in the field.

In particular, the first two issues substantially complicate designing and analysing comparative studies of effects of water availability in pots. Methods used in agricultural and physiological work to control substrate water potential, such as the use of polyethylene glycol (Burlyn & Kaufmann 1973; Turkan *et al.* 2005; also see Snow & Tingey 1985), do not allow plants to reach the low water potentials that critically influence survival and growth of many tropical species ( $\ll -3$  MPa, e.g. Baltzer *et al.* 2008; Kursar *et al.* 2009; Markesteijn *et al.* 2010). In pot experiments, soil water status has to be very carefully monitored and either differentially transpired water replaced across treatments (e.g. Sack 2004), or measurements of plant performance or physiological processes be related to measurements of soil or plant water status, rather than to duration of the dry treatment (Baltzer *et al.* 2009; Bonal & Guehl 2001; Kursar *et al.* 2009; ter Steege 1994). If soil water availability is not maintained constant across species and treatments (and/or carefully monitored) the desired effect of more specific control in greenhouse or laboratory experiments is lost, and the power of the experiment may be severely limited. Although the potential problems mentioned above can be dealt with, they are frequently not adequately accounted for, rendering the interpretation of the data difficult.

Throughout this chapter we use the term *drought resistance* as ‘the capacity of a plant to withstand periods of dryness’ (Larcher 2003), i.e. the ability to survive drought while minimising reductions in growth, and ultimately fitness. When using the term *drought resistance*, we refer to performance under drought conditions *relative* to performance under ‘optimal’ irrigated conditions, assessed in field experiments (see Engelbrecht & Kursar 2003). This approach allows the differentiation of the effects of low water availability, including both direct and indirect effects, from non-drought related factors that may additionally reduce performance and induce mortality during dry periods, e.g. pest pressure or low light conditions (Engelbrecht, Kursar & Tyree 2005). The term *drought resistance* is thus equivalent to response ratios (Hedges, Gurevitch & Curtis 1999). In contrast, we use the term *drought performance* simply to describe the performance of plants during dry periods, which is the outcome of all drought and non-drought related factors acting on the plants.

## 10.2 Regeneration dynamics in experimental field manipulations of water availability

In this section we review studies in which levels of water availability were experimentally manipulated. The majority of these studies involved irrigation to supplement precipitation, typically during dry periods, because removing water from a natural system is associated with substantial logistical difficulties, and the required structures may have indirect effects on regeneration (e.g. shading and seed rain exclusion through panels and gutters).

### 10.2.1 Germination

Seeds of most tropical woody species are desiccation-sensitive (i.e. recalcitrant; Daws, Garwood & Pritchard 2005, 2006; Vazquez-Yanes & Orozco-Segovia 1993). Nevertheless, water availability is unlikely to be a major factor limiting seed survival and germination for these species, because the peak of seed dispersal and germination often occurs in the wet season when water is abundant (Daws, Garwood & Pritchard 2005; Garwood 1983). Consistent with this, supplemental irrigation had no overall effect on seed germination in 12 species in an Amazonian rainforest (Paine, Harms & Ramos 2009). Similarly, in a study that simulated various patterns of rainfall in a seasonal tropical forest in Mexico, seed germination and seedling establishment rates differed little among rainfall treatments for three focal species (Blain & Kellman 1991). However, differential seed responses to water potential have been suggested to be important for determining habitat preferences of pioneer species, which have desiccation-tolerant seeds that germinate after gap formation (Daws *et al.* 2008), as well as for species associated with drier terra firme habitats (Paine, Harms & Ramos 2009). In addition, short dry stretches can occur during the

wet season (Burslem, Grubb & Turner 1996; Engelbrecht *et al.* 2006) and may lead to the desiccation of drought-sensitive seeds, which could affect their viability (Daws *et al.* 2007). Additionally, decreasing wet season duration could delay seed germination, giving seedlings less time to establish sufficient root systems before the start of the dry season. This may adversely affect seedlings' ability to withstand their first dry season, but such effects remain to be explored.

### 10.2.2 Growth and survival

A number of field studies examining the effects of supplemental irrigation on seedling growth and survival in tropical forests have accumulated over the past several years (Table 10.1). These studies focused on the forest understorey and were mostly, but not exclusively, conducted in seasonal moist forests in Central Panama. They clearly indicate widespread water limitation of seedling performance during the dry season: growth and/or survival generally increase with supplemental irrigation in the dry season compared with seedlings under naturally dry conditions (Figures 10.1 and 10.2) (Brenes-Arguedas, Coley & Kursar 2009; Bunker & Carson 2005; Engelbrecht & Kursar 2003; Engelbrecht *et al.* 2007; Fisher, Howe & Wright 1991; Paine, Harms & Ramos 2009; Yavitt & Wright 2008). For example, irrigation had a significant positive effect on height growth of both naturally regenerating and experimentally seeded species in Peru, and a positive effect on survival of the experimentally seeded species (Paine, Harms & Ramos 2009). Similarly, irrigation increased survival and growth of transplanted seedlings of 28 woody species relative to performance under severe dry season conditions (Figure 10.2) (Engelbrecht & Kursar 2003). Survival increased in 82% of the 28 species (with a significant effect in 57%), and growth increased in 92% (with a significant effect in 89%). Perhaps most strikingly, in several studies (Bunker & Carson 2005; Engelbrecht & Kursar 2003; Paine, Harms & Ramos 2009), growth rates shifted from negative (i.e. leaf and biomass loss) under dry season conditions, to positive in irrigated plots (Figure 10.1). The effects of dry season drought on seedlings growing in gaps have been examined in only a handful of studies. Consistent with understorey effects, dry season irrigation increased seedling growth and survival in gaps in a single species study in Panama (Fisher, Howe & Wright 1991), but watering at the end of the dry season did not increase growth in gaps for three species studied in the Bolivian Amazon (Poorter & Hayashida-Oliver 2000). Overall, for most species studied there is a clear trend for increased performance with supplemental irrigation during dry periods, indicating that they are indeed water-limited; however, the occurrence and magnitude of the effects are not entirely consistent across studies (see Box 10.2 for a discussion of the reasons contributing to such differences).

**Table 10.1** Effect of experimental manipulation of soil moisture availability in the field on seedling performance of woody tropical species.

Unless noted in footnotes, moisture was manipulated through supplementary irrigation; studies are sorted by habitat (understorey, gap), and by the average annual rainfall at the study site. A positive effect signifies overall higher performance at higher soil moisture conditions, a negative effect lower performance at higher soil moisture, and none, no significant overall effect. Numbers in parentheses give the number of species exhibiting a positive effect of irrigation, a negligible effect or a negative effect, respectively. The total number of species in the study is given as well. The habitat in which the study was conducted is given as understorey (U) and gaps (G). Studies were conducted on seedlings that were naturally regenerating (NR), transplanted (T) or sown (SS). Average annual rainfall (mm) at the study sites is provided (rounded to 100 mm). Where additional experimental treatments were applied, data refer to otherwise non-manipulated treatments only. Experiments in different habitats and/or sites within a study were treated separately. Where possible, overall positive or negative effects are based on statistical analyses provided in the paper. Where the comparison was not specifically analysed, we estimated the effect based on the effect sizes and standard errors given in the papers as data values, graphs or text. Effects on individual species are based on the sign of the effect (positive or negative), with species exhibiting a negligible effect (performance dry /performance irrigated  $\sim 1$ ; based on data or graphs) noted separately. BCNM, Barro Colorado Natural Monument.

	Dry season		Wet season		Annual		Number of species	Habitat	Approach	Annual rainfall	Country	Site	Study
	Growth	Survival	Growth	Survival	Growth	Survival							
Understorey:													
n.a.	<b>pos</b> (14;4;5)	n.a.	<b>none</b> <sup>1</sup>	n.a.	<b>pos</b> (14;3;7)	n.a.	24 <sup>2</sup>	U	T	1700	Panama	Gunn Hill	Brenes-Arquedas et al. (2009)
<b>pos</b> (26;2;0)	<b>pos</b> (23;5;0)	n.a.	n.a.	n.a.	n.a.	n.a.	28	U	T	2600 <sup>3</sup>	Panama	BCNM	Engelbrecht & Kursar (2003)
<b>none</b> (10;0;0)	<b>pos</b> (7;1;2)	<b>none</b> (2;6;2)	<b>none</b> (3;5;2)	<b>none</b> (5;2;3)	<b>none</b> (8;2;0)	<b>none</b> (8;2;0)	10	U	NR	2600	Panama	BCNM	Bunker & Carson (2005) <sup>13</sup>
<b>pos</b> (1;0;0)	<b>pos</b> (1;0;0)	n.a.	n.a.	n.a.	n.a.	n.a.	1	U	T	2600	Panama	BCNM	Fisher et al. (1991)
<b>pos</b> <sup>4</sup> (3;0;0)	n.a.	<b>none</b> <sup>4</sup> (1;1;1)	n.a.	n.a.	n.a.	n.a.	3	U	NR	2600	Panama	BCNM	Yavitt & Wright (2008)
n.a.	<b>pos</b> (20;0;0)	n.a.	n.a.	n.a.	n.a.	n.a.	20 <sup>5</sup>	U	T	2800 <sup>3</sup>	Panama	BCNM	Engelbrecht et al. (2007)
n.a.	<b>pos</b> (2;2;0)	n.a.	n.a.	n.a.	n.a.	n.a.	4	U	T	2600	Panama	BCNM <sup>6</sup>	Asquith & Mejia-Chang (2005)
n.a.	n.a.	n.a.	n.a.	<b>none</b> (1;3;0)	<b>pos</b> <sup>7</sup> (2;2;0)	<b>pos</b> <sup>7</sup> (2;2;0)	4	U	T	2600	Panama	BCNM	Tanner & Barberis (2007)

**Table 10.1 (cont.)**

Dry season			Wet season		Annual		Number of species	Habitat	Approach	Annual rainfall	Country	Site	Study
Growth	Survival	Growth	Survival	Growth	Survival								
n.a.	n.a.	n.a.	n.a.	n.a.	pos <sup>8</sup> (1;1;0)	2	U	NR	2600	Panama	BCNM	Mulkey, Wright & Smith (1993)	
pos <sup>1</sup>	pos <sup>1</sup>	n.a.	n.a.	none <sup>1</sup>	none <sup>1</sup>	12	U	SS	2600	Peru	Los Amigos	Paine <i>et al.</i> (2009)	
pos <sup>1</sup>	none <sup>1</sup>	n.a.	n.a.	pos <sup>1</sup>	none <sup>1</sup>	Unknown <sup>9</sup>	U	NR	2600	Peru	Los Amigos	Paine <i>et al.</i> (2009)	
n.a.	none (9;6;8)	n.a.	none <sup>1</sup>	pos	n.a.	24 <sup>2</sup>	U	T	3000	Panama	Lorenzo	Brenes-Arguedas <i>et al.</i> (2009)	
Gaps:													
pos (1;0;0)	pos (1;0;0)	n.a.	n.a.	n.a.	n.a.	1	G	T	2600	Panama	BCNM	Fisher <i>et al.</i> (1991)	
n.a.	n.a.	n.a.	pos <sup>10</sup> (6;0;0)	n.a.	n.a.	6	G	SS	2600 <sup>3</sup>	Panama	BCNM	Engelbrecht <i>et al.</i> (2005)	
n.a.	n.a.	n.a.	n.a.	n.a.	pos (1;1;0)	2	G	NR	2600	Panama	BCNM	Mulkey, Wright & Smith (1993)	
n.a.	n.a.	n.a.	n.a.	n.a.	none (0;1;0)	1 <sup>11</sup>	U, G <sup>12</sup>	NR	2600	Panama	BCNM	Mulkey & Wright (1996)	

<sup>1</sup> No data for individual species provided

<sup>2</sup> 23 species for survival

<sup>3</sup> Rainout shelters and supplementary irrigation were combined

<sup>4</sup> Based on height growth

<sup>5</sup> Species not considered in Engelbrecht and Kursar (2003)

<sup>6</sup> Various island and mainland sites

<sup>7</sup> Data over 4 years

<sup>8</sup> Data over 3 years

<sup>9</sup> 1856 seedlings, number of species not known

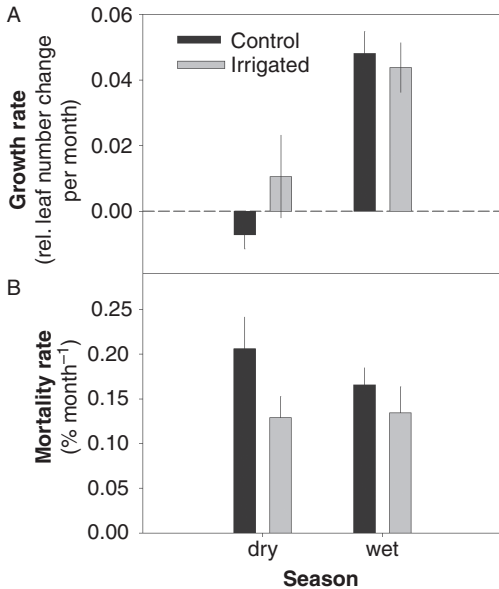
<sup>10</sup> Survival over 10 days with experimental manipulation

<sup>11</sup> Only refers to species not considered in Mulkey *et al.* (1993)

<sup>12</sup> Habitat not specified

<sup>13</sup> Only high irrigation treatment considered





**Figure 10.1** Effect of supplementary irrigation in the dry and wet season on growth (A) and mortality (B) of naturally regenerating seedlings of 10 woody species in the understorey of a lowland tropical moist forest on Barro Colorado Island (BCI), Panama. Growth rates were significantly lower in the dry season than in the wet season. Growth was not significantly affected by irrigation, although a consistent trend of higher growth under irrigated conditions was seen in all species. Mortality rates did not differ between seasons, but in the dry season irrigation led to significantly lower mortality rates. Data are means  $\pm 1$  SE. Drawn from data in Bunker and Carson (2005; the high irrigation treatment).

In the wet season, water availability is unlikely to be limiting. Consistent with this idea, supplementary irrigation has been shown to have generally no effect on growth and survival of seedlings in the moist forest understorey during the wet season (Figure 10.1) (Bunker & Carson 2005; Brenes-Arguedas, Coley & Kursar 2009; Fisher, Howe & Wright 1991). However, small seedlings of pioneer species growing in gaps were found to have increased mortality during short dry spells of only a couple of days in dry versus irrigated conditions in the wet season (Engelbrecht *et al.* 2006).

Supplemental irrigation can result in higher *annual* growth and survival rates (Tanner & Barberis 2007 for survival; Brenes-Arguedas, Coley & Kursar 2009 for growth), but this is not necessarily the case (Bunker & Carson 2005; Tanner & Barberis 2007 for growth). For example, Bunker and Carson (2005) found increased seedling survival in irrigated treatments during the dry season for 10 woody species in Panama, but no differences in survival across the full year. Thus, under some circumstances, other factors affecting performance in the wet season may cancel out positive effects of increased water availability in the dry season (Bunker & Carson 2005; Tanner & Barberis 2007).

### 10.2.3 Seedling size/age effects

Smaller plants are generally considered to be more vulnerable to drought stress than larger ones (Bunker & Carson 2005; Paine, Harms & Ramos 2009). Within species, the impact of low water availability indeed decreases with seedling size, which is determined by seedling age as well as genetic factors

**Box 10.2 Reasons for differential outcomes of supplemental irrigation studies**

Although there is a clear overall trend of higher seedling growth and survival with supplemental irrigation in the dry season, growth and survival are not necessarily simultaneously affected, and the size and significance of the effects vary among studies (Table 10.1). Several factors probably contribute to these differences, some of them ecologically meaningful, others due simply to differences in experimental design.

First, even at a single site, experiments conducted in years with differing drought severities are likely to yield different results, with more pronounced effects in drier years. Furthermore, drought intensity and soil properties vary locally and regionally, such that the same level of supplemental irrigation will probably have stronger effects on seedling growth and survival at sites where water is more limiting. The lack of an ecologically meaningful measure of water availability or drought intensity that is easy (and inexpensive) to measure and is comparable across sites and years currently hinders meaningful comparisons among forests and years. This also precludes a meta-analysis of such studies, allowing only a descriptive review of the literature (see Tables 10.1–10.3). To advance understanding of the effects of water availability and the extent of drought impacts, future studies must include a measure of soil water availability that is independent of plant species and size. Rainfall data alone are not sufficient, since differences in topography or soil characteristics, as well as evapotranspiration, also modulate soil water availability. Profiles of soil water potentials through the rooting zone of the seedlings will provide the most meaningful information. They can be assessed, for example, with psychrometers, the ‘filter paper technique’, or by gravimetric (or volumetric) soil water content, calibrated to soil water potentials through soil retention curves (e.g. Bonal & Guehl 2000; Engelbrecht & Kursar 2003; Markesteijn *et al.* 2010; Rascher *et al.* 2004).

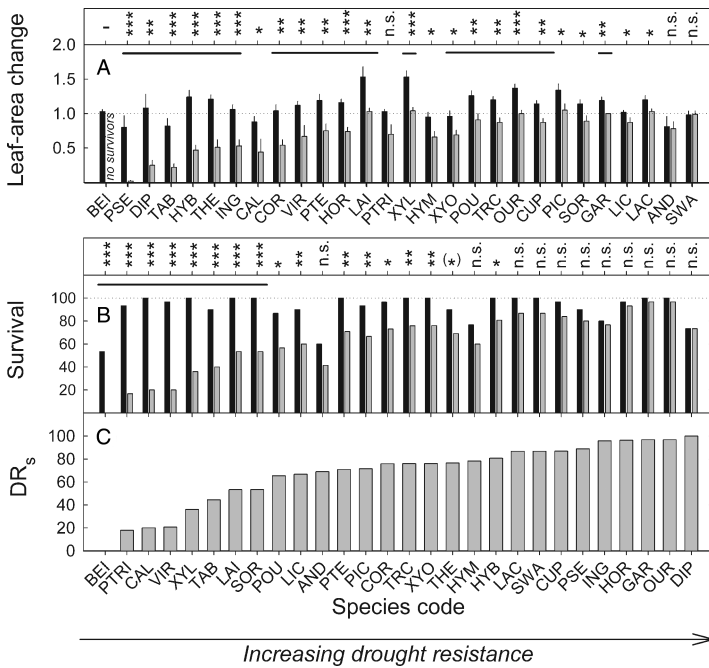
Furthermore, variation in seedling drought resistance among species can lead to strong sampling effects in studies that examine only a few species (see Westoby 2002). Often, study species are not explicitly chosen with respect to (or randomly with respect to) their drought resistance (or a preliminary indicator thereof), so that a study may be inadvertently restricted to either drought-resistant or drought-sensitive species. This may result in hugely different outcomes when trying to generalise from the study species to the community, or when trying to infer differences across sites or years. Thus, care must be taken when interpreting experiments that include only a small subset of species from the community. Future studies should aim to use explicit species sampling schemes to adequately take into account the large interspecific variation in species’ drought responses.

Additionally, differences in experimental study results can be due to differences in irrigation effects. Quantifying the strength of water

**Box 10.2 (cont.)**

limitation requires that drought stress is completely alleviated, i.e. species do not experience any drought stress in the supplemental irrigation treatment. This can be astonishingly hard to achieve experimentally, and may require very different amounts of irrigation in different sites and years. For example, in an irrigation study in a forest on the dry side of the Isthmus of Panama in the dry season, soil moisture did not show any appreciable increase despite water supplementation equivalent to the amount of average rainy-season rainfall (>200 mm), presumably owing to intense competition from neighbouring trees (the study had to be abandoned; Engelbrecht, unpublished data). Experiments that do not completely alleviate drought stress may reveal some effects, if water limitation exists, but will not quantify its full extent. In such cases, experiments are essentially simulating the effect of a less intense dry season or drought event, which may produce unexpected results. For example, in the irrigation study of Bunker *et al.* (2005), several species showed decreased growth at intermediate irrigation, but increased growth at high irrigation. Adjusting irrigation levels so that adequate and comparable water levels are achieved is especially critical in studies comparing irrigation effects across sites or years. Again, careful monitoring of soil water availability is critical.

In field irrigation studies, both effects on growth, but not survival (Bunker & Carson 2005; Yavitt & Wright 2008), and effects on survival, but not growth (Tanner & Barberis 2007), have been found. Effects on growth, but not survival, can be easily understood, since even slight drought stress at plant water potentials well above lethal levels (and even before wilting) can lead to decreased growth rates due to decreased turgor, stomatal closure limiting photosynthesis and generally inhibited metabolic processes (Hsiao 1973). Thus, in such studies, drought intensities (i.e. the extent and/or length of low water potentials) were simply not strong enough to induce death in the study species, an ecologically meaningful result. In contrast, effects on survival, but not on growth, are harder to explain, because, as described above, growth reductions *should* occur considerably before lethal water potentials are reached. One possible reason for detecting only survival effects is that growth rates can only be quantified for individuals that survive over the census interval. Studies that have few intermittent growth measurements may not detect lower growth before death since growth measurements exclude seedlings that show strong negative growth (e.g. leaf loss, stem dieback) and consequently die relatively quickly (i.e. before the first growth measurements are taken). Therefore, studies addressing effects of drought on growth should census plants frequently enough to avoid such effects.



**Figure 10.2** Interspecific variation in drought effects on growth and survival in transplanted seedlings of 28 co-occurring woody species in the understorey of a lowland tropical forest in Central Panama. (A) Leaf-area change, relative to initial leaf area, in transplanted seedlings under dry and irrigated conditions, (B) survival under dry and irrigated conditions, and (C) drought resistance ( $DR_s$ ) calculated as percent survival in dry conditions (grey) relative to irrigated conditions (black). Results of *t*-tests in (A) and of Fisher’s exact test in (B) for treatment differences within species are given as: \*\*\* $P < 0.0001$ , \*\* $P < 0.005$ , \* $P < 0.05$ , (\*) $P = 0.05$ , n.s.  $P > 0.05$  (not significant). Horizontal bars mark those species for which treatment differences were significant ( $P < 0.05$ ) after stepwise Bonferroni adjustment. When deciduous species are excluded, growth and survival responses to drought are positively correlated with each other. Redrawn from Engelbrecht and Kursar (2003). With permission from Springer Science and Business Media.

and environmental conditions. This is most directly shown by decreases in the effect of irrigation with seedling age or size (Bunker & Carson 2005; Paine, Harms & Ramos 2009; Poorter & Hayashida-Oliver 2000), and supported by observational studies (e.g. Delissio & Primack 2003). Across species, however, comparative irrigation studies of 28 understorey species (Engelbrecht & Kursar 2003) and six gap species (Engelbrecht *et al.* 2007) found no differences in drought resistance between species with larger vs. smaller seedlings. Increases of drought resistance with plant size or age are usually attributed to smaller and/or younger plants having smaller roots systems and less access to deeper soil layers with higher water availability (Cao 2000; Gibbons &

Newbery 2003), although the evidence for differences in rooting depth leading to the size dependence of drought resistance is limited (see Section 10.3). Within species, smaller seedlings may additionally, or alternatively, be less hardy (owing to unsuitable local conditions or genetics) and therefore more vulnerable to drought-induced mortality.

#### 10.2.4 Interspecific variation

Comparative experimental studies clearly indicate that the strength of the effect of drought on seedling performance varies widely among species, underscoring their differential capacity to withstand periods of low water availability (Brenes-Arguedas, Coley & Kursar 2009; Bunker & Carson 2005; Engelbrecht & Kursar 2003; Engelbrecht *et al.* 2007; Tanner & Barberis 2007). For example, among 48 native tree and shrub species in the forest understorey in Central Panama, performance in dry relative to irrigated conditions (i.e. drought resistance) varied from 0% to 100% (Figure 10.2) (Engelbrecht & Kursar 2003; Engelbrecht *et al.* 2007). As discussed below, the wide variation of drought resistance among species is consistent with the large variation among species in physiological and morphological traits relevant to plant water relations. We later review how these large interspecific differences in drought resistance have pronounced effects on population dynamics and species distribution patterns.

### 10.3 Mechanisms determining interspecific variation in seedling drought responses

Various traits and mechanisms have been suggested to underlie differences in drought resistance among seedlings of tropical tree species. Mechanisms are broadly divided into two categories: *desiccation avoidance* and *desiccation tolerance* (Larcher 2003). Mechanisms of desiccation avoidance are those that prevent or delay species from experiencing low tissue water potentials (the thermodynamic state of water, measured as pressure or suction in pascal, with lower (i.e. more negative) values indicating a lower 'availability' of water). Efficient mechanisms of desiccation avoidance minimise the decrease of plant water potentials under drought conditions. These traits include (1) maximising water uptake through deep and/or extended root systems; (2) water storage in stems, leaves or roots; and (3) minimising transpirational water loss through early stomatal closure and efficient cuticles, or drought deciduousness (leaf shedding).

Mechanisms of desiccation tolerance allow plants to continue functioning or, under more severe conditions, to survive despite a decrease of plant water potentials. These mechanisms include (4) mechanisms at the leaf (and meristem) level, e.g. maintaining cell turgor through high osmotic potentials and rigid cell walls, and maintaining vital cell processes through protection of membranes, enzymes and DNA, and (5) mechanisms in the water-conducting

tissues (xylem) that promote a high resistance to xylem cavitation, thus allowing plants to maintain water transport under conditions of low water availability.

The two groups of mechanisms have traditionally been treated as alternative strategies, even implying a trade-off between the two (Larcher 2003). However, all terrestrial vascular plants exhibit all of these mechanisms (with the exception of deciduousness) – all have roots, stomata and cuticles, water-containing tissues and water-conducting tissues, and are able to withstand some degree of water loss. Indeed, the evolution of these characters in vascular plants is the basis of their ecological success on land. What species differ in is the efficiency of the different mechanisms (and the expression of the associated traits) and how they combine to allow each species to withstand periods of low water availability.

The variation in drought resistance of species within and across systems may be governed by the variation in the efficiency of one dominant trait or a combination of several traits. For example, in Mediterranean systems, rooting depth has been shown to determine the drought survival of seedlings (Padilla & Pugnaire 2007). On the other hand, different combinations of traits may lead to the same integrated drought resistance. Evaluating the role and importance of potentially relevant traits (or their combination) in driving the variation in species' responses to drought in a community requires directly relating them to species' drought resistance. Apart from trait values, we need quantitative, comparative assessments of drought resistance via controlled experiments or, if such data are not available, comparative data on species performance or distribution with respect to drought intensity.

Numerous studies on the physiology of water relations of tropical woody plants have revealed enormous variation among species in water uptake, stomatal reactions, deciduousness, water storage and hydraulic architecture, resulting in differences in plant water balance and potentials (e.g. Bonal & Guehl 2001; Brodribb *et al.* 2003; Jackson *et al.* 1995; Markesteijn *et al.* 2011; Tyree & Ewers 1996). However, studies allowing for the rigorous evaluation of the importance of various traits and mechanisms in shaping plant drought resistance, and their performance and distribution under drought conditions, remain scarce. This is due to a scarcity of relevant comparative datasets on species performance responses to drought (i.e. drought resistance) combined with complementary data on the potentially relevant traits for the same set of species. Even datasets that combine trait data with quantitative data on species distribution patterns with respect to water availability remain scarce (but see Baltzer *et al.* 2008; Markesteijn & Poorter 2009), and to our knowledge no datasets exist that directly relate traits to comparative field performance under drought conditions. In the following we summarise the evidence for

the importance of different mechanisms for drought resistance of tropical seedlings from the few available comparative studies.

Differences in *rooting depth and volume*, which determine access to soil water, have long been suggested to be main drivers of variation in seedling drought performance across species in tropical forests. In Mediterranean systems, rooting depth has indeed been shown to be decisive in shaping seedling survival over dry periods (Padilla & Pugnaire 2007). However, seedling size, root–shoot ratio, rooting depth, and ‘rooting depth per leaf area’ were all unrelated to variation in seedling drought resistance among 28 understorey and 6 pioneer species in Central Panama (Engelbrecht *et al.* 2006; Engelbrecht *et al.* unpublished data; Kursar, Engelbrecht & Tyree 2003). Survival under irrigated versus control conditions was unrelated to root–shoot ratios in another study in Panama (Mulkey, Wright & Smith 1993), and dry season mortality in a moist forest in Thailand was unrelated to rooting depth (Marod *et al.* 2002). Similarly, in a comparison of dry and moist forest species, Markesteijn and Poorter (2009) found no relationship between rooting depth, or root length per leaf area, and species abundance in the two forest types, and even a decrease in root volume with stronger association to dry sites – despite various differences in biomass allocation to roots and root structure. In contrast, in a study comparing four Neotropical forests (in Costa Rica, Panama, Brazil and Peru), seedlings had deeper roots relative to leaf area at the most seasonal site (Paz 2003). The accumulating evidence suggests that under field conditions access to soil water resources through deep and/or extended root systems is not a decisive mechanism driving the variation among species in drought performance responses of tropical seedlings. However, root traits may vary across forest systems.

Plants can store water in their leaves, stems or roots, a characteristic that in tropical woody plants is mainly expressed in dry forests (Borchert 1994). Across species in a moist forest in Panama, leaf water content was not related to species’ drought resistance (Engelbrecht *et al.*, unpublished data), and in Bolivia, contrary to expectation, root water content increased with association to moist vs. dry forests (Markesteijn & Poorter 2009). The limited data therefore do not support an important role of water storage in drought responses of tropical seedlings, but more data, especially including stem water storage, are clearly needed.

Plants can minimise their transpirational water loss through early stomatal closure, an effective cuticle, or shedding their leaves during periods of low water availability, i.e. drought deciduousness. During the dry season, plants in the forest understorey exhibit reduced *stomatal conductance*, i.e. they close their stomata (Cao 2000; Engelbrecht, Wright & De Steven 2002; Mulkey *et al.* 1992; Mulkey, Wright & Smith 1993; Veenendaal *et al.* 1996; Wright

*et al.* 1992). However, comparative data on stomatal responses to drought in tropical seedlings, and how they relate to performance under drought conditions, remain exceedingly rare. In a detailed study of seedlings of three tropical tree species during a soil drying cycle in a growth chamber, Bonal and Guehl (2001) showed tremendous differences among species. In one species, stomata were extremely sensitive to soil drying, immediately reducing stomatal conductance with initiation of soil drying and reaching zero stomatal conductance at relatively high soil water contents. The most contrasting species maintained the stomata open until soil water contents were reduced to rather low levels (almost a third of saturation contents) and only reached full closure at much lower soil water contents than the other species. The differences in stomatal behaviour directly affected leaf water potentials, which remained high in the species with early stomatal closure, but decreased strongly with soil water content in the species whose stomata remained open, with the intermediate species showing intermediate leaf water potentials. We would expect that the species with sensitive stomatal response to drying would have the lowest growth rate, but the highest survival, whereas the species with delayed stomatal closure should exhibit faster growth, but lower survival. For growth, this pattern was indeed found, but the intermediate species showed even higher growth than both other species. Drought survival was not assessed in the study. In field studies in the tropics, stomatal conductance during the dry season in dry control versus irrigated plots was unrelated to survival (Mulkey, Wright & Smith 1993), and similarly, stomatal reaction to decreasing soil water contents did not reflect distribution patterns with respect to water availability (ter Steege 1994). Assessing stomatal responses to soil drought requires careful monitoring of soil and/or plant water status, especially for studies conducted in potted plants (see Box 10.1; also see Bonal & Guehl 2001). In cases where water status is not monitored (e.g. Slot & Poorter 2007), clear interpretation of results becomes difficult. At present, further research on the importance of stomatal responses for drought resistance of tropical trees is needed.

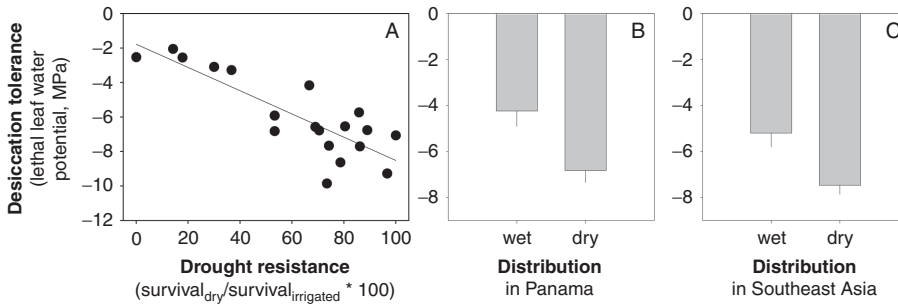
*Cuticular conductance* for water vapour in leaves is generally low, and when stomata are open it contributes little to overall plant water loss. However, as stomata close, cuticular water loss becomes increasingly important, and at stomatal closure it constitutes all of the plant water loss (Kerstiens 1996a, b). Differences in cuticular conductance might therefore be important for drought survival under severe drought stress, and thus species with lower cuticular conductance may be more drought-resistant. In seedlings of 20 tropical tree species, cuticular conductance (assessed as minimum leaf conductance) varied four-fold and differed significantly among species. However, it was not related to species' drought resistance (Engelbrecht *et al.*, unpublished data).



*Deciduous* trees generally occur under drier conditions in tropical forests (e.g. Malhi *et al.* 2009; Poorter, Bongers & Lemmens 2004). Leaf shedding decreases transpirational water loss and may therefore contribute to higher drought resistance (Borchert 1994; Reich & Borchert 1984). Even species whose adults are evergreen may have seedlings that shed their leaves under drought conditions (Engelbrecht & Kursar 2003). Unexpectedly, variation in deciduousness among species was unrelated to seedling drought resistance in Central Panama (Engelbrecht & Kursar 2003). Poorter and Markesteijn (2008) found longer survival times of deciduous species in pot experiments. However, such longer drought survival times of deciduous species in pots come with the caveat that soil drying can be substantially delayed for such species because of the reduced transpirational water loss, thus exposing them to less intense drought conditions (see Box 10.1). Rigorous evidence for an important role of deciduousness for drought performance of tropical seedlings is therefore still lacking.

The current evidence on individual traits associated with mechanisms of *desiccation avoidance*, presented above, does not support the idea that the traits individually are important in determining interspecific variation in drought resistance among seedlings of tropical woody plants. The effectiveness of the combined mechanisms of desiccation avoidance in a plant can be evaluated by assessing its leaf water potential under conditions of low water availability. If mechanisms of desiccation avoidance are important, leaf water potentials should remain high, whereas low leaf water potentials indicate that desiccation was not effectively avoided. Thus midday leaf water potentials provide an integrated measure of the effectiveness of mechanisms of desiccation avoidance. Midday leaf water potentials of 20 species in the dry season in Panama ranged from  $-1.2$  to  $-3.2$  MPa, but were not related to drought resistance (Engelbrecht *et al.*, unpublished data). This provides further support that *desiccation avoidance* does not govern seedling drought resistance in tropical forests.

An integrated measure of *desiccation tolerance* is lethal leaf water potential. If plants already die with minimal desiccation, i.e. at high water potentials, mechanisms of desiccation tolerance are not well developed, whereas low lethal water potentials indicate high desiccation tolerance. In a greenhouse study, Kursar *et al.* (2009) assessed lethal leaf water potential (and leaf water content) as the value at which 50% of the individuals of a species die (equivalent to LD 50). Across 19 species, lethal leaf water potential showed a highly significant negative correlation with species' drought resistance (independently assessed in a field experiment, Figure 10.3A; also see Tyree *et al.* 2003), and it also varied between species found in high vs. low rainfall areas (Figure 10.3B; Kursar *et al.* 2009). Specifically, drought-sensitive species die at high leaf water potentials whereas drought-resistant species can withstand



**Figure 10.3** Desiccation tolerance, assessed as lethal leaf water potentials, correlates with seedling drought resistance assessed experimentally in the field in Panama (A;  $n = 19$ ,  $R^2 = 0.70$ ,  $P < 0.0001$ ). Lethal leaf water potentials are significantly higher in wet forest species than moist forest species in Panama (B;  $t$ -test,  $P < 0.005$ , data for 25 species), and significantly higher in species restricted to wet aseasonal forests than in species occurring in drier seasonal forests on the Malay–Thai Peninsula in Southeast Asia (C;  $t$ -test,  $P < 0.005$ , data for 24 species). (A, B) Redrawn from Kursar *et al.* (2009); and (C) redrawn from Baltzer *et al.* (2008).

low water potentials. Additionally, across seedlings of 24 species, Baltzer *et al.* (2008) found significantly lower lethal leaf water potentials (and water contents) in species that occur in seasonally dry forests than in species restricted to wet evergreen forest south of the Kangar–Pattani Line (KPL) on the Malay–Thai Peninsula in Southeast Asia (Figure 10.3C). Combined, these datasets provide strong support for the idea that mechanisms of desiccation tolerance that allow plants to maintain tissue function or viability despite low water contents play an important role in determining variation in drought resistance across woody seedlings in tropical moist forests worldwide.

Which mechanisms of desiccation tolerance are actually important? Mechanisms at both the leaf level (mesophylls and epidermis) and in the xylem tissue may contribute. Wilting at lower water potentials (i.e. more negative turgor loss points), higher solute concentrations at full turgor (i.e. more negative solute potentials) and more rigid cell walls (i.e. higher bulk modulus of elasticity) are associated with lower lethal leaf water potentials and with species occurring in drier seasonal forests (Baltzer *et al.* 2008). These results demonstrate that there are strong inherent differences in leaf-level tissue characteristics consistent with mechanisms leading to higher desiccation tolerance in species in drier sites. Osmotic adjustments and changes in cell wall elasticity are known to occur under drought conditions (Tyree & Jarvis 1982; Eamus & Prior 2001), and interspecific differences in the acclimation potential of these parameters may additionally contribute to differences in lethal leaf water potentials. The extent to which compatible

solutes, i.e. solutes not involved in primary metabolism (Arndt *et al.* 2001; Chen & Murata 2002; Merchant *et al.* 2006), play a role in the desiccation tolerance of tropical seedlings through stabilising macromolecules has not yet been addressed.

Maintaining the functionality of the xylem, the water-conducting tissue, under drought conditions is critical initially to maintain transpirational water flow and photosynthesis, and under more advanced drought conditions to supply leaf and meristem tissues with sufficient water to stay above lethal water potentials. Under decreasing stem water potentials (increasing tension), xylem vessels cavitate and embolisms (air bubbles) form, which interrupt the water flow and thus reduce the stem hydraulic conductance (Tyree & Sperry 1989). Vulnerability to cavitation varies enormously among species of tropical plants (Brodribb *et al.* 2003; Choat, Sack & Holbrook 2007; Markesteijn *et al.* 2011; Tyree & Ewers 1996). No direct data are available to relate comparative xylem vulnerability of tropical seedlings to their desiccation tolerance (i.e. lethal leaf water potential or content). However, Kursar *et al.* (2009) found that leaf specific hydraulic conductivity (the hydraulic conductivity of the stem per leaf area) declined with increasing desiccation tolerance. Leaf specific hydraulic conductivity is usually positively related to xylem vulnerability (e.g. Markesteijn *et al.* 2011), in turn suggesting that species with higher xylem vulnerability are indeed less desiccation-tolerant. This is further supported by the finding of a significant increase in seedling wood density with the degree of association to dry forests in Bolivia (Markesteijn & Poorter 2009). High wood density is associated with small diameter xylem vessels that have higher resistance to xylem embolism than large vessels (Hacke *et al.* 2001).

To summarise, strong evidence has accumulated over the past several years that mechanisms of desiccation tolerance are decisive in determining differential seedling responses to drought, with both leaf and xylem level processes being relevant. However, contrary to longstanding assumptions and results from other ecosystems, currently there is no convincing empirical evidence that mechanisms of desiccation avoidance are important for shaping differences in seedling drought resistance in tropical moist and wet forests. These results will be important to consider when selecting 'soft traits' indicative of plant drought responses.

#### **10.4 Effects of temporal and spatial variation in water availability on tropical tree regeneration**

We can gain further insights into how species are affected by water availability by examining how current variation in water availability affects seedling dynamics and species distributions. In tropical forests, annual rainfall and dry season intensity vary widely and lead to pronounced spatial and temporal

variation in water availability (Walsh 1996). Plant responses to this variation can provide insight into how sensitive or resilient tropical species and communities will be to changes in precipitation, and can provide key baseline information that can be used in quantitative models of species distributions and forest composition under specific climate scenarios.

#### **10.4.1 Temporal variation in water availability**

In many tropical forests – including moist and wet ones – rainfall is seasonal, with one or two dry seasons per year (Walsh 1996). Even in aseasonal equatorial forests, dry periods of more than two weeks occur and can affect plants (e.g. Becker 1992; Burslem, Grubb & Turner 1996; Walsh & Newbery 1999). In addition to seasonal variation, there is large interannual variation in total and seasonal rainfall in the tropics. Extreme wet and dry years are often related to the El Niño–Southern Oscillation. In the moist and wet tropics, severe droughts often occur in association with El Niño climatic events (Allan, Lindesay & Parker 1996; Walsh & Newbery 1999). For example, the El Niño event of 1982–83 resulted in an unusually severe dry season and elevated tree mortality rates at Barro Colorado Island (BCI), Panama (Condit, Hubbell & Foster 1995), and the 1997–98 El Niño event caused widespread droughts in Southeast Asia (Bebber, Brown & Speight 2004). Even in the absence of El Niño conditions, pronounced regional droughts can occur, such as the 2005 drought in the Amazon basin (Phillips *et al.* 2009). In contrast, La Niña years generally have above average rainfall and lower solar irradiance owing to increased cloud cover (Wright 2005).

#### **10.4.2 Effects of seasonal variation in water availability**

Two alternative hypotheses can be proposed concerning seasonal effects on tropical seedlings. First, seedling performance may be higher in the dry season than in the wet season, because light, the most limiting resource in the understorey of tropical forests, occurs at higher levels in the dry season (Russo *et al.* 2012; Wright 2005), and at the same time, pest pressure may be lower, although that is not always the case (Coley 1983; Wolda 1978). Alternatively, seedling performance may be higher in the wet season, because low water availability limits growth and survival in the dry season so that seedlings are not able to take advantage of higher light levels. Evidence has now accumulated that seedling performance does indeed vary substantially between seasons. Table 10.2 lists studies examining effects of temporal variation in water availability on seedling performance. The majority of these studies support the latter hypothesis, that seedling performance is negatively affected by dry season water limitation.

In nearly all studies, seedling growth and/or survival were higher in the wet season than in the dry season (Table 10.2). This is consistent with studies that

**Table 10.2** Effect of temporal variation in soil moisture availability on seedling performance of woody tropical species.

A positive effect signifies overall higher performance at higher soil moisture conditions (i.e. in the wet season or in wet years), a negative effect lower performance at higher soil moisture, and none, no significant overall effect (as in Table 10.1). Numbers in parentheses give the number of species exhibiting a positive effect of a wetter period, a negligible effect, or a negative effect, respectively. Studies are sorted by habitat (understorey, gap), and by the average annual rainfall (mm) at the study site. BDFPP, Biological Dynamics of Forest Fragments Project. See Table 10.1 for further explanations.

Growth	Survival	Number of species	Habitat	Approach	Rainfall	Country	Site	Study
<b>Seasonal effects<sup>1,2</sup>:</b>								
n.a.	<b>pos</b> (2;0;0)	2	U	T	1000	Benin	Kandi	Biaou <i>et al.</i> (2011)
n.a.	<b>none</b> (2;0;0)	2	U	T	1100	Benin	Bassila	Biaou <i>et al.</i> (2011)
n.a.	pos <sup>3</sup>	>53 <sup>4</sup>	U <sup>5</sup>	NR	1100	Ghana	Pinkwae	Lieberman & Li (1992)
<b>pos</b> (2;0;0)	<b>pos</b> (2;0;0)	2	U	T	1300	Ghana	Tinte Bepo Forest Reserve	Veenendaal <i>et al.</i> (1996)
<b>none</b> (0;4;0)	<b>pos</b> (3;1;0)	4	U	T	1600 <sup>6</sup>	Costa Rica	Guanacaste Conservation Area	Gerhardt (1996)
<b>none</b> (0;4;0)	<b>pos</b> (4;0;0)	4	U	T	1600 <sup>7</sup>	Costa Rica	Guanacaste Conservation Area	Gerhardt (1996)
n.a.	<b>pos</b> (7;3;2)	12	U	NR	1700	Thailand	Mae Klog	Marod <i>et al.</i> (2002)
n.a.	<b>pos</b> (14;4;5)	24	U	T	1700	Panama	Gunn hill	Brenes-Arguedas <i>et al.</i> (2009)
<b>pos</b> (2;1;0)	n.a.	3	U	T	1800	Bolivia	El Tigre	Poorter & Hayashida-Oliver (2000)
n.a.	none (0;1;0)	1	U	NR	2200	Mexico	Santa Gertrudis	Cruz-Rodriguez & López-Mala (2004)
n.a.	<b>pos</b> (3;1;0)	4	U	NR	2300	Panama	Casarete <sup>8</sup>	Lopez & Kursar (2007)
<b>pos</b> (23;5;8)	<b>pos</b> (26;0;7)	36 <sup>9</sup>	U	NR	2600	Panama	BCNM	Comita & Engelbrecht (2009)
<b>pos</b> (10;0;0)	<b>none</b> (4;4;2)	10 <sup>10</sup>	U	NR	2600	Panama	BCNM	Bunker & Carson (2005)
n.a.	<b>pos</b> (5;2;0)	7	U	T	2600	Panama	BCNM	Myers & Kitajima (2007)

Table 10.2 (cont.)

Growth	Survival	Number of species	Habitat	Approach	Rainfall	Country	Site	Study
<b>pos</b> (1;0;0)	n.a.	1	U	T	2600	Panama	BCNM	Fisher <i>et al.</i> (1991)
<b>none</b> <sup>11</sup> (1;1;1)		3	U	NR	2600	Panama	BCNM	Yavitt & Wright (2008)
<b>none</b> (0;3;0)	<b>pos</b> <sup>12</sup> (3;0;0)	3	U	NR	2600	Malaysia	Pantai Aceh Forest Reserve	Turner (1990)
<b>neg</b> (2;0;4)	<b>pos</b> (5;0;1)	6	U	NR	2800	Malaysia	Danum Valley	Bebber, Brown & Speight (2004)
n.a.	<b>pos</b> <sup>3</sup>	3	U	NR	2800	Malaysia	Danum Valley	Bebber, Brown & Speight (2002)
n.a.	<b>none</b> (9;3;11)	24	U	T	3000	Panama	Lorenzo	Brenes-Arguedas <i>et al.</i> (2009)
n.a.	<b>pos</b> (1;0;0)	1	U	NR	5000	Cameroon	Korup National Park	Green & Newbery (2002)
none	<b>pos</b> <sup>3</sup>	64 <sup>4</sup>	UG <sup>13</sup>	NR	800	Jamaica	Hellshire Hills	McLaren & McDonald (2003)
<b>pos</b> (2;0;0)	n.a.	2	UG <sup>13</sup>	T	2200	Brazil	BDFPP	Lewis & Tanner (2000)
n.a.	<b>pos</b> (1;1;0)	2	G	T	1100	Benin	Kandi	Biaou <i>et al.</i> (2011)
n.a.	<b>none</b> (0;1;1)	2	G	T	1100	Benin	Bassila	Biaou <i>et al.</i> (2011)
<b>pos</b> (2;0;0)	<b>none</b> (2;0;0)	2	G	T	1300	Ghana	Tinte Bepo Forest Reserve	Veenendaal <i>et al.</i> (1996)
<b>pos</b> (2;1;0)	n.a.	3	G	T	1800	Bolivia	El Tigre	Poorter & Hayashida-Oliver (2000)
<b>pos</b> (1;0;0)	n.a.	1	G	T	2600	Panama	BCNM	Fisher, Howe & Wright (1991)
<b>pos</b> <sup>12</sup> (6;0;0)	<b>pos</b> (5;1;0) <sup>14</sup>	6	G	SS	2600	Panama	BCNM	Pearson <i>et al.</i> (2003)
<b>none</b> (0;1;0)	<b>pos</b> <sup>12</sup> (1;0;0)	1	G	NR	2600	Malaysia	Pantai Aceh Forest Reserve	Turner (1990)

Wet versus dry years:

n.a.	<b>pos</b> <sup>3</sup>	12	U	NR	1700	Thailand	Mae Klog Water shed research station	Marod <i>et al.</i> (2002)
n.a.	<b>none</b> <sup>15</sup>	1	U	NR	2300	Panama	Casarete <sup>8</sup>	Lopez & Kursar (2007)
<b>pos</b> <sup>16</sup>	<b>none</b> <sup>16</sup>	36 <sup>17</sup>	U	NR	2600	Panama	BCI	Comita & Engelbrecht (this study)
(19;3;7)	(3;32;1)							
n.a.	<b>none</b> (0;3;0)	3	U	NR	2600	Panama	BCI	Engelbrecht <i>et al.</i> (2002)
n.a.	<b>pos</b> <sup>18</sup> (1;0;0)	1	U	NR	2600	Panama	BCI	Gilbert <i>et al.</i> (2001)
<b>none</b> <sup>15</sup>	<b>pos</b> <sup>3</sup>	7	U	NR	2700	Malaysia	Lambir Hills, Borneo	Delissio & Primack (2002)

<sup>1</sup> The wet season usually refers to the one following the first dry season, the initial wet season was excluded

<sup>2</sup> In aseasonal sites, data refer to dry and wet periods

<sup>3</sup> No data for individual species provided

<sup>4</sup> Community level study

<sup>5</sup> Stratified random transects, assumed to be predominantly located in the understorey

<sup>6</sup> Evergreen site

<sup>7</sup> Deciduous site

<sup>8</sup> Seasonally flooded forest

<sup>9</sup> Growth for 33 species

<sup>10</sup> Refers to the 10 most abundant species with species specific data

<sup>11</sup> Refers to height growth

<sup>12</sup> Excluding initial wet season

<sup>13</sup> Understorey and gaps pooled cannot be distinguished from the data provided

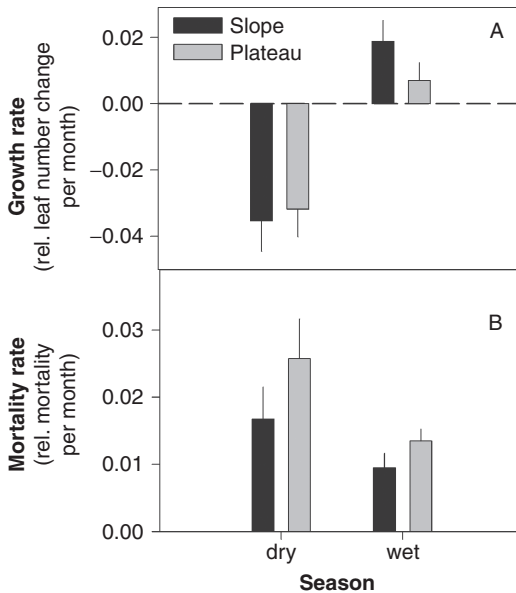
<sup>14</sup> Based on results for medium-sized gaps

<sup>15</sup> No consistent differences between wet and dry years

<sup>16</sup> Year with lowest vs. year with highest dry season rainfall; negligible effect for species if <10% difference

<sup>17</sup> Growth for 29 species

<sup>18</sup> After initial year



**Figure 10.4** Spatial and temporal differences in the performance of naturally regenerating seedlings in the understorey of a tropical moist forest in Panama. Seedlings were monitored in dry plateau and wet slope sites in the dry and the wet season. Relative growth rates (A) were significantly lower in the dry season than in the wet season, but did not differ between habitats. Mortality rates (B) were higher in the dry than in the wet season and higher in the dry plateau than in moist slope sites. Both growth and mortality varied significantly among species (see text). Data are means  $\pm 1$  SE for 36 species for mortality, and 33 species for growth. Redrawn from Comita and Engelbrecht (2009). With permission from the Ecological Society of America (ESA).

have found that plants in tropical forests can be exposed to considerable drought stress. At the height of the dry season, widespread wilting has been observed (Chiariello, Field & Mooney 1987; Engelbrecht *et al.*, unpublished data), and leaf water potentials down to  $-4.8$  MPa have been measured in moist tropical sites during the dry season (Eamus & Prior 2001; Engelbrecht *et al.*, unpublished data; Tobin, Lopez & Kursar 1999; Veenendaal *et al.* 1996), levels far below the conventional wilting point ( $-1.5$  MPa, Larcher 2003) and comparable to midsummer values in savanna datasets or Mediterranean climates (e.g. Eamus & Prior 2001).

In an extensive survey of seasonal growth and survival of seedlings of 36 woody species on Barro Colorado Island, Panama (Comita & Engelbrecht 2009), overall seedling mortality was significantly higher in the dry season than the wet season, particularly in the drier plateau habitat (Figure 10.4). Growth rates also differed significantly between seasons, with overall negative growth (i.e. leaf loss) in the dry season and positive growth in the wet season (Figure 10.4). This was partially, but not exclusively, due to drought-deciduous species. When examining performance of species separately, 80% of species showed higher growth and 65% higher survival in the wet season than in the dry season (Comita & Engelbrecht 2009). The magnitude of the differences in seasonal growth and survival varied among species, and some species showed a pronounced opposite trend, reflecting the wide variation in drought resistance among species. This study was conducted in a year with a relatively severe dry season, and patterns may differ among years with



differing precipitation (see Section 10.4.3 below). However, monthly survival (but not growth) rates were consistently lower in the dry season in three years with different rainfall regimes (Comita & Engelbrecht, unpublished data). The findings of these and other studies (Table 10.2) are consistent with widespread water limitation of seedling growth and drought-induced mortality during the dry season in seasonal tropical forests.

Drought has even been shown to be an important driver of seedling mortality in seasonally flooded forests, where inundation during the wet season is often thought to be the most extreme stress with which seedlings have to contend. In a study of four species in seasonally flooded forests in Darien, Panama, seedling mortality per month was three times as great in the dry season as in the wet season (Lopez & Kursar 2007). Similarly, decreased seedling growth and increased seedling mortality in response to drought has been observed for tree species in Amazonian floodplain forests (reviewed in Parolin *et al.* 2010).

Despite the fact that the majority of species examined exhibit lower seedling performance in the dry season, depending on species' drought resistance, dry season strength and microsite conditions, some species appear to be able to take advantage of higher light conditions and lower pest pressure in the dry season (e.g. Comita & Engelbrecht 2009; Yavitt & Wright 2008). In particular, drought-resistant species and individuals located in moist microsites should stand to benefit from dry season conditions.

Not only do rates of seedling mortality vary between seasons, but the agents of mortality can differ completely between wet and dry seasons. For example, in a study of 12 species in Thailand, drought and fire caused mortality in the dry season, whereas wet season mortality was caused by pathogens, insect herbivores and physical damage, as well as additional unknown causes (Marod *et al.* 2002). Furthermore, the importance of different agents for accumulated annual mortality differed substantially among species: whereas in one species all mortality was due to drought, in other species pathogens or physical damage were the main causes of death. These results highlight the differential selection pressures in the dry and wet season, and indicate that the importance of different mortality agents is likely to shift under altered precipitation regimes.

### **10.4.3 Effects of interannual variation in precipitation**

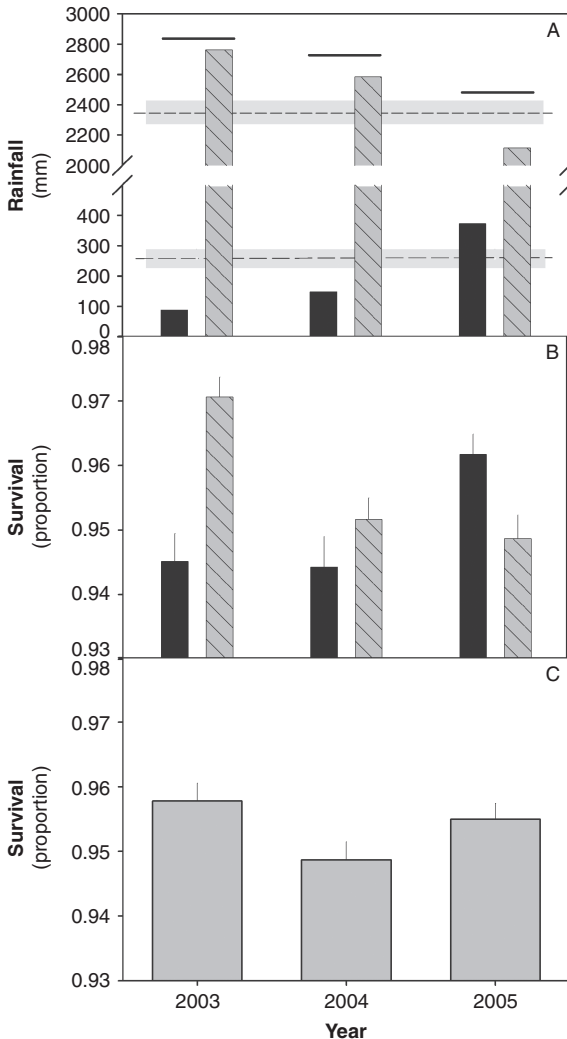
Year-to-year variation in total rainfall and dry season severity has also been shown to influence seedling dynamics (Table 10.2). For example, strong interannual variation in seedling mortality was found in a 5-year study in Thailand (Marod *et al.* 2002) and could be attributed to differences in annual rainfall: seedling survival was lowest in the driest year and highest when annual rainfall was highest. Further evidence for the role of water availability in

driving these patterns comes from the fact that these differences in annual survival were related to dry season mortality, which varied substantially among years (3.2–8.7% per month), but not to wet season mortality, which was relatively stable across years (11.6–13.8% per month).

A number of studies have specifically compared seedling performance in years with and without El Niño-related droughts. In northwest Borneo, higher seedling mortality and stem-dieback was observed over a 2-year census interval with a severe El Niño-associated drought compared with earlier (baseline) census intervals (Delisio & Primack 2003). In a 3-year study of *Prioria copaifera*, the dominant species in a seasonally flooded forest, seedling mortality was higher during a long El Niño dry season compared with a mild dry season, but seedling mortality rates were highest in a 'normal' dry season (Lopez & Kursar 2007).

At our study site in Central Panama, we monitored growth and survival of naturally occurring seedlings of 36 species over three years that differed substantially in precipitation patterns (Comita & Engelbrecht, unpublished data). The first year of the study, 2003, had a particularly severe dry season associated with an El Niño event (Figure 10.5A). Dry season rainfall in 2004 was also below average, but higher than in 2003. In contrast, dry season rainfall in 2005 was above average. Interestingly, wet season rainfall, as well as total annual rainfall, showed the opposite pattern, with precipitation highest in 2003 and lowest in 2005, thereby allowing us to separate out effects of dry season vs. total annual rainfall on seedling performance (Figure 10.5B).

We found that dry season survival was lowest in 2003 and 2004, years with below average dry season rainfall, and highest in 2005, the year with above average dry season rainfall (Figure 10.5B). Over the three years, wet season mortality rates similarly mirrored rainfall in the wet season, with the highest wet season survival in 2003 (the year with the highest wet season rainfall) and the lowest wet season survival in 2005 (the year with the lowest wet season rainfall). Interestingly, *annual* survival rates did not differ significantly among years (Figure 10.5C), in part owing to the opposing trends in dry and wet season mortality, but also owing to mixed responses of the 36 focal species (Figure 10.6), which were driven by differences in species' drought resistance (discussed below). These results demonstrate how a lack of community-level variation in seedling performance can mask large differences among species in responses to water availability. Ignoring such variation would lead to incorrect predictions about how species composition and diversity would shift in response to climate change. In addition, these results and others (e.g. Lopez & Kursar 2007, discussed above) suggest that while drought stress during severe dry seasons, such as those associated with El Niño events, often negatively affects seedling performance, annual mortality rates may not be strongly affected since non-drought-related mortality agents can also cause

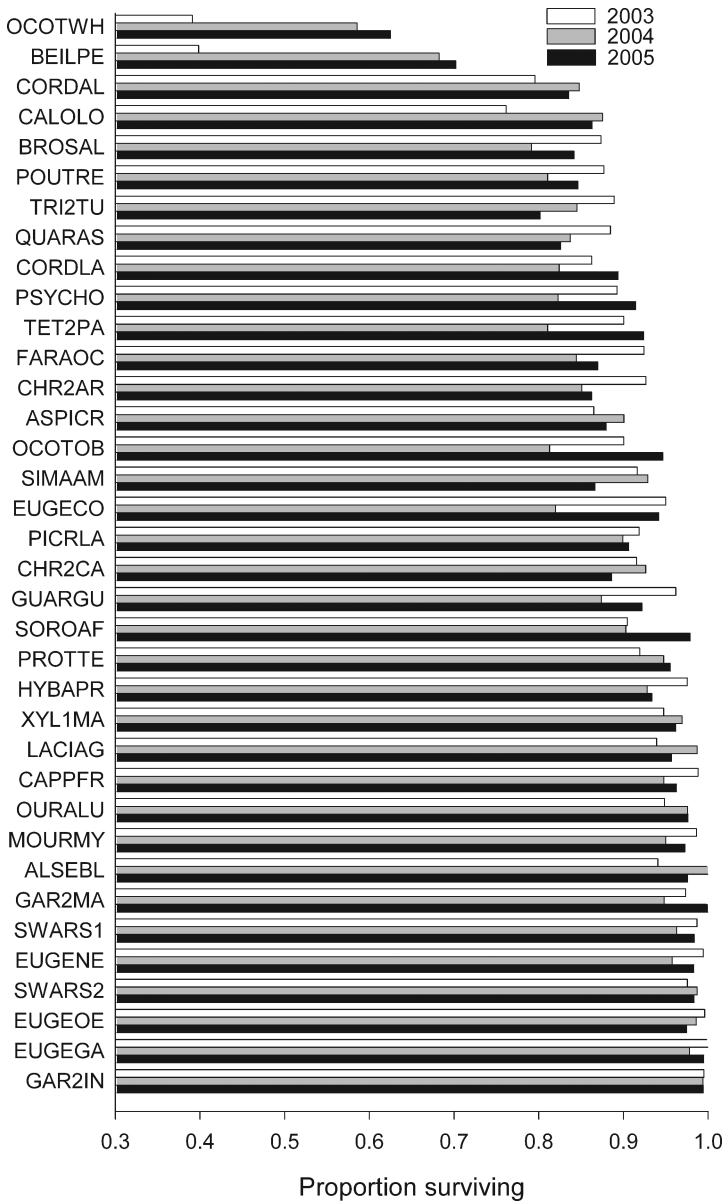


**Figure 10.5** Rainfall and survival of seedlings of 36 species in lowland tropical forest on BCI, Panama, in three years that differed in precipitation patterns. Cumulative dry and wet season rainfall (black bars and grey hatched bars, respectively) varied widely among the three years (A), as did total annual rainfall (bold horizontal lines). Dashed horizontal lines depict the 30-average seasonal rainfall  $\pm 1$  SE for the dry season (lower line) and wet season (upper line). (B) The proportion of seedlings surviving the 4-month dry season (black bar) and the 8-month wet season (grey hatched bar). Monthly survival rates were higher in the wet season than in the dry season in all three years (not shown). (C) The proportional annual seedling survival. Mean and SE values of the proportion surviving are corrected for differences in leaf number (within species) to account for changes in the size of surviving seedlings over time. Data in (A) are from ESP (2011).

high mortality rates. As a result, across years differing in precipitation patterns, the relationship between water availability and seedling performance is far from straightforward, further complicating attempts to predict how regeneration dynamics will respond to changing climate.

#### 10.4.4 Spatial variation in water availability

Annual rainfall varies widely across tropical regions. For example, across the Amazon basin, as well as in tropical West Africa, annual rainfall varies from about 1000 mm to more than 4000 mm (Sombroek 2001; Poorter *et al.* 2004; Quesada *et al.* 2009; Swaine 1996). Sharp rainfall gradients can also occur over



**Figure 10.6** Annual survival rates of naturally regenerating seedlings of 36 species on Barro Colorado Island, Panama, in three years that differed in precipitation (see Figure 10.5A). Values of proportion surviving are corrected for differences in leaf number (within species) to account for changes in the size of surviving seedlings over time.

relatively short distances. Across the Isthmus of Panama, rainfall varies from *c.* 1600 mm on the Pacific coast to *c.* 3100 mm on the Caribbean coast, over a distance of only 65 km (ACP 2011), and results in pronounced differences in soil moisture availability (Engelbrecht *et al.*, unpublished data). Such rainfall gradients are usually, but not always, associated with changes in dry season length (e.g. Clinebell *et al.* 1995; Davidar *et al.* 2007).

At local scales, soil moisture varies with topographic position, slope angle and position, soil texture (e.g. % clay), and canopy openness, leading some plants to experience significantly higher or lower water availability than individuals located only tens or hundreds of metres away. In particular, ridges and plateaus tend to have drier soils than slopes and valleys (Becker *et al.* 1988; Daws *et al.* 2002; Gibbons & Newbery 2003; Markesteijn *et al.* 2010), sandy soils are more drought-prone than loamy soils (Larcher 2003) and understorey sites drier than gaps (Becker *et al.* 1988; Poorter & Hayashida-Oliver 2000; Veenendaal *et al.* 1996). In the following, we will first discuss effects of local-scale variation in water availability on seedling performance, and then review available data on effects of larger-scale variation in rainfall.

#### 10.4.5 Effects of local-scale variation in soil moisture

Since soil moisture varies with topography and soil properties, differences in seedling performance among local habitats may be driven in large part by differences in soil water availability. It is important to note, however, that additional factors, including light and nutrient availability, and pest pressure, can vary among soil types or with topography (e.g. Fine, Mesones & Coley 2004; Gunatilleke *et al.* 2006; John *et al.* 2007; Palmiotto *et al.* 2004; Russo *et al.* 2012) so care must be taken when interpreting results of observational studies. Table 10.3 lists studies that have compared seedling performance between habitats that vary in soil moisture.

Differences in habitat soil moisture may initially shape regeneration through effects on germination and early seedling establishment. For example, seedling emergence and dry season survival of first year seedlings were higher in moist slope sites than in drier plateau sites on Barro Colorado Island, Panama (Daws *et al.* 2005). However, during the wet season, mortality was elevated on slopes, presumably owing to damage from overland water flow during intense rainfall or higher pathogen attack in the wetter slope sites. Thus, wetter habitats can be either beneficial or detrimental to early seedlings, depending on whether drought or physical damage and pathogen attack are more important causes of mortality.

The performance of later seedling stages has also been shown to vary among topographic habitat types. Higher mortality in drier plateau sites than in wetter slope sites was observed in the 50-ha Forest Dynamics Plot on Barro Colorado Island, with the difference between habitats particularly

**Table 10.3** Effect of spatial variation in soil moisture availability on seedling performance of woody tropical species.

A positive effect signifies overall higher performance at higher soil moisture conditions (i.e. wetter habitats or sites), a negative effect lower performance at higher soil moisture, and none, no significant overall effect. Numbers in brackets give the number of species exhibiting a positive effect of a moister habitat, a negligible effect, or a negative effect, respectively. The habitat comparison, based on topography, soils or rainfall regime, is specified for local-scale studies, and the rainfall regimes at the study sites for regional-scale comparisons. Studies are sorted by habitat (understorey, gap), and by the average annual rainfall (mm) at the study site.

Dry season <sup>1</sup>		Wet season		Annual		Number of species	Habitat	Approach <sup>11</sup>	Rainfall	Country	Site	Study
Growth	Survival	Growth	Survival	Growth	Survival							
Local scale:												
n.a.	<b>pos</b> <sup>2</sup>	n.a.	<b>neg</b> <sup>2</sup>	n.a.	n.a.	>58 <sup>3</sup>	U	NR	2600	Panama	BCNM	Daws <i>et al.</i> (2005)
<b>none</b> (17;1;15) <sup>4</sup>	<b>pos</b> (23;6;7) <sup>4</sup>	<b>pos</b> (22;1;10) <sup>4</sup>	<b>pos</b> (27;1;8)	<b>none</b> (20;2;11) <sup>4</sup>	<b>pos</b> (27;2;7) <sup>4</sup>	36 <sup>5</sup>	U	NR	2600	Panama	BCNM	Comita & Engelbrecht (2009)
<b>none</b> <sup>2</sup>	<b>none</b> <sup>2</sup>	<b>none</b> <sup>2</sup>	<b>none</b> <sup>2</sup>	n.a.	n.a.	6	U	NR	2800	Malaysia	Danum Valley	Bebber, Brown & Speight (2004)
n.a.	n.a.	n.a.	n.a.	<b>none</b> (0;3;3)	<b>none</b> (0;3;3)	6	U	T	3000	Malaysia	Lambir	Palmiotto <i>et al.</i> (2004)
n.a.	n.a.	n.a.	n.a.	<b>none</b> (1;3;0)	<b>none</b> <sup>6</sup> (0;3;1)	4	U <sup>7</sup>	T	3600	Madagascar	Tampolo	de Gouvenain <i>et al.</i> (2007)
n.a.	n.a.	n.a.	n.a.	<b>pos</b> (2;2;0)	<b>pos</b> (8;1;0)	4	U	T	5000	Sri Lanka	Sinhajara	Ashton <i>et al.</i> (1995)
n.a.	n.a.	n.a.	n.a.	<b>none</b> (2;2;2)	<b>pos</b> (3;3;0)	6	G	T	3000	Malaysia	Lambir	Palmiotto <i>et al.</i> (2004)
n.a.	n.a.	n.a.	n.a.	<b>none</b> (1;3;0)	<b>none</b> (0;3;1)	4	G	T	3600	Madagascar	Tampolo	de Gouvenain <i>et al.</i> (2007)
n.a.	n.a.	n.a.	n.a.	<b>pos</b> (4;0;0)	<b>none</b> (0;2;2)	4	G <sup>8</sup>	T	5000	Sri Lanka	Sinhajara	Ashton <i>et al.</i> (1995)

regional/large scale	pos	n.a.	none	pos	pos	long-short dry season/dry woodland	2	U	T	1000 vs. Benin 1200 <sup>9</sup>	Kandi	Biaou <i>et al.</i> (2011)
n.a.	pos (2;0;0)	n.a.	none (1;0;1)	pos (2;0;0)	pos (2;0;0)	long-short dry season/dry woodland	2	G	T	1000 vs. Benin 1200 <sup>9</sup>	Bassila	Biaou <i>et al.</i> (2011)
n.a.	pos (2;0;0)	n.a.	none (1;0;1)	pos (2;0;0)	pos (2;0;0)	long-short dry season/dry woodland	2	G	T	1000 vs. Benin 1200 <sup>9</sup>	Bassila	Biaou <i>et al.</i> (2011)
n.a.	pos (14;4;5)	n.a.	none (9;3;11)	neg (4;0;20)	n.a.	rainfall: low-high moist/wet forest	24 <sup>10</sup>	U	T	1700 vs. Panama 3000	Gunn Hill-Lorenzo	Brenes-Arguedas <i>et al.</i> (2009)
none	pos	none	none	none	pos	rainfall: low-high moist/wet forest	36	U	T	1600 vs. Panama 3000	Cardenas – Lorenzo	Engelbrecht (unpub. data)

<sup>1</sup> In aseasonal sites, data refer to dry and wet period

<sup>2</sup> No data for individual species provided

<sup>3</sup> Community-level study

<sup>4</sup> Considered negligible effect if <10% difference

<sup>5</sup> Growth for 33 species

<sup>6</sup> Data over 2 years

<sup>7</sup> Results refer to extremes of moisture and light gradient

<sup>8</sup> Results refer to gap centres

<sup>9</sup> 5 vs. 7 months dry season

<sup>10</sup> 23 species for survival

<sup>11</sup> NR = Naturally regenerating, T = transplanted

pronounced in the dry season (Figure 10.4), suggesting that differences between the two habitats in seedling performance was due primarily to water availability (Comita & Engelbrecht 2009). In particular, species whose adult trees are associated with the moist slope habitats showed higher mortality in the plateau versus the slope habitat in the dry season. On the other hand, species whose adults are associated with drier plateau habitats showed no difference in seedling mortality rates between the habitats, regardless of season (Comita & Engelbrecht 2009). The fact that differential mortality between the two habitats was most pronounced for species associated with moist sites, specifically in the dry season, again suggests that water availability was indeed a key driver of patterns of seedling performance.

The importance of water availability, rather than nutrients, in driving differences in species' performance among topographic habitats was convincingly shown in a transplant study in Malaysian Borneo (Palmiotto *et al.* 2004). For four out of six species studied, seedling growth rates varied significantly between drier ridges and wetter gullies, habitats that also differ in soil water holding capacity and nutrient status. Two of the species showed higher growth and two lower growth in gullies, indicating interspecific variation in resource requirements. The importance of varying water availability (and/or the development of anoxic conditions) for the observed habitat differences was confirmed by the fact that phosphorus additions had no significant effect on growth rates (despite elevated soil and tissue P concentrations). In the same study, seedling survival was significantly higher in the wetter gullies than on the drier ridge tops for three of the study species, but only when they were growing in gap sites. In summary, available data indicate that variation in water availability can play a substantial direct role in driving local performance differences among habitats.

#### **10.4.6 Effects of regional variation in rainfall**

Regional-scale variation in water availability may also influence seedling performance. A comparison of dynamics of naturally occurring seedlings at four tropical forest sites with different rainfall regimes (BCI, Panama; Pasoh, Malaysia; Nouragues, French Guinea; and Yasuní, Ecuador) showed that the most seasonal site (BCI) had the highest annual mortality rates (Metz *et al.* 2008). However, the second highest mortality rate occurred at the wettest, aseasonal site (Yasuní), and within-site spatial and temporal variation in seedling demographic rates exceeded differences among sites (Metz *et al.* 2008). Such comparisons are useful at the community level, but do not allow for comparisons of the performance of individual species under varying rainfall conditions, because of corresponding shifts in species composition.



Large-scale transplant experiments are therefore necessary to assess variation of seedling performance under different rainfall regimes (Table 10.3). In a transplant experiment with 24 woody plant species across a rainfall gradient in Panama ranging from c. 1700 mm to 3000 mm, Brenes-Arguedas *et al.* (2009) found overall very similar annual mortality rates for seedlings planted at the dry and the wet site (2.3% vs. 2.5% per month). At both sites, mortality was considerably higher in the seedlings' first dry season than in the subsequent wet season, but this effect was especially pronounced at the dry site. Overall leaf production at the dry site was double that at the wet site. However, these overall effects average out pronounced differences among the species that were related to their distribution with respect to rainfall, with each group having the highest survival in their place of origin: species occurring in dry areas exhibited higher survival at the dry site, and species restricted to moist sites had higher survival at the wet site. For growth, both groups had higher leaf production at the dry site, but the difference was especially pronounced for species restricted to wet sites. The pronounced mortality in the dry season in the dry site, which was alleviated through irrigation, shows that low water availability directly leads to mortality at that site. However, other results of the study hint towards the importance of additional factors in shaping performance differences between the sites. Understorey light levels and nutrients were higher in the dry site (Brenes-Arguedas *et al.* 2008, 2011), probably contributing to the considerably higher growth rates at that site. Additionally, leaf damage was higher at the wet site, further reducing growth rates there (Brenes-Arguedas, Coley & Kursar 2009). Because forest structure, understorey light levels, pathogen and herbivore pressure, and soil nutrients vary among forests and along rainfall gradients, it is challenging to separate out the effect of drought in such experiments. However, they give a realistic picture of the integrated responses of seedling performance and dynamics to the complex shifts of environmental factors with changing rainfall regimes, and are therefore highly relevant for understanding consequences of global climate change.

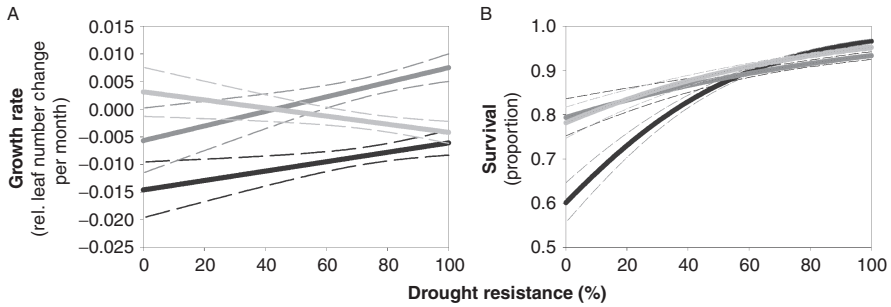
Two additional multi-species datasets from transplant experiments across rainfall gradients in tropical wet to moist forest, another one from Panama and one from Southeast Asia, also found strong differences in survival of seedlings of woody species between sites with different rainfall regimes, but neither found growth differences (Engelbrecht, unpublished data; Baltzer & Davies, personal communication). A comparison between transplanted seedlings at two woodland sites with different dry season lengths in Benin showed consistent results (Biaou *et al.* 2011): survival was considerably higher at the mesic than at the dry site, with an especially pronounced effect on the drought-sensitive species, but growth again did not differ between sites.

### 10.5 Species' drought resistance, regeneration dynamics, and species distributions and diversity

The studies reviewed above indicate that periods of low water availability typically have negative effects on seedling performance at the community level, but, at the same time, there exists huge variation among species in their responses. Variation in species' drought resistance – as quantified from irrigation experiments – has been shown to determine how individual species respond to natural variation in water availability. For example, Comita and Engelbrecht (2009) found that survival rates in drier plateau habitats were significantly positively correlated with species' drought resistance in the dry season (where drought resistance was measured in independent experiments; Engelbrecht *et al.* 2007). However, this was not the case in either the wet season or in wetter slope habitats. Similar patterns were found for growth rates (after excluding drought-deciduous species; Comita & Engelbrecht 2009). These results provide strong evidence that direct effects of low water availability lead to low survival and growth of seedlings of drought-sensitive species in drier habitats.

Species' drought resistance also determines how species respond to interannual variation in water availability. Overall, seedling survival rates were positively related to species' drought resistance in all three years of our study of naturally occurring seedlings in central Panama (Figure 10.7, Comita & Engelbrecht, unpublished data; described above in Section 10.4.3). However, the relationship was significantly stronger in the year with the driest dry season, indicating that drought-sensitive species do indeed have reduced survival in drought years (Figure 10.7). Interestingly, growth rates showed a positive relationship with species' drought resistance in years with below average dry season rainfall, but a negative relationship in the year with above average dry season rainfall (Figure 10.7). These results suggest that, despite their lower survival, drought-sensitive species are able to coexist with drought-resistant species owing to their higher growth in years when water is not as limiting. This is consistent with results from a regional-scale study that found that species occurring on the wetter side of the Isthmus of Panama had higher growth rates and were better able to take advantage of increased light availability when water was not limiting, compared with species occurring on the drier side (Brenes-Arguedas *et al.* 2011). Similarly, in a study of saplings and trees  $\geq 1$  cm dbh in Southeast Asia, species restricted to wet aseasonal forests had higher growth rates than species occurring in dry seasonal forests (Baltzer *et al.* 2007).

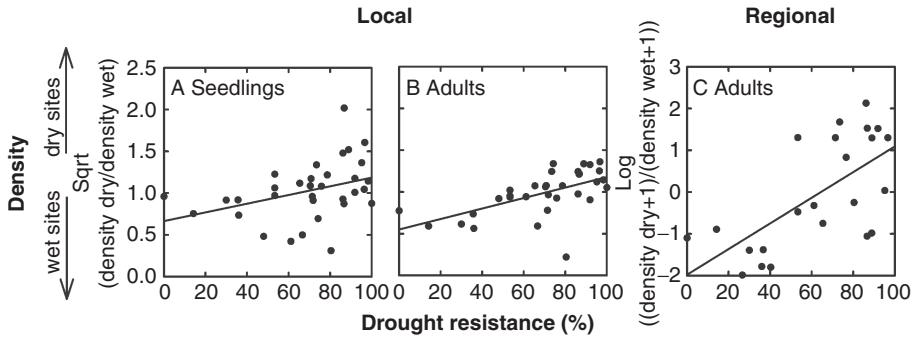
These studies suggest that variation in tropical tree species' drought resistance, combined with variation in water availability, plays a large and direct role in determining where and when species can successfully regenerate. This, in turn, suggests a key role for drought resistance in shaping distribution patterns of tropical tree species. Indeed, it has long been recognised that



**Figure 10.7** Relationship between species' drought resistance and (A) annual seedling growth and (B) survival in three years with different rainfall patterns on Barro Colorado Island, Panama. Data are for 2003 (black, very strong dry season), 2004 (dark grey, below average dry season rainfall) and 2005 (light grey, above average dry season rainfall). Data are means (solid lines), and 1 SE (dashed lines). All relationships were significant, and there was a significant growth  $\times$  year and survival  $\times$  year interaction. Mean and SE values of growth rates and proportion surviving are corrected for differences in leaf number (within species) to account for changes in the size of surviving seedlings over time. Drought resistance was independently assessed in a field irrigation experiment (Figure 10.2C; Engelbrecht *et al.* 2007).

water availability is a major correlate of distributions and diversity patterns of plant species (e.g. Currie & Paquin 1987; Hawkins *et al.* 2003; Kreft & Jetz 2007; Whittaker & Niering 1975). In lowland tropical forests, numerous regional-scale studies have found that diversity, species composition and species distributions strongly correlate with annual rainfall or dry season intensity (e.g. Bongers *et al.* 1999; Bongers, Poorter & Hawthorne 2004; Clinebell *et al.* 1995; Condit 1998; Davidar, Puyravaud & Leigh 2005; Gentry 1988; Hall & Swaine 1981; Hawkins *et al.* 2003; Holdridge *et al.* 1971; Medina 1999; Pyke *et al.* 2001; Slik *et al.* 2003; ter Steege *et al.* 2006). In addition, tropical forests undergo pronounced temporal shifts in species abundance and distribution on scales of decades, as well as thousands of years, that are associated with changes in rainfall patterns (e.g. Condit, Hubbell & Foster 1996; Enquist & Enquist 2011; Feeley *et al.* 2011; Mayle & Power 2008). Moreover, at local scales, many tropical plants show associations with topographic habitat types that vary in soil moisture (e.g. Harms *et al.* 2001; Newbery *et al.* 1996; Svenning 1999; Valencia *et al.* 2004; Webb & Peart 2000).

Despite obvious correlations with water availability, other factors, such as soil nutrients, light availability, pest pressure or historical mechanisms, can covary with water availability and therefore could be responsible for observed correlations between water availability and species' distributions (Baltzer *et al.* 2008; Brenes-Arguedas *et al.* 2009; Givnish 1999; ter Steege *et al.* 2003; Veenendaal & Swaine 1998). However, two recent studies strongly suggest a



**Figure 10.8** Relationship between species drought resistance and local and regional distribution patterns in lowland tropical forests in Central Panama. There was a significant relationship with drought resistance for local density in dry plateau vs. wetter slope sites for (A) seedlings ( $R^2 = 0.14$ ,  $P = 0.035$ ), and for (B) trees  $\geq 1$  cm dbh ( $R^2 = 0.34$ ,  $P = 0.0004$ ) in the BCI 50-ha Forest Dynamics Plot. There was also a significant relationship between drought resistance and the density of adults in a plot on the dry side vs. on the wet side of the Isthmus of Panama (C) ( $R^2 = 0.44$ ,  $P = 0.0006$ ). Redrawn from Engelbrecht *et al.* (2007).

direct, causal role of water availability in shaping tropical tree species' distributions at regional and local scales. Engelbrecht *et al.* (2007) examined distribution patterns of 48 tree and shrub species and found that species' drought resistance, assessed experimentally at the seedling stage, was significantly correlated with species distributions at the regional scale across 122 inventory plots spanning a strong rainfall gradient from the Pacific to the Caribbean side of the Isthmus of Panama (Figure 10.8). At the local scale, within a single large plot (50 ha) in the centre of the rainfall gradient, the distributions of species across topographic habitat types that vary in soil moisture (plateau vs. slope) were also significantly related to species' drought resistance both at the seedling and adult stage (Figure 10.8). In addition, it was shown that these correlations did not arise indirectly through species' responses to variation in light or nutrients (Engelbrecht *et al.* 2007). Similarly, Baltzer *et al.* (2008) found that species' distributions along a climatic gradient spanning the Malay–Thai Peninsula were related to experimentally assessed species' desiccation tolerance, not to historical factors, as had previously been suggested. Specifically, species whose distributions included seasonally dry forests were more desiccation-tolerant and showed different associated physiological characteristics than species restricted to wet aseasonal forests (see Section 10.3 above). Together, these studies provide strong evidence that species' drought resistance interacts with water availability to shape distribution patterns at local and regional scales in the tropics.

Water availability also plays a significant role in shaping patterns of diversity within and among tropical forests. In general, species diversity increases with precipitation and decreases with dry season length across tropical forests (Bongers, Poorter & Hawthorne 2004; Clinebell *et al.* 1995; Condit 1998; Davidar, Puyravaud & Leigh 2005; Gentry 1988; Hall & Swaine 1981; Hawkins *et al.* 2003; Holdridge *et al.* 1971; Medina 1999; Pyke *et al.* 2001; ter Steege *et al.* 2003). On local scales, habitats with high soil moisture tend to support higher tree species richness than drier habitats, although light and nutrient availability also vary with topography (e.g. Gunatilleke *et al.* 2006; Hubbell & Foster 1983; Hubbell *et al.* 1999). Experimental studies support the idea that water availability plays a direct role in shaping such patterns through effects on seedling diversity. In an irrigation experiment in Peru, watered plots had a higher density and higher species richness than unwatered plots, for both sown and naturally occurring seedlings (Paine, Harms & Ramos 2009). Similarly, irrigation had a significant, positive effect on seedling species richness in Panama (Bunker & Carson 2005). These results suggest that drought stress leads to the loss of drought-sensitive species through mortality, and thus decreases species diversity. Additionally, density-dependent mortality due to species-specific pests may be higher in wetter habitats, thus allowing for the coexistence of more species (Givnish 1999).

## 10.6 Conclusions and future research directions

Several conclusions can be drawn from the studies reviewed above. First, water availability is clearly an important driver of regeneration dynamics under current climatic conditions, particularly in seasonal tropical forests and during drought events. This is demonstrated by patterns of seedling recruitment, growth and survival in response to seasonal, interannual and spatial variation in water availability, as well as by experiments that show increased performance in response to supplemental watering during dry periods. Second, although low water availability (i.e. drought) tends to have negative consequences on seedling performance at the community level, there exists huge variation among species in their responses to drought. Variation in drought resistance among tropical woody plant species is governed by differences in physiological traits, primarily those that allow species to tolerate low water availability (i.e. mechanisms of desiccation tolerance). Third, the variation among species in drought resistance, and resulting variation in regeneration dynamics, plays a significant role in shaping differences in species distribution and diversity patterns across rainfall gradients (i.e. changes in annual precipitation and dry season length) at regional scales, and across local soil moisture gradients (associated with topography or soils).

How will altered precipitation patterns due to climate change affect tropical forests, given the relationship between water availability, regeneration

dynamics and species distributions? First, increases in dry season length or increases in the severity or frequency of drought events are expected to reduce recruitment, growth and survival of seedlings of drought-sensitive species, particularly in dry habitats and at the dry end of their ranges. As a result, within tropical tree communities, we anticipate a decrease in the abundance of drought-sensitive species, and a restriction of those species to wetter microsites (e.g. slopes and depressions). Failure to regenerate may eventually lead to local extinction of drought-sensitive species, resulting in a loss of diversity within the local community, and a contraction of species ranges at the regional scale, which will increase the probability of extinction at larger scales.

On the other hand, increased rainfall or decreased dry season length will not necessarily increase seedling performance at the community level or favour drought-sensitive species. The irrigation experiments reviewed above found that, although increased water availability increases seedling performance in the dry season, such effects do not necessarily add up to higher growth and survival over the course of the entire year. This is because other mortality agents may become increasingly important with higher water availability (e.g. pathogen and herbivore damage, and light and nutrient availability), and may compensate for decreased drought-related mortality. In addition, increases in the intensity of precipitation events, i.e. strong rainfall, may wash away seeds and young seedlings and also physically damage established seedlings and saplings. Thus, under increased rainfall, the 'winners' are more likely to be determined by resistance to physical damage and pest pressure or their competitive ability than by their drought resistance. Increased rainfall that leads to flooding would also favour tropical tree species that can tolerate anoxic conditions (Parolin *et al.* 2010).

If changing precipitation patterns mainly affect regeneration, such changes to tree community composition and diversity may not be observable for tens to hundreds of years or longer, since tropical tree species are very long-lived. However, if drought events or intense rainfalls are severe enough to increase adult tree mortality (e.g. Phillips *et al.* 2010), effects could be evident on a much shorter time scale. Increased adult mortality would additionally affect regeneration through increased formation of light gaps, which would favour pioneer species (Slik 2004).

To accurately predict how tropical tree species and communities will respond to changing precipitation through effects on regeneration, there are several areas of research that still need to be undertaken. First, the majority of studies of tropical tree species' response to water availability come from a relatively small number of sites, with the majority being conducted in lowland, seasonal, moist forests in the Neotropics. Studies from additional tropical areas (e.g. dry and wet forests, aseasonal and montane, Neotropical vs. Palaeotropical) are needed to further our understanding of

the differences in drought responses and drought resistance among communities and regions. It is important to note that careful monitoring of water availability will be necessary to allow for meaningful cross-site comparisons.

Second, there is a dearth of quantitative data on how water availability interacts with other abiotic factors (i.e. light, nutrients, temperature and CO<sub>2</sub>), and how it influences biotic interactions (e.g. pathogen or herbivore attack). These factors undoubtedly influence species performance and distributions, and are known to vary often with water availability (e.g. Givnish 1999; Swaine 1996; Veenendaal *et al.* 1996). However, how such interactions affect regeneration dynamics in tropical forest communities, and the ramifications for species distributions and diversity, remain to be explored.

Third, an improved mechanistic understanding of tropical tree species' physiological responses to drought is needed to develop meaningful proxies and identify 'soft traits' that correlate with species' drought resistance. This is particularly important for making projections of species' responses and effects on ecosystem functions in tropical forests, where the high diversity precludes detailed studies of all species in the community.

Fourth, although it is clear that there is wide variation among tropical tree species in drought resistance, little is known about variation within species, in terms of either phenotypic plasticity or genetic variation. Such information is key for assessing the potential of species to adapt to changing climate and to predict when and where species will be most affected (Williams *et al.* 2008). Furthermore, estimates of tropical tree species' migration potentials are needed to determine whether species will be able to track climate across the landscape (Clark *et al.* 2003).

Finally, efforts to predict the future of tropical forests under global climate change are currently hampered by the fact that existing climate change models can only predict precipitation patterns with extremely high uncertainty (IPCC 2007), particularly at regional to local spatial scales (e.g. Malhi *et al.* 2009).

In conclusion, our results highlight the sensitivity of tropical forest trees to variation in water availability. Thus, shifts in precipitation patterns will undoubtedly influence the population dynamics and distributions of individual species, with likely consequences for community composition, diversity and ecosystem functioning. The full extent of these changes remains unclear, but the resilience of these ecosystems will depend in large part on the degree to which large, contiguous, intact swaths of tropical forest are preserved.

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## References

- ACP (2011) ACP Physical Monitoring Downloads. [http://striweb.si.edu/esp/physical\\_monitoring/download\\_acp.htm](http://striweb.si.edu/esp/physical_monitoring/download_acp.htm)
- Allan, R., Lindesay, J. & Parker, D. E. (1996) *El Niño, Southern Oscillation and Climatic Variability*. Silver Spring, MD: Aubrey Books Intl Ltd.
- Allen, C. D., Macalady, A. K., Chenchouni, H. *et al.* (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.
- Arndt, S. K., Clifford, S. C., Wanek, W., Jones, H. G. & Popp, M. (2001) Physiological and morphological adaptations of the fruit tree *Ziziphus rotundifolia* in response to progressive drought stress. *Tree Physiology*, **21**, 705–715.
- Ashton, P. S. (1993) The community ecology of Asian rainforests, in relation to catastrophic events. *Journal of Biosciences*, **18**, 501–514.
- Ashton, P. H. S., Gunatilleke, C. V. S. & Gunatilleke, I. (1995) Seedling survival and growth of four *Shorea* species in a Sri Lankan rainforest. *Journal of Tropical Ecology*, **11**, 263–279.
- Asquith, N. M. & Mejia-Chang, M. (2005) Mammals, edge effects, and the loss of tropical forest diversity. *Ecology*, **86**, 379–390.
- Baltzer, J. L., Davies, S. J., Bunyavejchewin, S. & Noor, N. S. M. (2008) The role of desiccation tolerance in determining tree species distributions along the Malay–Thai Peninsula. *Functional Ecology*, **22**, 221–231.
- Baltzer, J. L., Davies, S. J., Noor, N. S. M., Kassim, A. R. & LaFrankie, J. V. (2007) Geographical distributions in tropical trees: can geographical range predict performance and habitat association in co-occurring tree species? *Journal of Biogeography*, **34**, 1916–1926.
- Bawa, K. S. & Markham, A. (1995) Climate change and tropical forests. *Trends in Ecology & Evolution*, **10**, 348–349.
- Bebber, D., Brown, N. & Speight, M. (2002) Drought and root herbivory in understorey *Parashorea* Kurz (Dipterocarpaceae) seedlings in Borneo. *Journal of Tropical Ecology*, **18**, 795–801.
- Bebber, D. P., Brown, N. D. & Speight, M. R. (2004) Dipterocarp seedling population dynamics in Bornean primary lowland forest during the 1997–8 El Niño–Southern Oscillation. *Journal of Tropical Ecology*, **20**, 11–19.
- Becker, P. (1992) Seasonality of rainfall and drought in Brunei Darussalam. *Brunei Museum Journal*, **7**, 99–109.
- Becker, P., Rabenold, P. E., Idol, J. R. & Smith, A. P. (1988) Water potential gradients for gaps and slopes in a Panamanian tropical moist forests dry season. *Journal of Tropical Ecology*, **4**, 173–184.
- Becker, P. & Wong, M. (1993) Drought-induced mortality in tropical heath forest. *Journal of Tropical Forest Science*, **5**, 416–419.
- Biaou, S. S. H., Holmgren, M., Sterck, F. J. & Mohren, G. M. J. (2011) Stress-driven changes in the strength of facilitation on tree seedling establishment in West African woodlands. *Biotropica*, **43**, 23–30.
- Blain, D. & Kellman, M. (1991) The effect of water supply on tree seed germination and seedling survival in a tropical seasonal forest in Veracruz, Mexico. *Journal of Tropical Ecology*, **7**, 69–83.
- Bonal, D. & Guehl, J. M. (2001) Contrasting patterns of leaf water potential and gas exchange responses to drought in seedlings of tropical rainforest species. *Functional Ecology*, **15**, 490–496.



- Bongers, F., Poorter, L. & Hawthorne, W. D. (2004) The forests of Upper Guinea: gradients in large species composition. In *Biodiversity of West African forests. An Ecological Atlas of Woody Plant Species* (eds L. Poorter, F. Bongers, F. N. Kouame & W. D. Hawthorne), pp. 41–52. Oxford, UK: CABI Publishing.
- Bongers, F., Poorter, L., Van Rompaey, R. & Parren, M. P. E. (1999) Distribution of twelve moist forest canopy tree species in Liberia and Cote d'Ivoire: response curves to a climatic gradient. *Journal of Vegetation Science*, **10**, 371–382.
- Borchert, R. (1994) Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology*, **75**, 1437–1449.
- Brenes-Arguedas, T., Coley, P. D. & Kursar, T. A. (2009) Pests vs. drought as determinants of plant distribution along a tropical rainfall gradient. *Ecology*, **90**, 1751–1761.
- Brenes-Arguedas, T., Rios, M., Rivas-Torres, G. *et al.* (2008) The effect of soil on the growth performance of tropical species with contrasting distributions. *Oikos*, **117**, 1453–1460.
- Brenes-Arguedas, T., Roddy, A. B., Coley, P. D. & Kursar, T. A. (2011) Do differences in understory light contribute to species distributions along a tropical rainfall gradient? *Oecologia*, **166**, 443–456.
- Brodribb, T. J., Holbrook, N. M., Edwards, E. J. & Gutierrez, M. V. (2003) Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant, Cell and Environment*, **26**, 443–450.
- Bunker, D. E. & Carson, W. P. (2005) Drought stress and tropical forest woody seedlings: effect on community structure and composition. *Journal of Ecology*, **93**, 794–806.
- Bunker, D. E., DeClerck, F., Bradford, J. C. *et al.* (2005) Species loss and aboveground carbon storage in a tropical forest. *Science*, **310**, 1029–1031.
- Burlyn, E. M. & Kaufmann, M. R. (1973) The osmotic potential of Polyethylene Glycol 6000. *Plant Physiology*, **51**, 914–916.
- Burslem, D. F. R. P., Grubb, P. J. & Turner, I. M. (1996) Responses to simulated drought and elevated nutrient supply among shade-tolerant tree seedlings of lowland tropical forest in Singapore. *Biotropica*, **28**, 636–648.
- Cao, K. F. (2000) Water relations and gas exchange of tropical saplings during a prolonged drought in a Bornean heath forest, with reference to root architecture. *Journal of Tropical Ecology*, **16**, 101–116.
- Chen, T. H. H. & Murata, N. (2002) Enhancement of tolerance of abiotic stress by metabolic engineering of betaines and other compatible solutes. *Current Opinion in Plant Biology*, **5**, 250–257.
- Chesson, P. L. & Warner, R. R. (1981) Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist*, **117**, 923–943.
- Chiariello, N. R., Field, C. B. & Mooney, H. A. (1987) Midday wilting in a tropical pioneer tree. *Functional Ecology*, **1**, 3–11.
- Choat, B., Sack, L. & Holbrook, N. M. (2007) Diversity of hydraulic traits in nine *Cordia* species growing in tropical forests with contrasting precipitation. *New Phytologist*, **175**, 686–698.
- Clark, J. S., Lewis, M., McLachlan, J. S. & HilleRisLambers, J. (2003) Estimating population spread: what can we forecast and how well? *Ecology*, **84**, 1979–1988.
- Clinebell, R. R., Phillips, O. L., Gentry, A. H., Stark, N. & Zuuring, H. (1995) Prediction of Neotropical tree and liana species richness from soil and climatic data. *Biodiversity and Conservation*, **4**, 56–90.
- Coley, P. D. (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs*, **53**, 209–233.
- Colwell, R. K., Brehm, G., Cardelus, C. L., Gilman, A. C. & Longino, J. T. (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, **322**, 258–261.
- Comita, L. S. & Engelbrecht, B. M. J. (2009) Seasonal and spatial variation in water

- availability drive habitat associations in a tropical forest. *Ecology*, **90**, 2755–2765.
- Condit, R. (1998) Ecological implications of changes in drought patterns: Shifts in forest composition in Panama. *Climatic Change*, **39**, 413–427.
- Condit, R., Hubbell, S.P. & Foster, R.B. (1995) Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs*, **65**, 419–439.
- Condit, R., Hubbell, S.P. & Foster, R.B. (1996) Changes in tree species abundance in a Neotropical forest: Impact of climate change. *Journal of Tropical Ecology*, **12**, 231–256.
- Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In *Dynamics of Populations* (eds P.J. den Boer & G.R. Gradwell), pp. 298–312. Wageningen, The Netherlands: Centre for Agricultural Publishing and Documentation.
- Costa, M.H. & Foley, J.A. (2000) Combined effects of deforestation and doubled atmospheric CO<sub>2</sub> concentrations on the climate of Amazonia. *Journal of Climate*, **13**, 18–34.
- Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A. & Totterdell, I.J. (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, **408**, 184–187.
- Cruz-Rodríguez, J.A. & López-Mala, L. (2004) Demography of the seedling bank of *Manilkara zorpota* (L.) Royen in a subtropical rain forest of Mexico. *Plant Ecology*, **172**, 227–235.
- Currie, D.J. & Paquin, V. (1987) Large-scale biogeographical patterns of species richness of trees. *Nature*, **329**, 326–327.
- da Costa, A.C.L., Galbraith, D., Almeida, S. *et al.* (2010) Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytologist*, **187**, 579–591.
- Davidar, P., Puyravaud, J.P. & Leigh, E.G. (2005) Changes in rain forest tree diversity, dominance and rarity across a seasonality gradient in the Western Ghats, India. *Journal of Biogeography*, **32**, 493–501.
- Davidar, P., Rajagopal, B., Mohandass, D. *et al.* (2007) The effect of climatic gradients, topographic variation and species traits on the beta diversity of rain forest trees. *Global Ecology and Biogeography*, **16**, 510–518.
- Daws, M.I., Bolton, S., Burslem, D., Garwood, N.C. & Mullins, C.E. (2007) Loss of desiccation tolerance during germination in neo-tropical pioneer seeds: Implications for seed mortality and germination characteristics. *Seed Science Research*, **17**, 273–281.
- Daws, M.I., Crabtree, L.M., Dalling, J.W., Mullins, C.E. & Burslem, D. (2008) Germination responses to water potential in Neotropical pioneers suggest large-seeded species take more risks. *Annals of Botany*, **102**, 945–951.
- Daws, M.I., Garwood, N.C. & Pritchard, H.W. (2005) Traits of recalcitrant seeds in a semi-deciduous tropical forest in Panama: some ecological implications. *Functional Ecology*, **19**, 874–885.
- Daws, M.I., Garwood, N.C. & Pritchard, H.W. (2006) Prediction of desiccation sensitivity in seeds of woody species: A probabilistic model based on two seed traits and 104 species. *Annals of Botany*, **97**, 667–674.
- Daws, M.I., Mullins, C.E., Burslem, D., Paton, S.R. & Dalling, J.W. (2002) Topographic position affects the water regime in a semideciduous tropical forest in Panama. *Plant and Soil*, **238**, 79–90.
- Daws, M.I., Pearson, T.R.H., Burslem, D., Mullins, C.E. & Dalling, J.W. (2005) Effects of topographic position, leaf litter and seed size on seedling demography in a semi-deciduous tropical forest in Panama. *Plant Ecology*, **179**, 93–105.
- de Gouvenain, R.L., Kobe, R.K. & Silander, J.A. (2007) Partitioning of understorey light and dry-season soil moisture gradients among seedlings of four rain-forest tree species in Madagascar. *Journal of Tropical Ecology*, **23**, 569–579.

- Delissio, L. J. & Primack, R. B. (2003) The impact of drought on the population dynamics of canopy-tree seedlings in an aseasonal Malaysian rain forest. *Journal of Tropical Ecology*, **19**, 489–500.
- Delissio, L. J., Primack, R. B., Hall, P. & Lee, H. S. (2002) A decade of canopy-tree seedling survival and growth in two Bornean rain forests: Persistence and recovery from suppression. *Journal of Tropical Ecology*, **18**, 645–658.
- Eamus, D. & Prior, L. (2001) Ecophysiology of trees of seasonally dry tropics: Comparisons among phenologies. *Advances in Ecological Research*, **32**, 113–197.
- Engelbrecht, B. M. J., Comita, L. S., Condit, R. *et al.* (2007) Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, **447**, 80–82.
- Engelbrecht, B. M. J., Dalling, J. W., Pearson, T. R. H. *et al.* (2006) Short dry spells in the wet season increase mortality of tropical pioneer seedlings. *Oecologia*, **148**, 258–269.
- Engelbrecht, B. M. J. & Kursar, T. A. (2003) Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. *Oecologia*, **136**, 383–393.
- Engelbrecht, B. M. J., Kursar, T. A. & Tyree, M. T. (2005) Drought effects on seedling survival in a tropical moist forest. *Trees-Structure and Function*, **19**, 312–321.
- Engelbrecht, B. M. J., Wright, S. J. & De Steven, D. (2002) Survival and ecophysiology of tree seedlings during El Niño drought in a tropical moist forest in Panama. *Journal of Tropical Ecology*, **18**, 569–579.
- Enquist, B. J. & Enquist, C. A. F. (2011) Long-term change within a Neotropical forest: assessing differential functional and floristic responses to disturbance and drought. *Global Change Biology*, **17**, 1408–1424.
- ESP (2011) BCI Physical Monitoring Downloads. [http://striweb.si.edu/esp/physical\\_monitoring/download\\_bci.htm](http://striweb.si.edu/esp/physical_monitoring/download_bci.htm)
- Feeley, K. J., Davies, S. J., Perez, R., Hubbell, S. P. & Foster, R. B. (2011) Directional changes in the species composition of a tropical forest. *Ecology*, **92**, 871–882.
- Fine, P. V. A., Mesones, I. & Coley, P. D. (2004) Herbivores promote habitat specialization by trees in Amazonian forests. *Science*, **305**, 663–665.
- Fisher, B. L., Howe, H. F. & Wright, S. J. (1991) Survival and growth of *Virola surinamensis* yearlings: water augmentation in gap and understory. *Oecologia*, **86**, 292–297.
- Garwood, N. C. (1983) Seed germination in a seasonal tropical forest in Panama: a community study. *Ecological Monographs*, **53**, 159–181.
- Gentry, A. H. (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden*, **75**, 1–34.
- Gerhardt, K. (1996) Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. *Forest Ecology and Management*, **82**, 33–48.
- Gibbons, J. M. & Newbery, D. M. (2003) Drought avoidance and the effect of local topography on trees in the understory of Bornean lowland rain forest. *Plant Ecology*, **164**, 1–18.
- Gilbert, G. S., Harms, K. E., Hamill, D. N. & Hubbell, S. P. (2001) Effects of seedling size, El Niño drought, seedling density, and distance to nearest conspecific adult on 6-year survival of *Ocotea whitei* seedlings in Panama. *Oecologia*, **127**, 509–516.
- Givnish, T. J. (1999) On the causes of gradients in tropical tree diversity. *Journal of Ecology*, **87**, 193–210.
- Green, J. J. & Newbery, D. M. (2002) Reproductive investment and seedling survival of the mast-fruiting rain forest tree, *Microberlinia bisulcata* A.Chev. *Plant Ecology*, **162**, 169–183.
- Grubb, P. J. (1977) The maintenance of species-richness in plant communities: the importance of regeneration niche. *Biological Reviews of the Cambridge Philosophical Society*, **52**, 107–145.
- Gunatilleke, C. V. S., Gunatilleke, I. A. U. N., Esufali, S. *et al.* (2006) Species-habitat

- associations in a Sri Lankan dipterocarp forest. *Journal of Tropical Ecology*, **22**, 371–384.
- Hacke, U. G., Sperry, J. S., Pockman, W. T., Davis, S. D. & McCulloch, K. A. (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*, **126**, 457–461.
- Hall, J. B. & Swaine, M. D. (1981) *Distribution and Ecology of Vascular Plants in a Tropical Rain Forest: Forest Vegetation in Ghana*. Geobotany Vol. 1. The Hague, Netherlands; Boston, MA: Dr W. Junk Publishers.
- Harms, K. E., Condit, R., Hubbell, S. P. & Foster, R. B. (2001) Habitat associations of trees and shrubs in a 50-ha Neotropical forest plot. *Journal of Ecology*, **89**, 947–959.
- Harper, J. L. (1977) *Population Biology of Plants*. London: Academic Press.
- Hawkins, B. A., Field, R., Cornell, H. V. *et al.* (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.
- Hedges, L. V., Gurevitch, J. & Curtis, P. S. (1999) The meta-analysis of response ratios in experimental ecology. *Ecology*, **80**, 1150–1156.
- Hoffmann, W. A., Schroeder, W. & Jackson, R. B. (2003) Regional feedbacks among fire, climate, and tropical deforestation. *Journal of Geophysical Research*, **108**, ACL4–1–11.
- Holdridge, L. R., Grenke, W. C., Hatheway, W. H., Liang, T. & Tosi, J. A. (1971) *Forest Environments in Tropical Life Zones*. Oxford: Pergamon Press.
- Hooper, D. U. & Vitousek, P. M. (1997) The effects of plant composition and diversity on ecosystem processes. *Science*, **277**, 1302–1305.
- Hsiao, T. C. (1973) Plant responses to water stress. *Annual Review of Plant Physiology*, **24**, 519–570.
- Hubbell, S. P. (1998) The maintenance of diversity in a Neotropical tree community: conceptual issues, current evidence, and challenges ahead. In *Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies* (eds. D. F. & J. A. Comiskey), pp. 17–44. Pearl River, NY: Parthenon Publishing.
- Hubbell, S. P. & Foster, R. B. (1983) Diversity of canopy trees in a Neotropical forest and implications for conservation. In *Tropical Rain Forest: Ecology and Management* (eds. S. L. Sutton, T. C. Whitmore & A. C. Chadwick), pp. 25–41. Oxford: Blackwell Scientific.
- Hubbell, S. P., Foster, R. B., O'Brien, S. T. *et al.* (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science*, **283**, 554–557.
- Hulme, M. & Viner, D. (1998) A climate change scenario for the tropics. *Climatic Change*, **39**, 145–176.
- IPCC (2007) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.
- Jackson, P. C., Cavelier, J., Goldstein, G., Meinzer, F. C. & Holbrook, N. M. (1995) Partitioning of water resources among plants of a lowland tropical forest. *Oecologia*, **101**, 197–203.
- Janzen, D. H. (1970) Herbivores and number of tree species in tropical forests. *American Naturalist*, **104**, 501–528.
- Jarvis, P. G. & Jarvis, M. S. (1963) The water relations of tree seedlings I. Growth and water use in relations to soil water potential. *Physiologia Plantarum*, **16**, 215–235.
- John, R., Dalling, J. W., Harms, K. E. *et al.* (2007) Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences USA*, **104**, 864–869.
- Kerstiens, G. (1996a) Cuticular water permeability and its physiological significance. *Journal of Experimental Botany*, **47**, 1813–1832.
- Kerstiens, G. (1996b) Diffusion of water vapour and gases across cuticles and through stomatal pores presumed closed. *Plant Cuticles* (ed. G. Kerstiens), pp. 121–134. Oxford: BIOS Scientific Publisher Ltd.
- Kreft, H. & Jetz, W. (2007) Global patterns and determinants of vascular plant diversity.

- Proceedings of the National Academy of Sciences USA*, **104**, 5925–5930.
- Kursar, T. A., Engelbrecht, B. M. J., Burke, A. *et al.* (2009) Tolerance to low leaf water status of tropical tree seedlings is related to drought performance and distribution. *Functional Ecology*, **23**, 93–102.
- Kursar, T. A., Engelbrecht, B. M. J. & Tyree, M. T. (2003) Soil moisture release curves for two tropical forests having similar rainfall but distinct tree communities. *Ecological Society of America Annual Meeting Abstracts*, **88**, 193–194.
- Larcher, W. (2003) *Physiological Plant Ecology*, 4th edn. Berlin: Springer.
- Lewis, S. L. & Tanner, E. V. J. (2000) Effects of above- and belowground competition on growth and survival of rain forest tree seedlings. *Ecology*, **81**, 2525–2538.
- Lieberman, D. & Li, M. (1992) Seedling recruitment patterns in tropical dry forest in Ghana. *Journal of Vegetation Science*, **3**, 375–382.
- Lopez, O. R. & Kursar, T. A. (2007) Interannual variation in rainfall, drought stress and seedling mortality may mediate monodominance in tropical flooded forests. *Oecologia*, **154**, 35–43.
- Malhi, Y., Aragao, L., Galbraith, D. *et al.* (2009) Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proceedings of the National Academy of Sciences USA*, **106**, 20610–20615.
- Malhi, Y. & Phillips, O. L. (2004) Tropical forests and global atmospheric change: a synthesis. *Philosophical Transactions of the Royal Society Series B: Biological Sciences*, **359**, 549–555.
- Malhi, Y., Roberts, J. T., Betts, R. A. *et al.* (2008) Climate change, deforestation, and the fate of the Amazon. *Science*, **319**, 169–172.
- Markesteijn, L., Iraipi, J., Bongers, F. & Poorter, L. (2010) Seasonal variation in soil and plant water potentials in a Bolivian tropical moist and dry forest. *Journal of Tropical Ecology*, **26**, 497–508.
- Markesteijn, L. & Poorter, L. (2009) Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *Journal of Ecology*, **97**, 311–325.
- Markesteijn, L., Poorter, L., Paz, H., Sack, L. & Bongers, F. (2011) Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant, Cell and Environment*, **34**, 137–148.
- Marod, D., Kutintara, U., Tanaka, H. & Nakashizuka, T. (2002) The effects of drought and fire on seed and seedling dynamics in a tropical seasonal forest in Thailand. *Plant Ecology*, **161**, 41–57.
- Mayle, F. E. & Power, M. J. (2008) Impact of a drier Early–Mid-Holocene climate upon Amazonian forests. *Philosophical Transactions of the Royal Society Series B*, **363**, 1829–1838.
- McLaren, K. P. & McDonald, M. A. (2003) The effects of moisture and shade on seed germination and seedling survival in a tropical dry forest in Jamaica. *Forest Ecology and Management*, **183**, 61–75.
- Medina, E. (1999) Tropical forests: diversity and function of dominant lifeforms. In *Handbook of Functional Plant Ecology* (eds F. Pugnaire & M. I. Vallejo), pp. 407–448. New York: Marcel Dekker.
- Merchant, A., Tausz, M., Arndt, S. K. & Adams, M. A. (2006) Cyclitols and carbohydrates in leaves and roots of 13 *Eucalyptus* species suggest contrasting physiological responses to water deficit. *Plant, Cell and Environment*, **29**, 2017–2029.
- Metz, M. R., Comita, L. S., Chen, Y. Y. *et al.* (2008) Temporal and spatial variability in seedling dynamics: a cross-site comparison in four lowland tropical forests. *Journal of Tropical Ecology*, **24**, 9–18.
- Miles, L., Grainger, A. & Phillips, O. (2004) The impact of global climate change on tropical forest biodiversity in Amazonia. *Global Ecology and Biogeography*, **13**, 553–565.
- Mulkey, S. S., Smith, A. P., Wright, S. J., Machado, J. L. & Dudley, R. (1992) Contrasting leaf phenotypes control seasonal variation in water-loss in a tropical

- forest shrub. *Proceedings of the National Academy of Sciences USA*, **89**, 9084–9088.
- Mulkey, S. S. & Wright, S. J. (1996) Influence of seasonal drought on the carbon balance of tropical forest plants. In *Tropical Forest Plant Ecophysiology* (eds S. S. Mulkey, R. L. Chazdon & A. P. Smith), pp. 217–243. New York: Chapman & Hall.
- Mulkey, S. S., Wright, S. J. & Smith, A. P. (1993) Comparative physiology and demography of 3 Neotropical forest shrubs: alternative shade-adaptive character syndromes. *Oecologia*, **96**, 526–536.
- Myers, M. A. & Kitajima, K. (2007) Carbohydrate storage enhances seedling shade and stress tolerance in a neotropical forest. *Journal of Ecology*, **95**, 383–395.
- Nakagawa, M., Tanaka, K., Nakashizuka, T. *et al.* (2000) Impact of severe drought associated with the 1997–1998 El Niño in a tropical forest in Sarawak. *Journal of Tropical Ecology*, **16**, 355–367.
- Neelin, J. D., Munnich, M., Su, H., Meyerson, J. E. & Holloway, C. E. (2006) Tropical drying trends in global warming models and observations. *Proceedings of the National Academy of Sciences USA*, **103**, 6110–6115.
- Nepstad, D. C., Tohver, I. M., Ray, D., Moutinho, P. & Cardinot, G. (2007) Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology*, **88**, 2259–2269.
- Newbery, D. M., Campbell, E. J. F., Proctor, J. & Still, M. J. (1996) Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia. Species composition and patterns in the understorey. *Vegetatio*, **122**, 193–220.
- Padilla, F. M. & Pugnaire, F. I. (2007) Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. *Functional Ecology*, **21**, 489–495.
- Paine, C. E. T., Harms, K. E. & Ramos, J. (2009) Supplemental irrigation increases seedling performance and diversity in a tropical forest. *Journal of Tropical Ecology*, **25**, 171–180.
- Palmiotto, P. A., Davies, S. J., Vogt, K. A. *et al.* (2004) Soil-related habitat specialization in dipterocarp rain forest tree species in Borneo. *Journal of Ecology*, **92**, 609–623.
- Parolin, P., Lucas, C., Piedade, M. T. F. & Wittmann, F. (2010) Drought responses of flood-tolerant trees in Amazonian floodplains. *Annals of Botany*, **105**, 129–139.
- Paz, H. (2003) Root/shoot allocation and root architecture in seedlings: Variation among forest sites, microhabitats, and ecological groups. *Biotropica*, **35**, 318–332.
- Pearson, T. R. H., Burslem, D. F. R. P., Goeriz, R. E. & Dalling, J. W. (2003) Regeneration niche partitioning in neotropical pioneers: effects of gap size, seasonal drought, and herbivory on growth and survival. *Oecologia*, **137**, 456–465.
- Phillips, O. L., Aragao, L., Lewis, S. L. *et al.* (2009) Drought sensitivity of the Amazon rainforest. *Science*, **323**, 1344–1347.
- Phillips, O. L., van der Heijden, G., Lewis, S. L. *et al.* (2010) Drought-mortality relationships for tropical forests. *New Phytologist*, **187**, 631–646.
- Poorter, L., Bongers, F., Kouame, F. N. & Hawthorne, W. D. (2004) *Biodiversity of West African Forests: An Ecological Atlas of Woody Plant Species*. Oxford: CABI Publishing.
- Poorter, L., Bongers, F. & Lemmens, R. H. M. J. (2004) West African forests; introduction. In *Biodiversity of West African Forests. An Ecological Atlas of Woody Plant Species* (eds L. Poorter, F. Bongers, F. N. Kouame & W. D. Hawthorne), pp. 5–14., Oxford: CABI Publishing.
- Poorter, L. & Hayashida-Oliver, Y. (2000) Effects of seasonal drought on gap and understorey seedlings in a Bolivian moist forest. *Journal of Tropical Ecology*, **16**, 481–498.
- Poorter, L. & Markesteijn, L. (2008) Seedling traits determine drought tolerance of tropical tree species. *Biotropica*, **40**, 321–331.
- Potts, M. D. (2003) Drought in a Bornean everwet rain forest. *Journal of Ecology*, **91**, 467–474.
- Pyke, C. R., Condit, R., Aguilar, S. & Lao, S. (2001) Floristic composition across a climatic gradient in a neotropical lowland forest. *Journal of Vegetation Science*, **12**, 553–566.

- Quesada, M., Sanchez-Azofeifa, G. A., Alvarez-Anorve, M. *et al.* (2009) Succession and management of tropical dry forests in the Americas: Review and new perspectives. *Forest Ecology and Management*, **258**, 1014–1024.
- Rascher, U., Bobich, E. G., Lin, G. H. *et al.* (2004) Functional diversity of photosynthesis during drought in a model tropical rainforest – the contribution of leaf area, photosynthetic electron transport and stomatal conductance to reduction in net ecosystem carbon exchange. *Plant, Cell and Environment*, **27**, 1239–1256.
- Reich, P. B. & Borchert, R. (1984) Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology*, **72**, 61–74.
- Russo, S. E., Zhang, L. & Tan, S. (2012) Covariation between understorey light environments and soil resources in Bornean mixed dipterocarp rain forest. *Journal of Tropical Ecology* **28**, 33–44.
- Sack, L. (2004) Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation? *Oikos*, **107**, 110–127.
- Slik, J. W. F. (2004) El Niño droughts and their effects on tree species composition and diversity in tropical rain forests. *Oecologia*, **141**, 114–120.
- Slik, J. W. F., Poulsen, A. D., Ashton, P. S. *et al.* (2003) A floristic analysis of the lowland dipterocarp forests of Borneo. *Journal of Biogeography*, **30**, 1517–1531.
- Slot, M. & Poorter, L. (2007) Diversity of tropical tree seedling responses to drought. *Biotropica*, **39**, 683–690.
- Snow, M. D. & Tingey, D. T. (1985) Evaluation of a system for the imposition of plant water stress. *Plant Physiology* **77**, 602–607.
- Sombroek, W. (2001) Spatial and temporal patterns of Amazon rainfall – Consequences for the planning of agricultural occupation and the protection of primary forests. *Ambio*, **30**, 388–396.
- Svenning, J. C. (1999) Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *Journal of Ecology*, **87**, 55–65.
- Swaine, M. D. (1996) Rainfall and soil fertility as factors limiting forest species distributions in Ghana. *Journal of Ecology*, **84**, 419–428.
- Tanner, E. V. J. & Barberis, I. M. (2007) Trenching increased growth, and irrigation increased survival of tree seedlings in the understorey of a semi-evergreen rain forest in Panama. *Journal of Tropical Ecology*, **23**, 257–268.
- ter Steege, H. (1994) Flooding and drought tolerance in seeds and seedlings of two *Mora* species segregated along a soil hydrological gradient in the tropical rain-forest of Guyana. *Oecologia*, **100**, 356–367.
- ter Steege, H., Pitman, N., Sabatier, D. *et al.* (2003) A spatial model of tree alpha-diversity and tree density for the Amazon. *Biodiversity and Conservation*, **12**, 2255–2277.
- ter Steege, H., Pitman, N. C. A., Phillips, O. L. *et al.* (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature*, **443**, 444–447.
- Timmermann, A., Oberhuber, J., Bacher, A. *et al.* (1999) Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature*, **398**, 694–697.
- Tobin, M. F., Lopez, O. R. & Kursar, T. A. (1999) Responses of tropical understorey plants to a severe drought: Tolerance and avoidance of water stress. *Biotropica*, **31**, 570–578.
- Toledo, M., Poorter, L., Pena-Claros, M. *et al.* (2011) Climate is a stronger driver of tree and forest growth rates than soil and disturbance. *Journal of Ecology*, **99**, 254–264.
- Turkan, I., Bor, M., Ozdemir, F. & Koca, H. (2005) Differential responses of lipid peroxidation and antioxidants in the leaves of drought-tolerant *P. acutifolius* Gray and drought-sensitive *P. vulgaris* L. subjected to polyethylene glycol mediated water stress. *Plant Science*, **168**, 223–231.
- Turner, I. M. (1990) The seedling survivorship and growth of three *Shorea* species in a

- Malaysian tropical rain forest. *Journal of Tropical Ecology*, **6**, 469–478.
- Tyree, M. T., Engelbrecht, B. M. J., Vargas, G. & Kursar, T. A. (2003) Desiccation tolerance of five tropical seedlings in Panama. Relationship to a field assessment of drought performance. *Plant Physiology*, **132**, 1439–1447.
- Tyree, M. T. & Ewers, F. W. (1996) Hydraulic architecture of woody tropical plants. In *Tropical Forest Plant Ecophysiology* (eds S. S. Mulkey, R. L. Chazdon & A. P. Smith), pp. 217–243. New York: Chapman & Hall.
- Tyree, M. T. & Jarvis, P. G. (1982) Water in tissues and cells. *Encyclopedia of Plant Physiology* (eds O. L. Lange, P. S. Nobel, C. B. Osmond & H. Ziegler), pp. 36–71. Berlin: Springer-Verlag.
- Tyree, M. T. & Sperry, J. S. (1989) Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Plant Molecular Biology*, **40**, 19–38.
- Valencia, R., Foster, R. B., Villa, G. *et al.* (2004) Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *Journal of Ecology*, **92**, 214–229.
- Vazquez-Yanes, C. & Orozco-Segovia, A. (1993) Patterns of seed longevity and germination in the tropical rainforest. *Annual Review of Ecology and Systematics*, **24**, 69–87.
- Veenendaal, E. M. & Swaine, M. D. (1998) Limits to tree species distribution in lowland tropical rainforests. *Dynamics of Tropical Communities: 37th Symposium of the British Ecological Society*. (eds D. M. Newbery, H. H. T. Prins & N. Brown), pp. 163–191. Oxford: Blackwell Scientific.
- Veenendaal, E. M., Swaine, M. D., Agyeman, V. K. *et al.* (1996) Differences in plant and soil water relations in and around a forest gap in West Africa during the dry season may influence seedling establishment and survival. *Journal of Ecology*, **84**, 83–90.
- Walsh, R. P. D. (1996) Climate. In *The Tropical Rainforest: An Ecological Study* (ed. P. W. Richards), pp. 159–205. Cambridge: Cambridge University Press.
- Walsh, R. P. D. & Newbery, D. M. (1999) The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact. *Philosophical Transactions of the Royal Society Series B*, **354**, 1869–1883.
- Webb, C. O. & Peart, D. R. (2000) Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology*, **88**, 464–478.
- Westoby, M. (2002) Choosing species to study. *Trends in Ecology & Evolution*, **17**, 587.
- Whittaker, R. H. & Niering, W. A. (1975) Vegetation of the Santa Catalina Mountains, Arizona 5. Biomass, production, and diversity along elevation gradient. *Ecology*, **56**, 771–790.
- Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A. & Langham, G. (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. *Plos Biology*, **6**, 2621–2626.
- Williamson, G. B., Laurance, W. F., Oliveira, A. A. *et al.* (2000) Amazonian tree mortality during the 1997 El Niño drought. *Conservation Biology*, **14**, 1538–1542.
- Wolda, H. (1978) Seasonal fluctuations in rainfall, food and abundance of tropical insects. *Journal of Animal Ecology*, **47**, 369–381.
- Wright, S. J. (2005) The El Niño Southern Oscillation influences tree performance in tropical rainforests. In *Tropical Rainforests: Past, Present, and Future* (eds E. Bermingham, R. E. Dickinson & C. Moritz), pp. 295–310. Chicago and London: University of Chicago Press.
- Wright, S. J., Machado, J. L., Mulkey, S. S. & Smith, A. P. (1992) Drought acclimation among tropical forest shrubs (*Psychotria*, Rubiaceae). *Oecologia*, **89**, 457–463.
- Yavitt, J. B. & Wright, S. J. (2008) Seedling growth responses to water and nutrient augmentation in the understorey of a lowland moist forest, Panama. *Journal of Tropical Ecology*, **24**, 19–26.