Floristic shifts versus critical transitions in Amazonian forest systems

JÉRÔME CHAVE

Laboratoire Evolution et Diversité Biologique,
CNRS & Université Paul Sabatier

6.1 Introduction

Tropical forests hold close to 250 Pg of carbon, with Latin America contributing half of this (Saatchi *et al.* 2011). Although the rates of deforestation appear to have decreased over the past decade, tropical deforestation still represents the bulk of the *c.* 1.1 PgC yr^{-1} of C emissions due to land-use change (Friedlingstein *et al.* 2010). The direct impact of deforestation and degradation has the potential to be mitigated through a performance-based mechanism such as REDD (Reducing Emissions from Deforestation and Forest Degradation), by monetising carbon held in both managed and unmanaged forests (Agrawal, Nepstad & Chhatre 2011). Additionally, tropical forests contribute to a terrestrial carbon sink (Le Quéré *et al.* 2009), offsetting fossil carbon emissions into the atmosphere through a physiological response of the vegetation (Lewis *et al.* 2009; Lloyd & Farquhar 2008). Thus tropical forests offer critically important ecosystem services by reducing the short-term effect of anthropogenic carbon emissions into the atmosphere.

However, in the face of global climate trends, the resilience of tropical forests has been called into question (Cox *et al.* 2000). South America is sensitive to a number of large-scale climatic anomalies, including the El Niño Southern Oscillation, the Pacific Decadal Oscillation and the North Atlantic Oscillation. All of these contribute to displacing the yearly course of the Inter-Tropical Convergence Zone (ITCZ) and increase the strength of the dry season in some regions (Garreaud *et al.* 2009; Marengo 2004). The 2005 and the 2010 climatic events over Amazonia have exemplified these atmospheric regime shifts, and these may occur more frequently during the twenty-first century. As a result of the increased likelihood of severe droughts, models suggest that Amazonian forests may shift by 2100 to a different biome type akin to a woodland savanna or dry forest (Cox *et al.* 2000, 2004; Huntingford *et al.* 2008; Malhi *et al.* 2009; Poulter *et al.* 2010). Aside from the radical implications for human and wildlife populations inhabiting Amazonia, this new biome type would have far less potential to hold carbon, and such a shift

would have important consequences for global life support services. Some of the predictions of this 'Amazon dieback' scenario have been empirically tested (Phillips *et al.* 2009). Theoretical work has also attempted to understand whether a shift showing alternative stable states is a likely outcome. Within a realistic range of precipitation regimes, a stability analysis comparing the current cover of three biome types – forest, savanna and treeless areas – has shown that forest and savanna do appear to behave as alternative stable states, substantiating the claim that climate change may trigger a critical transition from forest to savanna (Hirota *et al.* 2011; Staver, Archibald & Levin 2011). Although this approach needs to be backed by more empirical studies and confirmed by more detailed simulations, it appears to be a universal feature of tropical biome dynamics (Murphy & Bowman 2012). Thus, this body of knowledge collectively suggests that Amazonian forests are functioning today at the verge of a major environmental tipping point.

Support for the Amazon dieback scenario is one of the major findings of a new generation of Earth models where atmospheric global circulation models (GCMs) are synchronously coupled to dynamic global vegetation models (DGVMs). These DGVMs have a long tradition in vegetation modelling (Cramer *et al.* 2004; Krinner *et al.* 2005; Sitch *et al.* 2003), being related to the development of agricultural or forestry management models (Shugart 1984) and to the need to model short-term fluxes between atmosphere and biosphere in atmospheric physics. Here, I discuss two limitations of existing DGVMs that have until now been seldom addressed, but that are especially critical for an accurate modelling of tropical old-growth forests and woody savannas alike.

First, few DGVMs attempt to account for demographic stochasticity, in spite of the importance of these local processes in explaining the dynamics of unmanaged vegetation (Purves & Pacala 2008). One notable exception is the Ecosystem Demography model (ED model; Fisher *et al.* 2010; Moorcroft, Hurtt & Pacala 2001), where demographic stochasticity was taken into account through a spatial averaging procedure inspired from statistical physics (Iwasa, Andreasen & Levin 1987). With increased computer power, an alternative to the ED modelling strategy is to develop individual-based DGVMs for forests, for example Sato, Itoh and Kohyama's (2007) 'SEIB-DGVM'. While important efforts have been made in this direction in the recent literature, fusing ecosystem science and community ecology certainly represents a central challenge in the construction of a new generation of Earth models (Fisher *et al.* 2010).

A second limitation is that biodiversity is only simplistically represented in the current generation of DGVMs. Usually, a pool of only 10 or so plant functional types (PFTs) are available for populating DGVMs (Sitch *et al.* 2003), just two of which occur in tropical forests: tropical broadleaf evergreen trees

(woody vegetation with persistent leaves), and tropical broadleaf raingreen trees (semi-deciduous woody vegetation). Within a grid cell of *c.* 1° × 1° latitude/longitude, a fraction of each PFT is competing for space and resources. This simplification is easily understandable in view of the complexity of the task of modelling the interaction between a plant canopy and the atmospheric boundary layer (Jones 1992). However, what is known of the adaptive potential of organisms in changing environments (Davis, Shaw & Etterson 2005; Duputié *et al.* 2012) and of the evolutionary history of tropical tree families (Jaramillo *et al.* 2010; Wing *et al.* 2009) demands a critical reappraisal of over-simplistic approaches.

In this chapter, I examine lines of evidence for or against the Amazonian dieback scenario in light of ecological theory and palaeoenvironmental evidence. I then argue that a new generation of DGVMs must appropriately account for the physiology of tropical trees, including the contribution of both photosynthetic organs and the rest of the plants. I separate the contribution of photosynthetic organs (leaves) and of the rest of the plants (especially the stem and branches). Finally, I describe a possible implementation of this approach in an individual-based forest growth simulator.

6.2   The stability of Amazonian forests: historical insights

Tropical rain forests have been a dominant vegetation type on the Earth for much of the past 100 Ma. In his wonderful book on the evolution of tropical rain forests, Morley (2000) provided a synthesis of the fossil evidence for the tropical forest flora. Solid evidence now exists for the presence of multi-storeyed angiosperm-dominated forests from the late Cretaceous (Morley 2011), or in the early Tertiary for the Neotropics (Burnham & Johnson 2004; Wing *et al.* 2009). This suggests that the rise to dominance of tropical rain forests preceded the Cretaceous–Tertiary transition. This claim was also supported by molecular dating of phylogenetic trees for two predominantly tropical forest clades, the Malpighiales (Davis, Shaw & Etterson 2005), and the Ericales (Sytsma *et al.* 2006). A continuous palynological record dating back to 65 Ma BP from Colombia has confirmed that at least some areas in northern South America have been dominated by tropical forest taxa for much of the period from the Early Paleocene to the Early Miocene (Jaramillo, Rueda & Mora 2006), although a lot of vegetational changes have taken place over this period (Jaramillo, Rueda & Mora 2006; see also Jaramillo *et al.* 2010; Rull 1999). Together with the evolution of C4 photosynthesis, the rise to dominance of tropical rain forests is probably one of the very few key evolutionary advances in the history of terrestrial vegetation over the past 100 Ma (Brodribb & Feild 2010; Christin *et al.* 2008; McAdam & Brodribb 2012; Morley 2011).

Focusing on the Quaternary, oxygen isotope data from Brazil speleothems spanning the past 200 ka demonstrate that the climate of South America has

been altered by fluctuations in solar radiation, coupled with a large reorganisation of equatorial atmospheric circulation that led to a change in the position of the ITCZ (Cruz *et al.* 2009; Wang *et al.* 2007). Carbon isotope evidence from the Cariaco Basin, Venezuela, over the past 50 ka, suggests that the South American climate has been subject to large-scale oceanic shifts in the Atlantic meridional overturning circulation (Hughen *et al.* 2004). These climatic changes have been also traced in water level changes over the past 160 ka for Lake Pata, Brazil, close to the equator (Bush, Silman & Urrego 2002). Other areas of Amazonia appear to have been floristically quite stable over the past 50 ka, where the pollen cores show a dominance of arboreal pollen taxa, and little grass pollen, through much of this period (Burbridge, Mayle & Killeen 2004; Bush, Silman & Urrego 2004; Colinvaux, de Oliveira & Bush 1996; Haberle & Maslin 1999), except in an area that is today close to the forest–savanna ecotone: Serra dos Carajás, Brazil (Absy *et al.* 1991).

By far the most controversial climate-induced paleoecological event in South America is the one that occurred during the last glacial maximum (LGM), around 21 ka BP. There is evidence for a decline in precipitation and a decrease in temperature by up to 5 °C in some parts of this continent (Bush, Silman & Urrego 2004), in an atmosphere with CO_2 levels about half of those recorded today. Some authors have used this evidence to suggest that Amazonian forests were largely converted into savannas during the glacial periods. This fragmentation of Amazonian forests has been put forward as an explanation for the high diversity of this biome: many populations may have been maintained in allopatry through long periods in the Quaternary during which repeated episodes of forest fragmentation acted as a 'pump of speciation' (Bush 1994). Yet, there is no evidence for a widespread transition from a closed-canopy forest to a woodland savanna system either in the paleoecological record (Bush, Silman & Urrego 2004; Colinvaux *et al.* 2000; Haberle & Maslin 1999; Mayle *et al.* 2004, 2009) or in modelling studies (Cowling, Maslin & Sykes 2001). The pollen records reported by Colinvaux, de Oliveira and Bush (2000) and by Burbridge, Mayle and Killeen (2004) suggest that glacial-age Amazonian forests, with their mix of currently Andean and low-land Amazonian taxa, have no modern analogues. Pennington *et al.* (2000) proposed that in the LGM much of the current extent of the Amazonian forest was occupied by the now geographically restricted seasonally dry tropical forests. Together these studies suggest that a precipitation level of as much as 25% lower than today, and both lowered temperature and CO_2 concentration, did not result in a radical shift to an alternative stable state during the LGM. Rather, there was a smooth transition involving changes in the floristic assemblage, while maintaining a continuous canopy cover.

The LGM has often been perceived as the hallmark of past climatic changes. However, Amazonian paleoecology teaches us that tropical forests may have

undergone the most radical transition much later, during the Holocene. Over 30 years ago, Servant *et al.* (1981) were the first to provide evidence for arid phases in Bolivia during the Holocene; much more evidence has accumulated recently. For instance, there is evidence of an important dry event at around 7–5 ka BP (Absy *et al.* 1991; Burbridge, Mayle & Killeen 2004; Mayle *et al.* 2004), and this has recently been confirmed with a larger array of techniques (Bird *et al.* 2011; van Breukelen *et al.* 2008). This period of increased drought occurrence may have played a prominent role in the history of human populations in this region, as suggested by evidence from crop domestication (Piperno 2011). Figure 6.1 shows one of the few palynological cores in French Guiana (Ledru 2001). The peak in the pollen of pioneer species (*Cecropia* and *Vismia*), lasting over two centuries between around 1500 and 1300 BP, was attributed to either a human disturbance or to a sustained climatic event (grey peak close to the C14 calibration point at 1570±50 BP, see also Bird *et al.* 2011 for a comparable drought around 1500 BP in Peru). The Holocene history of northeast Amazonia remains poorly documented, but recently Freycon *et al.* (2010) used soil carbon isotope composition to detect whether past vegetation may have been dominated by plants with a C4 photosynthetic pathway
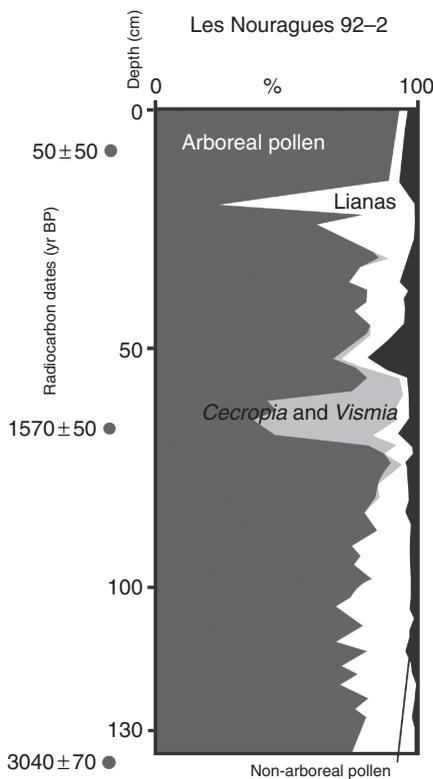

Figure 6.1 A 3000-yr palynological record, from a peat bog at the Nouragues Ecological Research Station, French Guiana. Redrawn from Ledru (2001).

(essentially savanna grasses), which show a lower ^{13}C discrimination than arboreal taxa (predominantly of the C3 photosynthetic pathway). They showed that even forest sites close to coastal savannas today have remained forested during much of the Holocene. Together, this suggests that even though Amazonian forests have been through important climatic fluctuations during the Holocene, they have been quite resilient to these changes.

How does the history of tropical forests help shed light on their future? It is likely that the future environmental conditions of tropical America will be very different from that of the LGM. Precipitation will not necessarily be less than today, but the frequency of long droughts is likely to increase, a phenomenon that may have occurred episodically from 10 to 6 ka BP (Mayle *et al.* 2009). In addition, atmospheric CO_2 concentrations and temperature will increase (Salazar, Nobre & Oyama 2007), and deforestation will contribute to altering the regional climate (Poulter *et al.* 2010). Comparing LGM simulations with those of vegetation status under projected climates by the end of the twenty-first century, Cowling, Cox and Betts (2004) showed that the likely feedbacks responsible for maintaining the integrity of Amazonian forest cover in the past were a reduction in both evapotranspiration (related with reduced rainfall) and plant respiration (related with lower temperature). This combination of response leading to a lower net primary productivity (NPP) but also a lower metabolism is unlikely to hold in the future. For these reasons, Cowling, Cox and Betts (2004) suggested that the Amazonian forest is near its resilience threshold.

This analysis calls for a more in-depth study of the resilience concept. Resilience is the capacity of an ecosystem to absorb disturbance without shifting to an alternative state and losing ecological functions (Holling 1973). Thus resilience encompasses two processes: 'resistance', the ability of a system to withstand a disturbance, and 'recovery', the ability of the system to return to its initial, pre-disturbance, state. This distinction largely depends on how frequent the disturbances are: if the shocks occur frequently and stochastically, the impact of these shocks depend on the ecosystem's resistance. If the perturbations occur rarely, ecosystem stability will be measured by the rate at which the system returns to equilibrium (Ives & Carpenter 2007). The LGM scenario of a shift in floristic composition within a persistent tropical forest canopy cover is consistent with the view of a 'resistant' system. Forests have been able to reshuffle their floristic makeup so as to maintain fundamental ecological functions (water recycling, carbon storage, radiation balance). It also appears that tropical forests have an ability to recover from pronounced disturbances, even though this recovery may take centuries (Ledru 2001; Mayle *et al.* 2009). This prediction is consistent with the idea of biodiversity conferring 'insurance value' (Yachi & Loreau 1998). Some tree species are dominant today because they are adapted to current local

environmental conditions. However, the large reservoir of species spanning a wide range of ecological functions enables the tropical forest system to navigate through a variety of pulse perturbations. Currently dominant species may decline in abundance under changing environmental conditions, but be replaced by other species that are rare today.

The consequence of this discussion is that the current classification of vegetation into a few PFTs ignores an important potential for the adaptation of ecological species assemblages to future climates. Current DGVMs therefore misrepresent the community-wide potential of the vegetation to adapt ecologically to novel environmental conditions. Next, I explore evidence in favour of this claim.

6.3   The leaf economics spectrum and the physiology of tropical trees

A great amount of work has been devoted to identifying PFTs within plants generally, and tropical tree species specifically, with the aim of simplifying the apparently overwhelming biological diversity of these ecosystems (Favrichon 1994; Picard & Franc 2003; Swaine & Whitmore 1988). The underlying theory of PFTs is that species in a given environment may be simply ranked along an axis of performance and persist in coexistence thanks to an ecological trade-off (Grime 1979; Swaine & Whitmore 1988). This idea is reminiscent of Robert MacArthur's model (1972) of a trade-off between ecological strategies with fast-growing species that die young (the r strategists) versus slow-growing species that survive for a long time (the K strategists). If this theory is valid, then functional traits should all covary along a single axis, and it is thought that carbon assimilation traits should thus suffice to describe the plant ecological strategy spectrum. This includes, in addition to competitive and successional traits, ecological traits that describe cold or drought tolerance (Harrison *et al.* 2010); drought tolerance is discussed further below.

Much of the physiological machinery implemented in current versions of DGVMs is based on a leaf-level view of plant physiology. Leaves are the most important organs for carbon fixation, and a general model of photosynthesis has been developed for them (Leuning *et al.* 1995; von Caemmerer 2000). Non-woody plants dominate a sizeable fraction of the planet's vegetation, and by focusing on leaf traits alone a universal way to classify plants into functional types becomes possible (Wright *et al.* 2004). As a result, an active field of research has been concerned with classifying plant species into PFTs using measurable leaf-level traits, or leaf functional traits (Cornelissen *et al.* 2003; Wright *et al.* 2004). These traits include such measures as total leaf area, leaf width, specific leaf area (leaf area per unit dry mass), elemental concentration in leaves (C, N, P and major elements like K, Ca, Mg, Al, Fe), and discrimination of stable isotopes of carbon and nitrogen ($\delta^{13}C$, $\delta^{15}N$). In addition, leaf

mechanical properties have been included in these multi-factorial analyses, and the implications for defence have been discussed (Onoda *et al.* 2011; Read & Stokes 2006). These traits are easily collected across a large number of plants and facilitate the compilation of global datasets (Kattge *et al.* 2011).

Numerous reports of the cross-species variation of some of these traits have been published across biomes (Wright *et al.* 2004), or within tropical rain forests (Baraloto *et al.* 2009; Fyllas *et al.* 2009; Ometto *et al.* 2006). They point to a cross-biome universality of leaf traits. Wright *et al.* (2004) showed that, across biomes, species mean traits fell into a single universal surface in a foliar functional trait space, confirming the idea that some trade-off explains the covariation of functional strategies, thus defining the leaf economics spectrum. Recently Fyllas *et al.* (2009) have carried out an extensive study of regional-scale variation for a range of foliar functional traits in Amazonian tree species to test the pertinence of a leaf economics spectrum within tropical vegetation biomes. They conclude that variation in key foliar functional traits is associated with variation in tree growth. For instance, high fertility soils are associated with higher growth rates, lower leaf mass per area (LMA, the inverse of specific leaf area) and higher nutrient concentration per dry weight (N, P, K and Mg). Trees growing on more fertile soils have more nutrients (especially N and P) to invest into the photosynthetic apparatus, hence the correlation observed by Fyllas *et al.* (2009). This result provides strong, albeit correlative, support for developing DGVMs parameterised with foliar functional traits (Clark *et al.* 2011; Mercado *et al.* 2011). It is consistent with the broadly accepted assumption that PFTs can be defined by a simple suite of foliar traits.

The above PFT classification assumes that carbon assimilation is the major limiting factor in plant growth. However, short but stressful events may considerably compromise the fitness of populations, leading to an increased death rate and/or to reduced overall performance. The likelihood of sudden events that considerably reduce the population fitness has been explored in much greater detail for plants growing in the temperate zone where frost tolerance is an important dimension of the phenological timing of trees (Chuine 2000). In the tropics, one of the most important of these stressful events is the occurrence of prolonged drought periods (McDowell 2011). At an ecosystem scale, it has been demonstrated experimentally that droughts have a significant short-term impact on the ecosystem functioning of tropical forests (Markewitz *et al.* 2010). At the plant scale, stomatal closure is the main line of defence against drought, but beyond a certain point cell turgor will be lost, leading to leaf wilting (Nobel 2009). The ability of an ecosystem to withstand severe droughts depends on the ability of the species to resist wilting. It has thus become a major quest to find functional plant traits that would correlate with drought tolerance.

Recently, Bartlett, Scoffoni and Sack (2012) have provided a useful perspective on the issue of measuring leaf tolerance to drought. They have demonstrated that, across biomes, leaf water potential at wilting (or at turgor loss point, Π_{tlp}) is the best predictor of leaf drought tolerance. Leaf water potential at turgor loss point is a negative pressure (measured in MPa) since water is in tension within the leaf. Drought is measured by the soil negative pressure imposed upon the water column of the plant. If soil water potential falls below a threshold (often assumed to be −1.5 MPa), ecosystem-wide consequences for plant survival are to be expected. Several responses are possible in dry conditions. The plant may reduce its tolerance through osmotic regulation, leading to a reduction in Π_{tlp} (Nobel 2009). This plasticity is limited, however (Wenhui & Prado 1998; Zhu & Cao 2009). Deciduous plants drop their leaves before they wilt, to save as much water as possible. Importantly, deciduousness in dry tropical forest species is not only aimed at maximising water use efficiency, but appears to be primarily a herbivore avoidance, or phenological escape, strategy (Janzen 1981; Marquis, Morais & Diniz 2002). Prado *et al.* (2004), in a detailed study of a range of cerrado plant species, have shown that during the dry season, evergreen species such as *Didymopanax vinosum* Cham. & Schlecht maintain their photosynthetic capacity (*A*) at the same time as regulating evapotranspiration (*E*) to levels comparable to that of the wet season. In contrast, deciduous species (e.g. *Bauhinia rufa* (Bongard) Stendel) regulate their water use efficiency (*A*/*E*) by reducing both *A* and *E*. The leaf turgor loss point is also often lower in evergreen species than the average community, although the relationship between deciduousness and tolerance to leaf wilting is not clear (Wenhui & Prado 1998).

Figure 6.2 represents the covariation of leaf water potential at the turgor loss point against the ratio of wet to dry mass of leaves. It summarises a number of interesting findings. First, the dry forest species of Hao *et al.* (2008) tend to have a lower Π_{tlp} than the moist forest species of Zhu and Cao (2009), as also pointed out by Bartlett *et al.* (2012). There appears to be a relatively good correlation between Π_{tlp} and the ratio of wet to dry mass of leaves ($r^2 = 0.63$). Second, a phylogenetically controlled comparison between dry forest species and woodland savanna species (the grey circles and grey triangles, respectively, in Figure 6.2) suggests that Π_{tlp} is not necessarily lower in woodland savanna species than in adjacent dry forest species. Pending more detailed studies, this suggests that the phylogenetic signal is low for Π_{tlp}. Further genus-specific leaf tolerance studies, in *Cordia* (Choat, Sack & Holbrook 2007) and *Ficus* (Patiño *et al.* 1995), deserve to be mentioned in this respect. Third, Zhu and Cao's (2009) study confirms that osmotic regulation, leading to a drop of Π_{tlp} between the wet and the dry season, is an important component of drought tolerance. Remarkably, the three liana species studied by Zhu and Cao (2009) show little to no osmotic regulation. Fourth, and
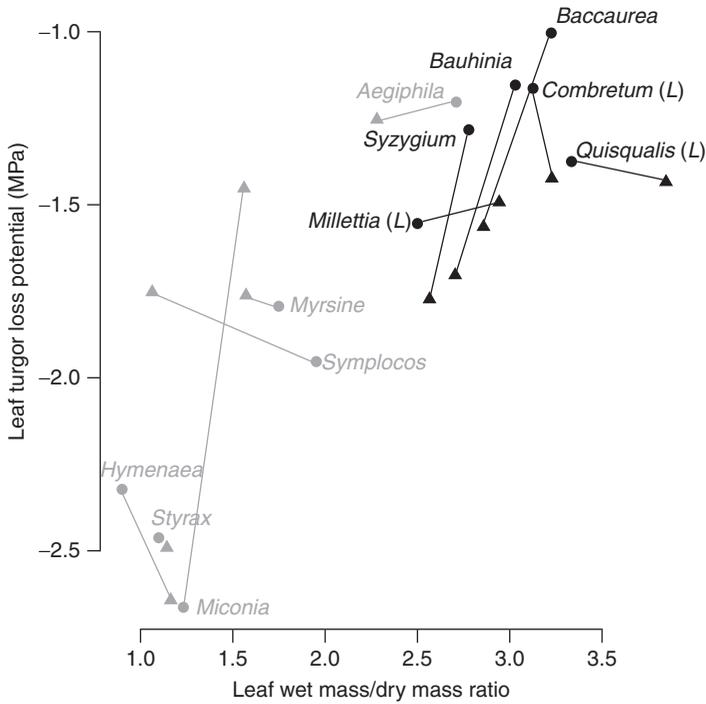
Figure 6.2 Correlation between the leaf turgor loss potential (Π_{tlp}, in MPa) and the ratio of wet mass over dry mass for leaves. Grey symbols are from Hao *et al.* (2008), black symbols are from Zhu and Cao (2009). In Hao *et al.*'s (2008) study, six congeneric species pairs were compared, where each pair has one forest species (grey circles) and one cerrado species (grey triangles). In Zhu and Cao's (2009) study, six species were measured both in the wet season (black circles) and in the dry season (black triangles). Species denoted with (L) in Zhu and Cao's (2009) study are lianas.

finally, lianas' leaf water potential at the turgor loss point does not differ from that of trees, in spite of their propensity to keep their leaves even in semi-deciduous forests (Schnitzer & Bongers 2002).

Do some commonly measured leaf traits covary strongly with leaf tolerance to wilting? Niinemets (2001) has proposed that LMA should be a good correlate of drought tolerance because it is associated with leaf wall stiffness. However, Bartlett, Scoffoni and Sack (2012) showed that LMA is a poor predictor of Π_{tlp} measurements globally, suggesting that leaf wall stiffness as an indicator of leaf drought tolerance does not hold globally across plants. In the few publications focusing on dry tropical environments, a relatively good correlation has been found between leaf drought tolerance and LMA (Bucci *et al.* 2004; Meinzer *et al.* 2008a; Poorter *et al.* 2009), but this evidence remains too thin to discount the possibility that Π_{tlp} may represent an independent axis of variation in the leaf economy spectrum, and that drought tolerance is inadequately

represented in the analysis by Wright *et al.* (2004). Besides, LMA is associated with other functions as well, and it is also a remarkably plastic trait (Poorter *et al.* 2009).

6.4   Whole-plant physiology of tropical trees

A second important issue relevant to the construction of PFTs is that tropical trees are not just leaf surfaces. Most of their carbon is held in self-supporting structures (trunks) and resource-foraging structures (roots). Leaf water is supplied through the xylem, and the whole plant water status is critically dependent on the health of woody tissue. Wood protection in particular may represent a non-negligible energetic investment for a tropical tree, as suggested by the variation in bark thickness across tree species (Brando *et al.* 2012; Paine *et al.* 2010). Much research has been conducted on wood structure, because tropical timber represents an important international economic market. Wood production is a critical allocation strategy for photosynthates, since growth in height leads to a competitive advantage in forested environments. Many wood functional traits may be measured that are likely to be even more important in predicting tree growth rates than leaf-level traits. For instance, just by looking at a wood core in the trunk of a tropical tree, critical demographic data may be inferred quite easily, at least if the tree shows an annual growth pattern (Rozendaal & Zuidema 2011; Worbes 2002).

Simple functional traits have been proposed for inclusion in DGVM development, such as wood density, or the distribution of conduit sizes (Chave *et al.* 2009; Patiño *et al.* 2009; Zanne *et al.* 2010). Wood density has generated a great deal of recent interest because it is believed to integrate a number of important stem processes (Baas *et al.* 2004). It has been speculated that wood density may correlate with the ability of a woody plant to withstand whole-plant water stress (Hacke *et al.* 2001; Jacobsen *et al.* 2005; see also below). Wood density is also clearly related to tree mechanical stability (Chave *et al.* 2009; van Gelder, Poorter & Sterck 2006), and correlates negatively with mortality rates across a broad range of forests (Kraft *et al.* 2010). Finally, wood density has been found to be strongly related to total stem sapflow, and thus total plant transpiration, in a limited number of studies (Bucci *et al.* 2004, 2008; McCulloh *et al.* 2011; Meinzer *et al.* 2008a).

In addition to causing leaf wilting, drought may cause irreversible damage to the plant as a result of cavitation in the xylem conduits (Cochard 2006; Tyree & Zimmermann 2002). Xylem failure during exceptional episodes of drought may occur more frequently in the future. Engelbrecht and Kursar (2003) have demonstrated that seedlings of a range of species respond very differently to drought stresses. Seedling drought tolerance may indeed be a critical element of the fitness of tree populations in seasonal climates, and a key explanation of patterns of plant distribution across environmental

gradients (Engelbrecht *et al.* 2007). However, rapid changes in climate may also increase the risk of xylem failure of large trees. For instance, Zhang *et al.* (2009) have shown that larger individuals of the legume tree *Sclerolobium paniculatum* were more likely to show branch damage and to die than smaller trees under the same drought conditions (see Rood *et al.* 2000 for a temperate tree example). This shows that DGVMs should pay special attention to modelling xylem-failure induced mortality in trees, and not only mortality related to carbon starvation (see e.g. Fisher *et al.* 2010; McDowell 2011). An obvious trait to model the risk of xylem failure is the pressure at which a stem has lost 50% of its hydraulic conductivity (P_{50}). In their meta-analysis, Maherali *et al.* (2004) reported 41 P_{50} measurements for moist tropical forest species (mostly from Tyree, Patiño & Becker 1998 and Zotz, Tyree & Cochard 1994), and only 19 for dry tropical forest species. They found that vulnerability to cavitation was on average almost three times larger in moist tropical forest than in dry tropical forest trees. Additional values not included in Maherali *et al.*'s (2004) compilation for dry and moist tropical forests confirm this first analysis (Brodribb *et al.* 2003; Bucci *et al.* 2006; Chen *et al.* 2009; Lopez *et al.* 2005; Markesteijn *et al.* 2011; Meinzer *et al.* 2003, 2008b; Zhu & Cao 2009; see Figure 6.3, and appendix). Figure 6.3 shows that moist tropical forest species appear to be more vulnerable to drought-induced xylem failure than dry forest or woodland savanna species. However, with the exception of Meinzer *et al.* (2003, 2008b), these previous studies have tended to ignore
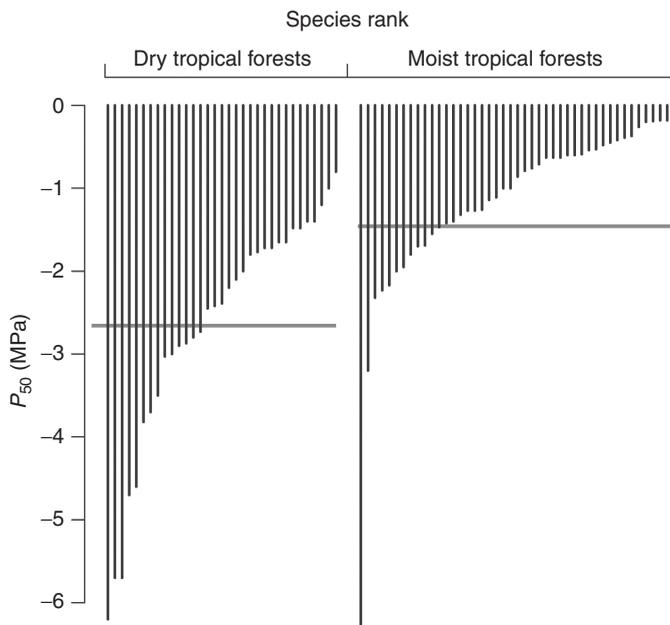

Figure 6.3 Xylem vulnerability to cavitation (pressure at which 50% of the xylem hydraulic conductivity has been lost) for dry and moist tropical forests. This meta-analysis shows that dry forest species are on average half as vulnerable to xylem cavitation as moist tropical forest species. The mean values are drawn as grey horizontal lines (mean $P_{50} = -2.66$ MPa, $n = 33$, for dry tropical forests; mean $P_{50} = -1.41$ MPa, $n = 66$, for moist tropical forests). However, the range of variation is large and comparable in both biome types.

the species that dominate Amazonian forests. Thus this conclusion merits further scrutiny in this region. Xylem water potential at 50% loss of hydraulic conductivity varies a lot across species in both biomes, and spans almost the same range of variation. This is suggestive that, under a stronger drought, more species may be at risk in moist tropical forests than in dry tropical forests, yet the survivors may be enough to maintain a closed-canopy cover and a large fraction of the biomass stocks.

How should we account for non-leaf traits in the development of DGVMs? Under MacArthur's (1972) trade-off theory, whole-plant traits should covary in a predictable way and define simple plant ecological 'syndromes'. For instance, fast-growing trees should also invest less into wood construction costs because they invest more into photosynthesis (per dry mass). Although such a trade-off in allocation is expected across broad environmental gradients and across biomes, this pattern does not appear to hold within moist tropical forests. Baraloto *et al.* (2010) showed that leaf traits are not correlated with stem-related functional traits, and the leaf-investment and stem-investment strategies appeared to be uncorrelated. Thus, for PFTs based on leaf traits, it is impossible to predict how the plant will allocate carbon into wood production. Further, based on this analysis it is expected that species able to invest a lot in both wood and leaf construction can still persist in the ecosystem. Chen *et al.* (2009) arrived at a similar result, using more traits but only six species in the family Euphorbiaceae s.l. Fyllas, Quesada and Lloyd (2012) have taken this idea one step further through a global approach based on functional traits measured not only on leaves but also on whole plant traits, including wood traits. They conducted an ordination analysis on a suite of traits, much like Baraloto *et al.* (2010) but at a regional scale, and subsequently clustered the species into discrete groups using a K-mean cluster algorithm. They found that their species could be naturally clustered into four groups, possibly defining novel types of PFTs. These four groups correspond to a combination of light demand strategies (as measured by potential gas exchange rates) and overall tree stature. However, there was still large variation in species traits within each of these four PFTs. It should be noted that the uncoupling of leaf and stem traits remains a debated subject. Leaf and wood traits appear to be more correlated in xeric habitats than in moist forest ones. Indeed, the two studies where a convergence of wood and leaf traits was observed were conducted in woodland savanna and dry forest (Bucci *et al.* 2004; Mendez-Alonzo in press).

The special case of lianas merits a separate discussion. Tropical forests are remarkable for having a large abundance of lianas (Schnizter & Bongers 2002), which may increase in abundance with changing climates (Phillips *et al.* 2002). These lianas, as parasitic plants, do not need to invest as much carbon into wood construction. They have large conduits and a higher water conductivity

leading to higher transpiration (Andrade *et al.* 2005; Feild & Balun 2008; Zhu & Cao 2009). Lianas thus represent a disproportionate amount of carbon turnover (NPP) and of ecosystem transpiration in comparison with the biomass they hold (e.g. Restom & Nepstad 2001). They also have a distinctive response to drought, since many lianas of semideciduous forests keep their leaves during the dry season (Schnitzer & Bongers 2002; see also Figure 6.2). It would be important to further appraise the importance of accounting for the presence of lianas in DGVMs and to model their contribution to NPP and to ecosystem transpiration. Likewise, other life forms found almost exclusively in moist tropical forests, such as hemiepiphytes, may play an important ecosystem-level role (Patiño *et al.* 1995; Zotz, Tyree & Cochard 1994).

In conclusion, in spite of an enormous effort to better understand the physiology of tropical plants, a number of key points remain undocumented, especially regarding the drought tolerance of large tropical trees. As a result, current efforts to reduce these physiological behaviours to a few discrete groups have not met with great success. Most attempts to construct plant functional types have been restricted to leaf traits (Schulze *et al.* 1994; Wright *et al.* 2004), and available evidence now suggests that existing trait databases do not include appropriate proxies for xylem conductivity and for xylem vulnerability to cavitation. Comparing a range of species with respect to different ecological functions, it has often been found that traits sometimes covary but cannot easily be partitioned into discrete groups (Baraloto *et al.* 2010; Goldstein *et al.* 2008; Figure 6.3). This argument should not be overlooked when considering plant functional types as an operational concept in the building of dynamic vegetation models. It is possible that PFTs could be replaced with more detailed population-based models that couple the dynamics of the species assemblage with ecosystem processes, or that many more PFTs could be included to account for the observed variability in plant traits.

6.5   Discussion

The idea that the presence of a few species may help the persistence of ecological functions through environmental disturbances is far from novel in ecology and has been widely discussed in the ecosystem science literature. However, evidence for such a scenario is wanting in tropical forests because it is difficult to reconcile the long generation times of tree species, and the hypothetical nature of environmental change scenarios, with any experimental test. Here, I have shown that the current generation of coupled biosphere–atmosphere Earth models still include too many uncertainties when it comes to making predictions about the future of Amazonian tropical forests. If the Amazon dieback scenario has spurred considerable controversy, evidence in its favour remains scarce, and existing models produce very different projections for Amazonia at the end of the twenty-first century. However, global

trends of an increase in temperature will probably be accompanied by stronger and/or more frequent droughts over Amazonia. Research on drought tolerance of Amazonian forests remains surprisingly scarce given the importance of the challenge, but available evidence suggests that both the leaves and the xylem of average moist tropical forest tree species are not as well adapted to drought as dry tropical forest and woodland savanna species. Thus, whether drought-tolerant trees will be able to supplant drought-intolerant ones within the moist tropical forest matrix, and given the short timeframe, remains an open question.

When building DGVMs, it is perhaps inevitable to use plant functional traits. A range of issues are associated with measuring and using these traits, as discussed above. Traits do not necessarily correlate directly with relevant physiological processes, and they may not be useful in a process-based model. Furthermore, plant functional traits cannot be considered as constant for species across their whole geographical range and/or environmental gradients. A recent detailed analysis of how whole-plant traits covary with environmental conditions has been published by Patiño *et al.* (2012). One of the strongest correlations in their dataset was for the decline of sapwood density with increasing soil fertility (see also Fyllas *et al.* 2009), a relationship also known by foresters. A remarkable experiment has been conducted in the Brazilian cerrado to further explore this question (Bucci *et al.* 2006). By fertilising the soil for 36 months for five tree species, the authors showed that only the addition of nitrogen had a significant effect, and that nitrogen addition resulted in a decline in both sapwood density and in vulnerability to cavitation (the trees growing in an N-enriched soil had lower P_{50} values than the controls). The study of Bucci *et al.* (2006) therefore suggests that most of the traits discussed here are either directly correlated to demographic variables (such as stem growth rate) or are intrinsically variable. This variability, together with the adaptive potential of tree species, cannot be overemphasised. Such trait–environment covariation has never been included in DGVMs, in spite of their obvious importance. More experimental and empirical results are needed before generalisations are possible on this front.

It would be desirable to implement a finer-grained description of tropical forest vegetation dynamics, allowing for a more accurate description of inter-specific and inter-individual variability. The problem raised here is one of parameter aggregation: it is often the case that by aggregating traits originally measured on individuals into a few discrete categories, the statistical properties of the entire dataset are altered. Although this problem has a remarkably long history in ecology (Iwasa, Andreasen & Levin 1987) and in forest model simulators (Hurtt *et al.* 1998; Ritchie & Hann 1997), it has been overlooked in recent attempts to develop DGVMs, in part owing to the lack of accessible databases on functional traits. One option for a new generation of DGVMs is to

develop individual-based versions to account for the physiological processes at play in tropical forest ecosystems. Only the outline of such an approach is presented here, based on a previous development of an individual-based spatially explicit forest growth simulator described in Chave (1999) and called TROLL. In the original version of this dynamic forest growth simulator, each tree with a trunk diameter of 1 cm or above is simulated. At most, one individual can occupy a grid cell of 1 × 1 m, thus allowing a maximum number of 10 000 individuals per hectare. Individuals compete for free cell space as in cellular automata (Hurtt & Pacala 1995), but they also compete for light resources. Solar radiation above the canopy may be computed from geometrical considerations of solar movement, and it may be decomposed into a direct and a diffuse component (Leuning *et al.* 1995; Monteith & Unsworth 2007). In agreement with the Beer–Lambert law, light intensity in a forest declines exponentially from the top of the canopy to the ground level (Hirose 2005). To model this light attenuation, I took a discrete approach whereby the leaf density is computed in each voxel of side 1 m within the canopy, assuming a turbid medium approximation within each voxel (Le Roux *et al.* 2001). Death could result from a stochastic process, insufficient light availability (see also Pacala *et al.* 1996), carbon starvation (Fisher *et al.* 2010) or xylem embolism (Cochard 2006). The TROLL model also includes a detailed treefall gap formation module in which falling trees topple neighbours according to their relative height and size. Tree geometry is modelled explicitly by including, in addition to trunk dbh, total tree height, crown radius and crown depth. All of the parameters are defined for each species, hence there is no need to lump species into PFTs (but the intraspecific variability in ecological traits is ignored).

One challenge is to develop a leaf-level photosynthesis module averaged over sufficiently long time scales so as to avoid the issues of modelling the relationship between stomatal conductance g_c to local environmental conditions (Lloyd & Farquhar 2008). This could be tackled by relating the mean ratio of intracellular to atmospheric CO_2 concentration, c_i/c_a, and carbon isotopic discrimination in leaves as modelled by $\delta^{13}C$ (Domingues, Martinelli & Ehleringer *et al.* 2007, 2010; Farquhar, Ehleringer & Hubick 1989). Indeed, carbon isotopic discrimination has been measured in a large range of trees empirically (Baraloto *et al.* 2010; Ometto *et al.* 2006). A second challenge is to include a detailed model of drought resistance, including the susceptibility of a plant's leaves and of its water column to sudden droughts. Empirical data to model leaf drought tolerance remains scarce, as reviewed above, but empirical evidence relating basic wood properties such as sapwood density and resistance to xylem cavitation is now strong and convincing. Finally, this model poses a serious computational challenge, which has been a major impediment to the development of global individual-based DGVMs in the

past. To test this, I simulated the dynamics of a relatively small permanent plot (16 ha, 1 m spatial resolution). With these conditions, the TROLL model admits a maximum of 160 000 individuals at a time. Briefly, the test runs showed that species diversity can be maintained in the system while ecosystem variables (NPP, stem size distribution, biomass) reach an equilibrium within a few centuries. These results will be developed in a forthcoming work, but the point here is that such models are easily scalable using the impressive computer power available today. Importantly, they also offer an important means of performing direct and ecologically intuitive data assimilation.

To conclude, it is tempting to suggest that the oversimplification of plant functional types in existing DGVMs account, at least in part, for the predicted critical transition between forest and savanna in South America over the twenty-first century. Real ecosystems are species-rich, and some of their species (e.g. *Hymenaea courbaril* L.) thrive both in closed-canopy forests and in woodland savannas. Although they are scattered in the forest today, their fitness may be favoured by changing climates, and they would then rise to dominance in the decades to come. This floristic turnover, which cannot be modelled in the current generation of DGVMs, would help to maintain a closed canopy cover, and help minimise changes in ecosystem functions in the carbon, water and element cycles, and in the energy budget of the forest. Next generations of DGVMs should seek to bridge the divide between ecosystem science and community ecology, and account for biological diversity and for population processes.

Acknowledgements

Appendix 6.1

Compilation of values of xylem water potential at 50% loss of hydraulic conductivity (P_{50}) used to estimate the xylem vulnerability to cavitation, for tropical forest environments. Monocots, gymnosperms and mangrove species were excluded from this compilation.

Species	Family	Forest type	P_{50} (MPa)	Country	Reference
Bursera simaruba (L.) Sarg.	Burseraceae	Dry	−1	Costa Rica	Brodribb *et al.* (2003)
Calycophyllum candidissimum (Vahl) DC	Rubiaceae	Dry	−2.87	Costa Rica	Brodribb *et al.* (2003)
Enterolobium cyclocarpum (Jacq.) Griseb.	Fabaceae	Dry	−2.73	Costa Rica	Brodribb *et al.* (2003)
Hymenaea courbaril L.	Fabaceae	Dry	−3	Costa Rica	Brodribb *et al.* (2003)
Quercus oleoides Schltdl. & Cham.	Fagaceae	Dry	−3.03	Costa Rica	Brodribb *et al.* (2003)
Rehdera trinervis (S.F. Blake) Moldenke	Verbenaceae	Dry	−2.8	Costa Rica	Brodribb *et al.* (2003)
Simarouba glauca DC	Simaroubaceae	Dry	−2	Costa Rica	Brodribb *et al.* (2003)
Swietenia macrophylla King	Meliaceae	Dry	−2.2	Costa Rica	Brodribb *et al.* (2003)
Blepharocalyx salicifolius (Kunth) O. Berg	Myrtaceae	Dry	−1.72	Brazil	Bucci *et al.* (2006)
Caryocar brasiliense Cambess.	Caryocaraceae	Dry	−1.48	Brazil	Bucci *et al.* (2006)
Ouratea hexasperma (A. St.-Hil.) Baill.	Ochnaceae	Dry	−1.48	Brazil	Bucci *et al.* (2006)
Qualea parviflora Mart.	Vochysiaceae	Dry	−1.65	Brazil	Bucci *et al.* (2006)
Schefflera macrocarpa (Cham. & Schltdl.) Frodin	Araliaceae	Dry	−1.72	Brazil	Bucci *et al.* (2006)
Aleurites moluccana (L.) Willd.	Euphorbiaceae	Moist	−2.17	China	Chen *et al.* (2009)
Bischofia javanica Blume	Phyllanthaceae	Moist	−1.27	China	Chen *et al.* (2009)
Codiaeum variegatum (L.) Rumph. ex A. Juss.	Euphorbiaceae	Moist	−2.23	China	Chen *et al.* (2009)
Drypetes indica (Müll. Arg.) Pax & K. Hoffm.	Putranjivaceae	Moist	−2.32	China	Chen *et al.* (2009)
Hevea brasiliensis (Willd. ex A. Juss.) Müll. Arg.	Euphorbiaceae	Moist	−1.27	China	Chen *et al.* (2009)
Macaranga denticulata (Blume) Müll. Arg.	Euphorbiaceae	Moist	−1.14	China	Chen *et al.* (2009)
Acosmium cardenasii H.S. Irwin & Arroyo	Fabaceae	Dry	−6.2	Bolivia	Markesteijn *et al.* (2011)
Anadenanthera colubrina (Vell.) Brenan	Fabaceae	Dry	−5.7	Bolivia	Markesteijn *et al.* (2011)
Aspidosperma cylindrocarpon Müll. Arg.	Apocynaceae	Dry	−2.9	Bolivia	Markesteijn *et al.* (2011)
Aspidosperma tomentosum Mart.	Apocynaceae	Dry	−4.7	Bolivia	Markesteijn *et al.* (2011)
Astronium urundeuva (Allemão) Engl.	Anacardiaceae	Dry	−1.8	Bolivia	Markesteijn *et al.* (2011)

Species	Family		Value	Country	Reference
Bougainvillea modesta Heimerl	Nyctaginaceae	Dry	−3.7	Bolivia	Markesteijn *et al.* (2011)
Casearia gossypiosperma Briq.	Salicaceae	Dry	−4.6	Bolivia	Markesteijn *et al.* (2011)
Cecropia concolor Willd.	Urticaceae	Dry	−0.8	Bolivia	Markesteijn *et al.* (2011)
Ceiba speciosa (A. St.-Hil.) Ravenna	Malvaceae	Dry	−1.4	Bolivia	Markesteijn *et al.* (2011)
Centrolobium microchaete (Mart. ex Benth.) H.C. Lima	Fabaceae	Dry	−1.2	Bolivia	Markesteijn *et al.* (2011)
Guibourtia hymenaefolia (Moric.) J. Léonard	Fabaceae	Dry	−5.7	Bolivia	Markesteijn *et al.* (2011)
Solanum riparium Pers.	Solanaceae	Dry	−2.1	Bolivia	Markesteijn *et al.* (2011)
Trichilia elegans A. Juss.	Meliaceae	Dry	−3.5	Bolivia	Markesteijn *et al.* (2011)
Anacardium excelsum (Kunth) Skeels	Anacardiaceae	Moist	−1.56	Panama	Meinzer *et al.* (2003)
Cordia alliodora (Ruiz & Pav.) Oken	Boraginaceae	Moist	−3	Panama	Meinzer *et al.* (2003)
Ficus insipida Willd.	Moraceae	Moist	−1.66	Panama	Meinzer *et al.* (2003)
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin	Araliaceae	Moist	−1.68	Panama	Meinzer *et al.* (2003)
Chrysophyllum cainito L.	Sapotaceae	Moist	−2.1	Panama	Meinzer *et al.* (2008b)
Ficus insipida Willd.	Moraceae	Moist	−1.91	Panama	Meinzer *et al.* (2008b)
Manilkara bidentata (A. DC.) A. Chev.	Sapotaceae	Moist	−2.65	Panama	Meinzer *et al.* (2008b)
Protium panamense (Rose) I.M. Johnst.	Burseraceae	Moist	−1.73	Panama	Meinzer *et al.* (2008b)
Tachigali versicolor Standl. & L.O. Williams	Fabaceae	Moist	−1.63	Panama	Meinzer *et al.* (2008b)
Tapirira guianensis Aubl.	Anacardiaceae	Moist	−1.82	Panama	Meinzer *et al.* (2008b)
Trattinnickia aspera (Standl.) Swart	Burseraceae	Moist	−1.07	Panama	Meinzer *et al.* (2008b)
Vochysia ferruginea Mart.	Vochysiaceae	Moist	−1	Panama	*Meinzer et al.* (2008b)
Curatella americana L.	Dilleniaceae	Dry	−1.4	Venezuela	Sobrado (1996)
Beureria cumanensis O.E. Schulz	Boraginaceae	Dry	−3.82	Venezuela	Sobrado (1997)
Capparis aristiguetae Iltis	Capparaceae	Dry	−2.45	Venezuela	Sobrado (1997)
Coursetia ferruginea (Kunth) Lavin	Fabaceae	Dry	−2.42	Venezuela	Sobrado (1997)
Lonchocarpus pubescens (Willd.) DC.	Fabaceae	Dry	−1.77	Venezuela	Sobrado (1997)
Morisonia americana L.	Capparaceae	Dry	−2.39	Venezuela	Sobrado (1997)
Pithecellobium dulce (Roxb.) Benth.	Fabaceae	Dry	−1.65	Venezuela	Sobrado (1997)

Species	Family	Forest type	P_{50} (MPa)	Country	Reference
Aglaia glabrata Teijsm. & Binn.	Meliaceae	Moist	−0.71	Brunei	Tyree *et al.* (1998)
Amyxa pluricornis (Radlk.) Domke	Thymelaeaceae	Moist	−0.63	Brunei	Tyree *et al.* (1998)
Canarium caudatum King	Burseraceae	Moist	−1.47	Brunei	Tyree *et al.* (1998)
Cotylelobium burckii Heim	Dipterocarpaceae	Moist	−0.45	Brunei	Tyree *et al.* (1998)
Diospyros brachiata King & Gamble	Ebenaceae	Moist	−0.42	Brunei	Tyree *et al.* (1998)
Diospyros hermaphroditica Bakh. ex Steenis	Ebenaceae	Moist	−0.6	Brunei	Tyree *et al.* (1998)
Diospyros mindanaensis Merr.	Ebenaceae	Moist	−0.79	Brunei	Tyree *et al.* (1998)
Dipterocarpus globosus Vesque	Dipterocarpaceae	Moist	−0.18	Brunei	Tyree *et al.* (1998)
Dryobalanops aromatica C.F. Gaertn.	Dipterocarpaceae	Moist	−0.26	Brunei	Tyree *et al.* (1998)
Heritiera sumatrana Kosterm.	Malvaceae	Moist	−1.69	Brunei	Tyree *et al.* (1998)
Homalium moultonii Merr.	Salicaceae	Moist	−6.3	Brunei	Tyree *et al.* (1998)
Isonandra lanceolata Thwaites	Sapotaceae	Moist	−0.48	Brunei	Tyree *et al.* (1998)
Lophopetalum subobovatum King	Celastraceae	Moist	−0.59	Brunei	Tyree *et al.* (1998)
Mallotus wrayi King ex Hook. f.	Euphorbiaceae	Moist	−0.53	Brunei	Tyree *et al.* (1998)
Nephelium lappaceum L.	Sapindaceae	Moist	−0.76	Brunei	Tyree *et al.* (1998)
Payena endertii H.J. Lam	Sapotaceae	Moist	−0.63	Brunei	Tyree *et al.* (1998)
Pentace adenophora Kosterm.	Malvaceae	Moist	−0.19	Brunei	Tyree *et al.* (1998)
Santiria mollis Engl.	Burseraceae	Moist	−0.2	Brunei	Tyree *et al.* (1998)
Shorea faguetiana Heim.	Dipterocarpaceae	Moist	−0.37	Brunei	Tyree *et al.* (1998)
Shorea mecistopteryx Ridl.	Dipterocarpaceae	Moist	−0.63	Brunei	Tyree *et al.* (1998)
Shorea ovalis Bl.	Dipterocarpaceae	Moist	−0.39	Brunei	Tyree *et al.* (1998)
Sindora leiocarpa Backer ex K. Heyne; de Wit	Fabaceae	Moist	−0.86	Brunei	Tyree *et al.* (1998)
Stemonurus umbellatus Becc.	Stemonuraceae	Moist	−0.18	Brunei	Tyree *et al.* (1998)
Syzygium ampullarium (Stapf) Merr. & L.M. Perry	Myrtaceae	Moist	−0.6	Brunei	Tyree *et al.* (1998)

Species	Family	Biome	Value	Country	Reference
Syzygium bankense (Hassk.) Merr. & L.M. Perry	Myrtaceae	Moist	−1.26	Brunei	Tyree *et al.* (1998)
Syzygium muelleri (Miq.) Miq.	Myrtaceae	Moist	−0.54	Brunei	Tyree *et al.* (1998)
Xerospermum laevigatum Radlk.	Sapindaceae	Moist	−0.18	Brunei	Tyree *et al.* (1998)
Baccaurea ramiflora Lour.	Phyllanthaceae	Moist	−2	China	Zhu & Cao (2009)
Bauhinia variegata L.	Fabaceae	Moist	−1.55	China	Zhu & Cao (2009)
Combretum latifolium Blume	Combretaceae	Moist	−1.11	China	Zhu & Cao (2009)
Millettia pachycarpa Benth.	Fabaceae	Moist	−1.32	China	Zhu & Cao (2009)
Quisqualis indica L.	Combretaceae	Moist	−1.42	China	Zhu & Cao (2009)
Syzygium szemaoense Merr. & L.M. Perry	Myrtaceae	Moist	−1.95	China	Zhu & Cao (2009)
Cordia alliodora (Ruiz & Pav.) Oken	Boraginaceae	Moist	−3.2	Panama	Zotz *et al.* (1994)
Ficus citrifolia Mill.	Moraceae	Moist	−1.7	Panama	Zotz *et al.* (1994)
Ochroma pyramidale (Cav. ex Lam.) Urb.	Malvaceae	Moist	−1	Panama	Zotz *et al.* (1994)
Ouratea lucens (Kunth) Engl.	Ochnaceae	Moist	−1.8	Panama	Zotz *et al.* (1994)
Pseudobombax septenatum (Jacq.) Dugand	Malvaceae	Moist	−1	Panama	Zotz *et al.* (1994)
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin	Araliaceae	Moist	−1.4	Panama	Zotz *et al.* (1994)
Ouratea lucens (Kunth) Engl.	Ochnaceae	Moist	−1.9	Panama	Lopez *et al.* (2005)
Swartzia simplex (Sw.) Spreng.	Fabaceae	Moist	−2.8	Panama	Lopez *et al.* (2005)
Psychotria horizontalis Sw.	Rubiaceae	Moist	−2.6	Panama	Lopez *et al.* (2005)
Hybanthus prunifolius (Humb. & Bonpl.) Schultze-Menz.	Violaceae	Moist	−4.1	Panama	Lopez *et al.* (2005)
Prioria copaifera Griseb.	Fabaceae	Moist	−0.8	Panama	Lopez *et al.* (2005)
Carapa guianensis Aubl.	Meliaceae	Moist	−0.8	Panama	Lopez *et al.* (2005)
Ficus citrifolia Mill.	Moraceae	Moist	−1.4	Panama	Lopez *et al.* (2005)
Bursera simaruba (L.) Sarg.	Burseraceae	Moist	−3.2	Panama	Lopez *et al.* (2005)
Cordia alliodora (Ruiz & Pav.) Oken.	Boraginaceae	Moist	−1.6	Panama	Lopez *et al.* (2005)

References

Absy, M. L., Cleef, A., Fournier, M. *et al.* (1991) Mise en évidence de quatre phases d'ouverture de la forêt dense dans le Sud-Est de l'Amazonie au cours des 60,000 dernières années: première comparaison avec d'autres régions tropicales. *Comptes Rendus de l'Académie des Sciences Paris, Série II*, **312**, 673–678.

Agrawal A., Nepstad, D. & Chhatre, A. (2011) Reducing emissions from deforestation and forest degradation. *Annual Review in Environmental Resources*, **36**, 373–396.

Andrade, J. L., Meinzer, F. C., Goldstein, G. & Schnitzer, S.A. (2005) Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest. *Trees*, **19**, 282–289.

Baas, P., Ewers, F. W., Davis, S. D. & Wheeler, E. A. (2004). Evolution of xylem physiology. In *The Evolution of Plant Physiology* (eds. A. R. Hemsley & I. Poole), pp. 273–295. London, San Diego: Elsevier Academic Press.

Baraloto, C., Paine, C. E. T., Patiño, S. *et al.* (2009) Functional trait variation and sampling strategies in species-rich plant communities. *Functional Ecology*, **24**, 208–216.

Baraloto, C., Paine, C. E. T., Poorter, L. *et al.* (2010) Decoupled leaf and stem economics in rainforest trees. *Ecology Letters*, **13**, 1338–1347.

Bartlett, M. K., Scoffoni, C. & Sack, L. (2012) The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecology Letters*, **15**, 393–405.

Bird, B. W., Abbott, M. B., Rodbell, D. T. & Vuille, M. (2011) Holocene tropical South American hydroclimate revealed from lake sediment d18O record. *Earth and Planetary Science Letters*, **310**, 192–202.

Brando P. M., Nepstad, D. C., Balch, J. K. *et al.* (2012) Fire-induced tree mortality in a neotropical forest: the role of tree size, wood density and fire behavior. *Global Change Biology*, **18**, 630–641.

van Breukelen, M. R., Vonhof, H. B., Hellstrom, J. C., Wester, W. C. G. & Kroon, D. (2008) Fossil dripwater in stalagmites reveals Holocene temperatures and rainfall variation in Amazonia. *Earth and Planetary Science Letters*, **275**, 54–60.

Brodribb, T. J. & Feild, T. S. (2010) Leaf hydraulic evolution led a surge in leaf photosynthetic capacity during early angiosperm diversification. *Ecology Letters*, **13**, 175–183.

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.

Bucci, S. J., Goldstein, G., Meinzer, F. C. *et al.* (2004) Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant. *Tree Physiology*, **24**, 891–899.

Bucci, S. J., Scholz, F. G., Goldstein, G. *et al.* (2006) Nutrient availability constrains the hydraulic architecture and water relations of savannah trees. *Plant, Cell and Environment*, **29**, 2153–2167.

Bucci, S. J., Scholz, F. G., Goldstein, G. *et al.* (2008) Controls on stand transpiration and soil water utilization along a tree density gradient in a Neotropical savanna. *Agricultural and Forest Meteorology*, **148**, 839–849.

Burbridge, R. E., Mayle, F. E. & Killeen, T. J. (2004) Fifty-thousand-year vegetation and climate history of Noel Kempff Mercado National Park, Bolivian Amazon. *Quaternary Research*, **61**, 215–230.

Burnham, R. J. & Johnson, K. R. (2004) South American palaeobotany and the origins of Neotropical rainforests. *Philosophical Transactions of the Royal Society London Series B*, **359**, 1595–1610.

Bush, M. B. (1994) Amazonian speciation: a necessarily complex model. *Journal of Biogeography*, **21**, 5–17.

Bush, M. B., Miller, M. C., de Oliveira, P. E. & Colinvaux, P.A. (2002) Orbital forcing signal

in sediments of two Amazonian lakes. *Journal of Paleolimnology*, **27**, 341–352.

Bush, M. B., Silman, M. R. & Urrego, D. H. (2004) 48,000 years of climate and forest change in a biodiversity hot spot. *Science*, **303**, 827–829.

von Caemmerer, S. (2000) *Biochemical Models of Leaf Photosynthesis*. Victoria, Australia: CSIRO Publishing.

Chave, J. (1999) Study of structural, successional and spatial patterns in tropical rain forests using TROLL, a spatially explicit forest model, *Ecological Modelling*, **124**, 233–254.

Chave, J., Coomes, D., Jansen, S. *et al.* (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.

Chen, J. W., Zhang, Q., Li, X. S. & Cao, K. F. (2009) Independence of stem and leaf hydraulic traits in six Euphorbiaceae tree species with contrasting leaf phenology. *Planta*, **230**, 459–168.

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.

Christin, P. A., Besnard, G., Samaritani, E. *et al.* (2008) Oligocene CO_2 decline promoted C4 photosynthesis in grasses. *Current Biology*, **18**, 37–43.

Chuine, I. (2000) A unified model for budburst of trees. *Journal of Theoretical Biology*, **207**, 337–347.

Clark, D. B., Mercado, L. M., Sitch, S. *et al.* (2011) The Joint UK Land Environment Simulator (JULES), Model description – Part 2: Carbon fluxes and vegetation *Geoscientific Model Development Discussions*, **4**, 641–688.

Cochard, H. (2006) Cavitation in trees. *Comptes Rendus de Physique*, **7**, 1018–1026.

Colinvaux, P. A., de Oliviera, P. E., Moreno, J. E., Miller, M. C. & Bush, M. B. (1996) A long pollen record from lowland Amazonia: forest and cooling in glacial times. *Science*, **274**, 85–88.

Colinvaux, P. A., de Oliveira, P. E. & Bush, M. B. (2000) Amazonian and neotropical plant communities on glacial time-scales: the failure of the aridity and refuge hypotheses. *Quaternary Science Review*, **19**, 141–169.

Cornelissen, J. H. C., Lavorel, S., Garnier, E. *et al.* (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.

Cowling, S. A., Cox, P. M. & Betts, R. A. (2004) Contrasting simulated past and future responses of the Amazon rainforest to atmospheric change. *Philosophical Transactions of the Royal Society B*, **359**, 539–548.

Cowling, S. A., Maslin, M. A. & Sykes, M. T. (2001) Paleovegetation simulations of lowland Amazonia and implications for neotropical allopatry and speciation. *Quaternary Research*, **55**, 140–149.

Cox, P. M., Betts, R. A., Collins, M. *et al.* (2004) Amazonian forest dieback under climate-carbon cycle projections for the 21st century. *Theoretical Applied Climatology*, **78**, 137–156.

Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A. & Totterdell, I. J. (2000) Acceleration of global warming due to carbon-cycling feedbacks in a coupled climate model. *Nature*, **408**, 184–187.

Cramer, W., Bondeau, A., Schaphoff, S. *et al.* (2004) Tropical forests and the global carbon cycle: impacts of atmospheric carbon dioxide, climate change and rate of deforestation. *Philosophical Transactions of the Royal Society B*, **359**, 331–343.

Cruz, F. W., Wang, X., Auler, A. *et al.* (2009) Orbital and millennial-scale precipitation changes in Brazil from speleothem records. In *Past Climate Variability in South America and Surrounding Regions* (eds. F. Vimeux *et al.*) Developments in Paleoenvironmental Research 14. Berlin: Springer.

Davis, C. C., Webb, C. O., Wurdack, K. J., Jaramillo, C. A. & Donoghue M. A. (2005) Explosive radiation of Malpighiales supports a mid-Cretaceous origin of modern

tropical rain forests. *American Naturalist*, **165**, E36–E65.

Davis, M. B., Shaw, R. G. & Etterson, J. R. (2005) Evolutionary responses to changing climates. *Ecology*, **86**, 1706–1714.

Domingues, T. F., Martinelli, L. A. & Ehleringer, J. R. (2007) Ecophysiological traits of plant functional groups in forest and pasture ecosystems from eastern Amazonia, Brazil. *Plant Ecology*, **193**, 101–112.

Domingues, T. F., Meir, P., Feldpausch, T. R. *et al.* (2010) Co-limitation of photosynthetic capacity by nitrogen and phosphorus in West Africa woodlands. *Plant, Cell & Environment*, **33**, 959–980.

Duputié, A., Massol, F., Chuine, I., Kirckpatrick, M. & Ronce, O. (2012) How do genetic correlations affect species range shifts in a changing environment? *Ecology Letters*, **15**, 251–259.

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., Comita, L. S., Condit, R. *et al.* (2007) Drought sensitivity shapes species distribution patterns in tropical forests *Nature*, **447**, 80–82.

Farquhar, G. D., Ehleringer, J. R. & Hubick, K. T. (1989) Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, **40**, 503–537.

Favrichon, V. (1994) Classification des espèces arborées en groupes fonctionnels en vue de la réalisation d'un modèle de dynamique de peuplement en foret guyanaise. *Revue d'Écologie (Terre et Vie)*, **49**, 379–403.

Feild, T. S. & Balun, L. (2008) Xylem hydraulic and photosynthetic function of Gnetum (Gnetales) species from Papua New Guinea. *New Phytologist*, **177**, 665–675.

Fisher, R., McDowell, N., Purves, D. *et al.* (2010) Assessing uncertainties in a second-generation dynamic vegetation model

caused by ecological scale limitations. *New Phytologist*, **187**, 666–681.

Freycon, V., Krencker, M., Schwartz, D., Nasi, R. & Bonal, D. (2010) The impact of climate changes during the Holocene on vegetation in Northern French Guiana. *Quaternary Research*, **73**, 220–225.

Friedlingstein, P., Houghton, R. A., Marland, G. *et al.* (2010) Update on CO_2 emissions. *Nature Geosciences*, **3**, 811–812.

Fyllas, N. M., Patiño, S., Baker, T. R. *et al.* (2009) Basin-wide variations in foliar properties of Amazonian forests: Phylogeny, soils and climate. *Biogeosciences*, **6**, 2677–2708.

Fyllas, N. M., Quesada, C. A. & Lloyd, J. (2012) Deriving plant functional types for Amazonia for use in vegetation dynamics models. *Perspectives in Plant Ecology, Evolution, and Systematics*, **14**, 97–110.

Garreaud, R. D., Vuille, M., Compagnucci, R. & Marengo, J. (2009) Present-day South American climate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **281**, 180–195.

van Gelder, H. A., Poorter, L. & Sterck, F. J. (2006) Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. *New Phytologist*, **171**, 367–378.

Goldstein, G., Meinzer, F. C., Bucci, S. J. *et al.* (2008) Water economy of Neotropical savanna trees: six paradigms revisited. *Tree Physiology*, **28**, 395–404.

Grime, J. P. (1979) *Plant Strategies and Vegetation Processes*. Chichester: Wiley.

Haberle, S. G. & Maslin, M. A. (1999) Late Quaternary vegetation and climate change in the Amazon basin based on a 50,000 year pollen record from the Amazon Fan, ODP Site 932. *Quaternary Research*, **51**, 27–38.

Hacke, U. G., Sperry, J. S., Pockman, W. T., Davis, S. D. & McCulloh, K. A. (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*, **126**, 457–461.

Hao, G. Y., Hoffmann, W. A., Scholtz, F. G. *et al.* (2008) Stem and leaf hydraulics of congeneric tree species from adjacent

tropical savanna and forest ecosystems. *Oecologia*, **155**, 405–415.

Harrison, S. P., Prentice, I. C., Barboni, D. *et al.* (2010) Ecophysiological and bioclimatic foundations for a global plant functional classification. *Journal of Vegetation Science*, **21**, 300–317.

Hirose, T. (2005) Development of the Monsi–Saeki theory on canopy structure. *Annals of Botany*, **95**, 483–494.

Hirota, M., Holmgren, M., van Nes, E. H. & Scheffer, M. (2011) Global resilience of tropical forest and savanna to critical transitions. *Science*, **334**, 232–235.

Holling, C. S. (1973) Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, **4**, 1–23.

Hughen, K. A., Lehman, S., Southon, J. *et al.* (2004) 14C activity and global carbon cycle changes over the past 50,000 years. *Science*, **303**, 202–207.

Huntingford, C., Fisher, R. A., Mercado, L. *et al.* (2008) Towards quantifying uncertainty in predictions of Amazon 'dieback'. *Philosophical Transactions of the Royal Society B*, **363**, 1857–1864.

Hurtt, G. C., Moorcroft, P. R., Pacala, S. W. & Levin, S. (1998) Terrestrial models and global change: challenges for the future. *Global Change Biology*, **4**, 581–590.

Hurtt, G. C. & Pacala, S. W. (1995) The consequences of recruitment limitation: Reconciling chance, history, and competitive differences between plants. *Journal of Theoretical Biology*, **176**, 1–12.

Ives, A. R. & Carpenter, S. R. (2007) Stability and diversity of ecosystems. *Science*, **317**, 58–62.

Iwasa, Y., Andreasen, V. & Levin, S. (1987) Aggregation in model ecosystems. I. Prefect aggregation. *Ecological Modelling*, **37**, 287–302.

Jacobsen, A. L., Ewers, F. W., Pratt, R. B., Paddock III, W. A. & Davis, S. D. (2005) Do xylem fibers affect vessel cavitation resistance? *Plant Physiology*, **139**, 546–556.

Janzen, D. H. (1981) Patterns of herbivory in a tropical deciduous forest. *Biotropica*, **13**, 271–282.

Jaramillo, C., Ochoa, D., Contreras, L. *et al.* (2010) Effects of rapid global warming at the Paleocene–Eocene boundary on Neotropical vegetation. *Science*, **330**, 957–961.

Jaramillo, C., Rueda, M. J. & Mora, G. (2006) Cenozoic plant diversity in the Neotropics. *Science*, **311**, 1893–1896.

Jones, H. G. (1992). *Plants and Microclimate*, 2nd edn. Cambridge: Cambridge University Press.

Kattge, J., Diaz, S., Lavorel, S. *et al.* (2011) TRY – a global database of plant traits. *Global Change Biology*, **17**, 2905–2935.

Kraft, N. J. B., Metz, M. R., Condit, R. S. & Chave, J. (2010) The relationship between wood density and mortality in a global tropical forest dataset. *New Phytologist*, **188**, 1124–1136.

Krinner, G., Viovy, N., de Noblet-Ducoudré, N. *et al.* (2005) A dynamic global vegetation model for studies of the coupled atmosphere–biosphere system. *Global Biogeochemical Cycles*, **19**, GB1015.

Le Quéré, C., Raupach, M. R., Canadell, J. G. *et al.* (2009) Trends in the sources and sinks of carbon dioxide. *Nature Geosciences*, **2**, 831–836.

Le Roux, X., Lacointe, A., Escobar-Gutierrez, A. & Le Dizès, S. (2001) Carbon-based models of individual tree growth: A critical appraisal. *Annals of Forest Science*, **58**, 469–506.

Ledru, M.-P. (2001) Late Holocene rainforest disturbance in French Guiana. *Review of Paleobotany and Palynology*, **115**, 161–176.

Leuning, R., Kelliher, F. M., De Pury, D. G. G. & Schulze, E. D. (1995) Leaf nitrogen, photosynthesis, conductance and transpiration: scaling from leaves to canopies. *Plant, Cell & Environment*, **18**, 1183–1200.

Lewis, S. L., Lloyd, J., Sitch, S., Mitchard, E. T. A & Laurance, W. F. (2009) Changing ecology of tropical forests: evidence and drivers. *Annual*

Reviews of Ecology Evolution and Systematics, **40**, 529–549.

Lloyd, J. & Farquhar, G. D. (2008) Effects of rising temperatures and [CO_2] on the physiology of tropical forest trees. *Philosophical Transactions of the Royal Society B*, **363**, 1811–1817.

Lopez, O. R., Kursar, T. A., Cochard, H. & Tyree, M. T. (2005) Interspecific variation in xylem variability to cavitation among tropical tree and shrub species. *Tree Physiology*, **25**, 1553–1562.

MacArthur, R. H. (1972) *Geographical Ecology: Patterns in the Distribution of Species*. Princeton: Princeton University Press.

Maherali, H., Pockman, W. T. & Jackson, R. B. (2004) Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology*, **85**, 2184–2199.

Malhi, Y., Aragão, L. E. O. C., 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.

Marengo, J. (2004) Interdecadal and long-term rainfall variability in the Amazon basin. *Theoretical and Applied Climatology*, **78**, 79–96.

Markesteijn, L., Poorter, L., Paz, H. & Sack, L. (2011) Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant, Cell and Environment*, **34**, 137–148.

Markewitz, D., Devine, S., Davidson, E. A., Brando, P. & Nepstad, D. C. (2010) Soil moisture depletion under simulated drought in the Amazon: impacts on deep root uptake. *New Phytologist*, **187**, 592–607.

Marquis, R. J., Morais, H. C. & Diniz, I. R. (2002), Interactions among Cerrado plants and their herbivores: unique or typical? In *The Cerrados of Brazil – Ecology and Natural History of a Neotropical Savanna* (eds. P. S. Oliveira & R. J. Marquis), pp. 306–328. New York: University Presses of California, Columbia and Princeton.

Mayle, F. E., Beerling, D. J., Gosling, W. D. & Bush, M. B. (2004) Responses of Amazonian ecosystems to climatic and atmospheric CO2 changes since the Last Glacial Maximum. *Philosophical Transactions of the Royal Society B*, **359**, 499–514.

Mayle, F. E., Burn, M. J., Power, M. & Urrego, D. H. (2009) Vegetation and fire at the Last Glacial Maximum in tropical South America. In *Past Climate Variability in South America and Surrounding Regions* (eds. F. Vimeux *et al.*) Developments in Paleoenvironmental Research 14. Berlin: Springer.

McAdam, S. A. & Brodribb, T. J. (2012) Stomatal innovation and the rise of seed plants. *Ecology Letters*, **15**, 1–8.

McCulloh, K. A., Meinzer, F. C., Sperry, J. S. *et al.* (2011) Comparative hydraulic architecture of tropical tree species representing a range of successional stages and wood density. *Oecologia*, **167**, 27–37.

McDowell, N. G. (2011) Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology*, **155**, 1051–1059.

Meinzer, F. C., Campanello, P. I., Domec, J. C. *et al.* (2008a) Constraints on physiological function associated with branch architecture and wood density in tropical forest trees. *Tree Physiology*, **28**, 1609–1617.

Meinzer, F. C., James, S. A., Goldstein, G. & Woodruff, D. R. (2003) Whole water transport scales with sapwood capacitance in tropical forest canopy trees. *Plant, Cell & Environment*, **26**, 1147–1155.

Meinzer, F. C., Woodruff, D. A., Domec, J. C. *et al.* (2008b) Coordination of leaf and stem water transport properties in tropical forest trees. *Oecologia*, **156**, 31–41.

Mendez-Alonzo, R. *et al.* (in press) Coordination between leaf and stem economics in a tropical dry forest. *Ecology*.

Mercado, L. M., Patiño, S., Domingues, T. F. *et al.* (2011) Variations in Amazon forest productivity correlated with foliar nutrients and modelled rates of photosynthetic carbon supply. *Philosophical Transactions of the Royal Society B*, **366**, 3316–3329.

Monteith, J. L. & Unsworth, M. H. (2007) *Principles of Environmental Physics*, 3rd edn. Burlington, San Diego, London: Academic Press.

Moorcroft, P. R., Hurtt, G. C. & Pacala, S. W. (2001) A method for scaling vegetation dynamics: the ecosystem demography model (ED). *Ecological Monographs*, **71**, 557–586.

Morley, R. J. (2000) *Origin and Evolution of Tropical Rain Forests*. Chichester, New York: Wiley.

Morley, R. J. (2011) Cretaceous and Tertiary climate change and the past distribution of megathermal rainforests. In *Tropical Rainforest Responses to Climatic Change*, 2nd edn (eds. M. B. Bush, J. R. Flenley & W. D Gosling), pp. 1–34. Berlin-Heidelberg: Springer.

Murphy, B. P. & Bowman, D. M. J. S. (2012) What controls the distribution of tropical forest and savanna? *Ecology Letters*, **15**, 748–758.

Niinemets, U. (2001) Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology*, **82**, 453–469.

Nobel, P.S. (2009) *Physiochemical and Environmental Plant Physiology*, 5th edn. San Diego: Academic Press.

Ometto, J. P. H. B., Ehleringer, J. R., Domingues, T.F. *et al.* (2006) The stable carbon and nitrogen isotopic composition of vegetation in tropical forests of the Amazon Basin, Brazil. *Biogeochemistry*, **79**, 251–274.

Onoda, Y., Westoby, M., Adler, P. B. *et al.* (2011) Global patterns of leaf mechanical properties. *Ecology Letters*, **14**, 301–312.

Pacala, S. W., Canham, C. D., Saponara, J. *et al.* (1996) Forest models defined by field measurements, estimation, error analysis and dynamics. *Ecological Monographs*, **66**, 1–43.

Paine, C. E. T., Stahl, C., Courtois, E., Patiño, S. & Baraloto, C. (2010) Functional explanations for bark thickness in tropical forest trees. *Functional Ecology*, **24**, 1202–1210.

Patiño, S., Fyllas, N. M., Baker, T. R. *et al.* (2012) Coordination of physiological and structural traits in Amazon forest trees. *Biogeosciences*, **9**, 775–801.

Patiño, S., Lloyd, J., Paiva, R. *et al.* (2009) Branch xylem density variations across the Amazon Basin. *Biogeosciences*, **6**, 545–568.

Patiño, S., Tyree, M. T. & Herre, E. A. (1995) Comparison of hydraulic architecture of woody plants of differing phylogeny and growth form with special reference to free-standing and hemi-epiphytic Ficus species from Panama. *New Phytologist*, **129**, 125–134.

Pennington, R. T., Prado, D. E. & Pendry, C. A. (2000) Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography*, **27**, 261–273.

Phillips, O. L., Martinez, R. V., Arroyo, L. *et al.* (2002) Increasing dominance of large lianas in Amazonian forests. *Nature*, **418**, 770–774.

Phillips, O. L., Aragão, L. E. O. C., Lewis, S. L. *et al.* (2009) Drought sensitivity of the Amazon rainforest. *Science*, **323**, 1344–1347.

Picard, N. & Franc, A. (2003) Are ecological groups of species optimal for forest dynamics modelling. *Ecological Modelling*, **163**, 175–186.

Piperno D. R. (2011) Prehistoric human occupation and impacts on Neotropical forest landscapes during the Late Pleistocene and Early/Middle Holocene. In *Tropical Rainforest Responses to Climatic Change*, 2nd edn (eds. M. B. Bush, J. R. Flenley & W. D Gosling). pp. 185–212. Berlin-Heidelberg: Springer.

Poorter, H., Niinemets, U., Poorter, L., Wright, I. J. & Villar, R. (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist*, **182**, 565–588.

Poulter, B., Aragão, L., Heyder, U. *et al.* (2010) Net biome production of the Amazon basin in the 21st century. *Global Change Biology*, **16**, 2062–2075.

Prado, C. H. B. A., Wenhui, Z., Rojas, M. H. C. & Souza, G. M. (2004) Seasonal leaf gas exchange and water potential in a woody cerrado species community. *Brazilian Journal of Plant Physiology*, **16**, 7–16.

Purves, D. & Pacala, S. (2008) Predictive models of forest dynamics. *Science*, **320**, 1452–1453.

Read, J. & Stokes, A. (2006) Plant biomechanics in an ecological context. *American Journal of Botany*, **93**, 1546–1565.

Restom, T. G. & Nepstad, D. C. (2001) Contribution of vines to the evapotranspiration of a secondary forest in eastern Amazonia. *Plant and Soil*, **236**, 155–163.

Ritchie, M. W. & Hann D. W. (1997) Implications of disaggregation in forest growth and yield modeling. *Forest Science*, **43**, 223–233.

Rood, S. B., Patiño, S., Coombs, K. & Tyree, M. T. (2000) Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. *Trees*, **14**, 248–257.

Rozendaal, D. M. A. & Zuidema, P. A. (2011) Dendroecology in the tropics: a review. *Trees*, **25**, 3–16.

Rull, V. (1999) Palaeofloristic and palaeovegetational changes across the Paleocene-Eocene boundary in northern South America. *Review of Palaeobotany and Palynology*, **107**, 83–95.

Saatchi, S. S., Harris, N. L., Brown, S. *et al.* (2011) Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences USA*, **108**, 9899–9904.

Salazar, L. F., Nobre, C. A. & Oyama, M. D. (2007) Climate change consequences on the biome distribution in tropical South America. *Geophysical Research Letters*, **34**, L09708.

Schnitzer, S. A. & Bongers, F. (2002) The ecology of lianas and their role in forests. *Trends in Ecology & Evolution*, **17**, 223–230.

Schulze, E.-D., Kelliher, F. M., Korner, C., Lloyd, J. & Leuning, R. (1994) Relationships among maximum stomatal conductance, carbon assimilation rate and plant nitrogen nutrition: a global ecology scaling exercise. *Annual Review of Ecology and Systematics*, **25**, 629–660.

Servant, M., Fontes, J. C., Rieu, M. & Saliège, X. (1981) Phases climatiques arides holocènes dans le Sud-Ouest de l'Amazonie (Bolivie). *Comptes Redus de l'Académie des Sciences Paris, Série II*, **292**, 1295–1297.

Shugart, H. H. (1984) *A Theory of Forest Dynamics*. New York: Springer.

Sitch, S., Smith, B., Prentice, I. C. *et al.* (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic vegetation model. *Global Change Biology*, **9**, 161–185.

Sobrado, M. A. (1996) Embolism vulnerability of an evergreen tree. *Biologia Plantarum*, **38**, 297–301.

Sobrado, M. A. (1997) Embolism vulnerability in drought-deciduous and evergreen species of a tropical dry forest. *Acta Oecologica*, **18**, 383–391.

Staver, A. C., Archibald, S. & Levin, S. A. (2011) The global extent and determinants of savanna and forest as alternative stable states. *Science*, **334**, 230–232.

Swaine, M. D. & Whitmore, T. C. (1988) On the definition of ecological species groups in tropical rain forests. *Plant Ecology*, **75**, 81–86.

Sytsma, K. J., Walker, J. B., Schönenberger, J. & Anderberg, A. A. (2006) Phylogenetics, biogeography, and radiation of Ericales. *Annual BSA Meeting, Botany 2006*, Chicago, CA, Abstract volume 71.

Tyree, M. T., Patiño, S. & Becker, P. (1998) Vulnerability to drought-induced embolism of Bornean heath and dipterocarp forest trees. *Tree Physiology*, **18**, 583–588.

Tyree, M. T. & Zimmermann, M. H. (2002). *Xylem Structure and the Ascent of Sap*, 2nd edn (ed. T. E. Timell), pp. 283. Berlin: Springer-Verlag.

Wang, X., Auler, A. S., Edwards, R. L. *et al.* (2007) Wet periods in northeastern Brazil over the past 210 kyr linked to distant climate anomalies. *Nature*, **432**, 740–743.

Wenhui, Z. & Prado, C. H. B. A. (1998) Water relations balance parameters of 30 woody species from Cerrado vegetation in the wet and dry season. *Journal of Forestry Research*, **9**, 233–239.

Wing, S. L., Herrera, F., Jaramillo, C. A. *et al.* (2009) Late Paleocene fossils from the Cerrejón

Formation, Colombia, are the earliest record of Neotropical rainforest. *Proceedings of the National Academy of Sciences USA* **106**, 18627.

Worbes, M. (2002) One hundred years of tree-ring research in the tropics: a brief history and an outlook to future challenges. *Dendrochronologia*, **20**, 217–231.

Wright, I. J., Reich, P. B., Westoby, M. *et al.* (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.

Yachi, S. & Loreau, M. (1998) Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences USA*, **96**, 1453–1458.

Zanne, A. E., Westoby, M., Falster, D. S. *et al.* (2010) Angiosperm wood structure: Global patterns in vessel anatomy and their relation to wood density and potential conductivity. *American Journal of Botany*, **97**, 207–215.

Zhang, Y. J., Meinzer, F. C., Hao, G. Y. *et al.* (2009) Size-dependent mortality in a Neotropical savanna tree: the role of height-related adjustments in hydraulic architecture and carbon allocation. *Plant, Cell and Environment*, **32**, 1456–1466.

Zhu, S.-D. & Cao, K.-F. (2009) Hydraulic properties and photosynthetic rates in co-occurring lianas and trees in a seasonal tropical rainforest in southwestern China. *Plant Ecology*, **204**, 295–304.

Zotz, G., Tyree, M. T. & Cochard, H. (1994) Hydraulic architecture, water relations and vulnerability to cavitation of *Clusia uvitana* Pittier: a C3-CAM tropical hemiepiphyte. *New Phytologist*, **127**, 287–295.