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Drought tolerance as predicted by leaf water potential at turgor loss point varies strongly across species within an Amazonian forest

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Summary

1. Amazonian droughts are predicted to become increasingly frequent and intense, and the vulnerability of Amazonian trees has become increasingly documented. However, little is known about the physiological mechanisms and the diversity of drought tolerance of tropical trees due to the lack of quantitative measurements.
2. Leaf water potential at wilting or turgor loss point (π_{tlp}) is a determinant of the tolerance of leaves to drought stress, and contributes to plant-level physiological drought tolerance. Recently, it has been demonstrated that leaf osmotic water potential at full hydration (π_0) is tightly correlated with π_{tlp}. Estimating π_{tlp} from osmometer measurements of π_0 is much faster than the standard pressure-volume curve approach of π_{tlp} determination. We used this technique to estimate π_{tlp} for 165 trees of 71 species, at three sites within forests in French Guiana. Our dataset represents a significant increase in available data for this trait for tropical tree species.
3. Tropical trees showed a wider range of drought tolerance than previously found in the literature, π_{tlp} ranging from -1.4 to -3.2 MPa. This range likely corresponds in part to adaptation and acclimation to occasionally extreme droughts during the dry season.
4. Leaf-level drought tolerance varied across species, in agreement with the available published observations of species variation in drought-induced mortality. On average, species with a more negative π_{tlp} (i.e., with greater leaf-level drought tolerance) occurred less frequently across the region than drought-sensitive species.

5. Across individuals, π_{tlp} correlated positively but weakly with leaf toughness (R^2=0.22, P=0.04) and leaf thickness (R^2=0.03, P=0.03). No correlation was detected with other functional traits (leaf mass per area, leaf area, nitrogen or carbon concentrations, carbon isotope ratio, sapwood density or bark thickness).
6. The variability in π_{tlp} among species indicates a potential for highly diverse species responses to drought within given forest communities. Given the weak correlations between π_{tlp} and traditionally measured plant functional traits, vegetation models seeking to predict forest response to drought should integrate improved quantification of comparative drought tolerance among tree species.

Key-words: climate change, French Guiana, functional traits, plant water relations, tropical trees, wilting

Introduction

Amazonian forests play a fundamental role in global biogeochemical cycles (Malhi *et al.* 2008; Boyce *et al.* 2010; Saatchi *et al.* 2011; Harper *et al.* 2013). However, these forests have been predicted to be vulnerable to drought intensification in simulations coupling a global climate model and a dynamic global vegetation model (Cox *et al.* 2000; Huntingford *et al.* 2008). This critically discussed “Amazonian dieback” scenario predicts significant increases in mortality rates for Amazonian trees, leading to a catastrophic transition into a savannah-type vegetation (Malhi *et al.* 2009; Good *et al.* 2013; Huntingford *et al.* 2013). The observed increase in Amazonian tree mortality during the 2005 and 2010 droughts illustrated this vulnerability (Phillips *et al.* 2009; Lewis *et al.* 2011; Saatchi *et al.* 2013; Hilker *et al.* 2014), and such droughts may increase in frequency and intensity in the future (Malhi *et al.* 2008; Lewis *et al.* 2011; Joetzjer *et al.* 2013).

Through-fall exclusion experiments in Amazonia confirmed that an increased drought intensity resulted in reduced tree growth and increased tree mortality, leading in turn to a net carbon release of the ecosystem (Nepstad *et al.* 2002; Fisher *et al.* 2007; Brando *et al.* 2008). These experiments also revealed species differences in tree vulnerability, with some but not all species presenting increased mortality rates due to water stress (Nepstad *et al.* 2007; da Costa *et al.* 2010). Previous studies also found strong species differences in physiological drought tolerance among selected species within a given vegetation type (Engelbrecht *et al.* 2007; Baltzer *et al.* 2008; Kursar *et al.* 2009; Blackman, Brodribb & Jordan 2012; McDowell *et al.* 2013). Drought may thus strongly shape tropical tree species distributions through species-specific effects on growth and mortality (Engelbrecht *et al.* 2007; Jabot & Chave 2011). However, the diversity of species responses to drought has been poorly accounted for in vegetation models (Sitch *et al.* 2008; Powell *et al.* 2013; Xu *et al.* 2013). Improving the representation of drought responses across species-rich tropical tree communities therefore remains a critical research objective. This study aimed to document the drought tolerance of Amazonian trees, with a special focus on variation among species, by implementing a novel method for rapidly measuring leaf-level drought tolerance.

One well-established approach to study the drought tolerance of plants is to quantify their physiological responses to water supply at the seedling stage using reciprocal transplant experiments (Cao 2000; Engelbrecht *et al.* 2007; Kursar *et al.* 2009; Urli *et al.* 2013). Although this approach has yielded insightful findings, it is applicable to a limited number of species, and only at the seedling stage. It cannot be readily applied to canopy trees that account for most of the biomass of the ecosystem and that have been found to be particularly vulnerable to water stress in several studies (Nepstad *et al.* 2007; da Costa *et al.* 2010). A different route consists of measuring plant functional traits for many species, especially for use in vegetation models (Fyllas, Quesada & Lloyd 2012). The search for traits that may be used as proxies of plant tolerance to drought has generated an important literature (Niinemets 2001; Hacke *et al.* 2001; Lamont, Groom & Cowling 2002). However, the use of structural traits – in particular leaf mass per area (LMA), leaf thickness, leaf toughness, and wood density – as a proxy for drought tolerance remains controversial (Zanne *et al.* 2010; Bartlett, Scoffoni & Sack 2012b; Fortunel *et al.* 2014). Thus physiological traits with strong mechanistic links with plant responses to water stress are needed to explore drought tolerance patterns in tropical forests. These traits would also facilitate exploring the relationship between drought tolerance and rarity in tropical forest trees and therefore improve understanding of the drivers of tropical forest diversity and composition.

In a recent review, Bartlett, Scoffoni & Sack (2012b) argued that leaf water potential at wilting (or turgor loss point, henceforth denoted π_{tlp}), strongly underlies ecological drought tolerance and species distributions relative to water supply within and across biomes (see also Lenz, Wright & Westoby 2006). This plant functional trait represents the leaf water potential that induces wilting. Thus, leaves with a more negative π_{tlp} (measured in MPa) remain turgid at more negative water potentials, and tend to maintain critical processes, such as leaf hydraulic conductance, stomatal conductance, and photosynthetic gas exchange, under drier conditions (Cheung, Tyree & Dainty 1975; Abrams, Kubiske & Steiner 1990; Brodribb *et al.* 2003; Bartlett *et al.* 2012b; Guyot, Scoffoni & Sack 2012). Thus a more negative value for π_{tlp} contributes to greater leaf-level and therefore also plant-level drought tolerance.

Previously, π_{tlp} has been estimated from pressure-volume curves, which measure the decline of leaf water potential as the leaf dehydrates. This standard method of π_{tlp} determination is time-consuming and impractical for the hundreds of species occurring in most tropical forests (Koide *et al.* 1989). However, another pressure-volume curve trait, the leaf osmotic potential at full hydration (π_o), was repeatedly found to be an excellent correlate for π_{tlp} (Sack *et al.* 2003; Lenz *et al.* 2006; Blackman, Brodribb & Jordan 2010; Scoffoni *et al.* 2011; Bartlett *et al.* 2012b). Based on the above correlation, and finding its basis in the fundamental equations describing leaf physiology, Bartlett *et al.* (2012a) inferred modelled values of π_{tlp} from osmometer measurements of π_o. The π_o – π_{tlp} relationship was calibrated using diverse species, including tropical rainforest species. This method has the advantage of being much faster than the standard pressure-volume curve approach.

Here we used this method to gather new π_{tlp} data for 71 woody plant species in French Guiana, and to compare these data with previously published data for species of other tropical forests. We used this new dataset to test hypotheses for the diversity of tropical forest tree drought tolerance, as estimated by the π_{tlp}, its relationships with species rarity, its variability with local environmental conditions, and its potential coordination with other functional traits. We hypothesized that (1) because drought tolerance arising from adaptation and/or acclimation incurs a significant cost, species with high drought tolerance would be relatively infrequent in moist tropical forests and thus π_{tlp} would correlate negatively with species rarity; (2) π_{tlp} depends on local environmental conditions, and thus, individuals growing in soils with a lower water retention capacity are more drought-tolerant; and (3) π_{tlp} would be correlated, even if weakly, with other functional traits previously hypothesized to be associated with drought tolerance or lower water availability, such as higher leaf mass per area and wood density.

Materials and methods

Study sites and sampling strategy

Field measurements were conducted at three plots within two moist tropical forests in French Guiana. The Nouragues Ecological Research Station is located 120 km south of Cayenne within an undisturbed forest, ca. 50 km from Cacao, the closest village (4°05’ N, 52°40’ W; Bongers *et al.* 2001). The bedrock is varied at this site: the majority of the forest grows on metamorphic bedrock of the Paramaca series, covered with clay soil, while a smaller area surrounding the granitic outcrop has granitic and crystalline bedrocks covered with soil with a mixture of clay and sand derived from the bedrock (Grimaldi & Riéra 2001). Data were collected in two 1-ha permanent plots, one on clay soil (NL11 on Grand Plateau, hereafter referred to as the “clay site”), and the other on clay-sand soil (NH20 on Petit Plateau, hereafter referred to as the “clay-sand site”). The Paracou Research Station is located close to the village of Sinnamary and 20 km from the coast (5°15’ N, 52°55’ W; Gourlet-Fleury, Guehl & Laroussinie 2004). The bedrock is a metamorphic formation of the Precambrian Shield, dominated by schists and sandstones. Soils are limited in depth by a lateritic pan, which has a low permeability and leads to lateral drainage during heavy rains (Ferry *et al.* 2010). At Paracou, we collected data from one 1-ha plot (P006, hereafter referred to as the “sandstone site”). Having different textures, soils at the three sites are expected to present contrasting water holding capacities, with clay-sand and sandstone sites being more drained than the clay site. All three sites receive c.a. 3000 mm/yr rainfall, with significant seasonal and inter-annual variation due to the movement of the Inter-Tropical Convergence Zone. A long wet season lasts from December to July, often interrupted by a short dry period in March. The dry season lasts from the end of August to November with 2-3 months with precipitation < 100 mm/mo.

In 2007 and 2008, the three 1-ha plots were fully censused for trees ≥ 10 cm diameter at breast height (DBH) (Baraloto *et al.* 2010a), and species richness ranged between 150 and 200 species per hectare. During that initial sampling phase, all trees (with DBH ≥ 10 cm) in each plot were sampled for many leaf and stem functional traits, including toughness (estimated by punch tests, using a penetrometer), carbon and nitrogen concentrations, carbon isotope ratio ($\delta^{13}C$), and sapwood density and bark thickness (methods used in the determination of these traits are described in Baraloto *et al.* 2010a).

Measurements of leaf drought tolerance traits were conducted in September 2012 at the peak of the dry season. The trees were selected so that the most locally-abundant species were represented in our sampling, to ensure that at least two individuals per species were collected per plot, and to maximize species-level variation in wood density, which has often been associated with drought tolerance (Hacke *et al.* 2001; Santiago *et al.* 2004; Chave *et al.* 2009; Markesteijn *et al.* 2011a; b). Small branches were collected by climbing the trees using the French-spike method (Fonderies Lacoste, Excideuil, France; De Castilho *et al.* 2006) or directly from the ground using a clipping pole. When climbing the selected trees, we also occasionally sampled neighbouring trees, which explains why a few species were sampled only once in the final dataset. In total, we collected leaves for 165 trees (48, 63 and 54 from the clay, clay-sand site, and sandstone sites, respectively), from 71 species (33, 40 and 19 species from the clay, clay-sand and sandstone sites, respectively), representing 29 families (nomenclature follows the Plant List http://www.theplantlist.org/).

Measurements of leaf thickness, leaf area, leaf dry mass and leaf mass per area (LMA) were conducted on the same leaves as for leaf drought tolerance traits in September 2012. Leaf thickness was computed as the mean of thickness measurements at the bottom, middle and top of the leaf, measured on the fresh leaves using digital calipers (Mitutoyo, Japan). Thick woody petioles were removed and fresh leaves were scanned using a portable scanner (Canon LiDE 60, Canon USA, Lake Success, NY, USA). Leaf area was measured manually from the scans using the ImageJ software (http://imagej.nih.gov/ij/). Leaves were then oven-dried at 65°C for 48 h and weighted for estimating leaf dry mass and computing LMA (leaf dry mass divided per leaf area).

Measurement of π_{tlp} *values*

We assessed the leaf turgor loss point, π_{tlp}, from a previously established linear relationship with the osmotic potential at full hydration (π_{o}), in turn directly measured with a vapour pressure osmometer (Vapro 5520, Wescor, Logan, UT) (Bartlett *et al.* 2012a).

Branches were collected from the selected trees and placed in opaque bags with wet paper towel, then recut under water at least two nodes distal to the original cut and allowed to rehydrate overnight covered with plastic, and branch ends underwater. Three mature leaves were collected from each rehydrated branch and stored in Whirl-Pak bags (Nasco, Fort Atkinson, WI, USA) with a wet paper towel. One disc was sampled from each leaf centrally between the midrib and margin with an 8-mm-diameter cork borer, avoiding first- and second-order veins. The discs were wrapped in foil and frozen by immersion in liquid nitrogen (LN_2) for at least 2 minutes, then immediately punctured 10-15 times with sharp-tipped forceps and sealed in the osmometer chamber, using the standard 10 μL chamber well. The discs were exposed to air for less than 40 seconds for all steps between removing the leaf from the Whirl-Pak bag and sealing the disc in the osmometer. The equilibrium solute concentration value c_0 (in mmol kg^{-1}) was recorded from the osmometer when the difference between consecutive 2-minute measurements fell below 5 mmol kg^{-1}. This value was converted to π_o values from the osmometer (π_{osm}) using the van't Hoff equation relating solute concentration to vapour pressure:

$$\pi_{osm} = -\frac{2.5}{1000} \times c_0 \qquad (1)$$

where the numerator of the first term represents R×T = 2.5 L MPa mol^{-1} at 25°C, with R the ideal gas constant and T the temperature in degrees Kelvin.

The value of π_{tlp} was estimated from π_{osm} using the previously published regression equation relating π_{osm} to pressure-volume curve turgor loss point values, developed from 30 woody species representing a wide range of leaf structural features and habitat preferences (n=30 species, R^2=86%, p<2.10^{-12}, π_{osm} range=[-3.03, -0.64] MPa and π_{tlp} range=[-3.00, -1.02] MPa ; Bartlett *et al.* 2012a):

$$\pi_{tlp} = 0.832 \times \pi_{osm} - 0.631 \qquad (2)$$

This correlation was established using osmometer π_o values (π_{osm}) and π_{tlp} values measured with the standard but very time-consuming pressure-volume curve method, for 15 diverse species sampled in gardens adjacent to the University of California, Los Angeles campus, originating from a range of vegetation zones from chaparral to tropical wet forest, and 15 species growing in natural conditions in Chinese tropical rainforest (Bartlett *et al.* 2012a). The fit of Equation (2) was not significantly different for these two subgroups, consistent with expectations from theory that this estimation of turgor loss point is independent of leaf structure and habitat preference and can be applied to species across vegetation zones (Bartlett *et al.* 2012a). The π_{osm} range of the correlation dataset encompassed the full range of the π_{osm} values measured in this study (π_{osm} range=[-3.02, -0.94] MPa). When this correlation dataset was restricted to the tropical rainforest species group only, the π_{osm} range (π_{osm} range=[-1.70, -0.70] MPa; Bartlett *et al.* 2012a) encompassed 86% of the range of our measured π_{osm} values. All π_{osm} and π_{tlp} data are available (see Appendix S1 in Supporting Information).

Data analysis

We compared the π_{tlp} values for the measured trees with a published compilation of π_{tlp} values for moist tropical forests measured during the wet season (n=50 for moist tropical forests, data available in the Supplementary material of Bartlett *et al.* 2012b). We tested for species differences in π_{tlp} for a subset of 13 species for which at least 5 individuals were sampled (n=82 individuals). We also tested for species differences in π_{tlp} within two well-sampled families (with at least 4 sampled species for which at least 5 individuals were sampled; Fabaceae, n=4 species and 26 individuals; Lecythidaceae, n=4 species and 25 individuals). We used linear models (ANOVA), with species as a fixed effect, and tested for pairwise species differences with Tukey tests. The relative contribution of within- and across-species differences to π_{tlp} variability was quantified with variance partitioning (Sokal & Rohlf 1987).

To test the significance of the variation of π_{tlp} values among study sites, we used linear models (ANOVA), with site treated as a fixed effect. Tukey tests were used to determine which pairwise comparisons were significantly different.

We also investigated the relationship between species mean π_{tlp} and regional occupancy, estimated as the number of occurrences across 478 0.25°×0.25° grid cells within the Guiana Shield (Mouillot *et al.* 2013). Regional occupancy measures one dimension of species rarity, not necessarily correlated with local abundance. We conducted a Spearman rank-order correlation test (r_s) between species-averaged π_{tlp} and regional occupancy.

We tested correlations between π_{tlp} and leaf-level plant functional traits measured on the same leaves (area, thickness and mass per area) at the individual level. We also tested the correlation between species-averaged π_{tlp} and previously measured species-averaged leaf-level and stem-level plant functional traits (toughness, carbon and nitrogen concentrations, δ^{13}C, sapwood density and bark thickness). The latter traits were measured five years earlier (in 2007; Baraloto *et al.* 2010a) and not on the same leaves for each individual. Hence, we tested these correlations for species means to minimize the effect of temporal and intra-canopy variability within individuals. For this second set of analyses, we included only species for which trait values had been measured for at least 3 individuals for both π_{tlp} and the tested trait (n ranged from 14 to 19 species).

All statistical analyses were conducted using the R software (version 3.0.2; R Core Team 2013).

Results

Variation in mean π_{tlp} across species

The π_{tlp} varied strongly across species (Fig. 1; ANOVA, $P<1.10^{-6}$), with 40% of the variance in π_{tlp} associated with species differences (n=13 species and 82 individuals). Strong species differences were exemplified by *Dicorynia guianensis* (Fabaceae) and *Eschweilera coriacea* (Lecythidaceae), which had less negative π_{tlp} values than the average (-1.71 ± 0.16 MPa and -1.83 ± 0.06 MPa, respectively) and *Lecythis poiteaui* (Lecythidaceae), which had a more negative π_{tlp} than average (-2.58 ± 0.16 MPa). *Protium* (Burseraceae) individuals also had significantly more negative π_{tlp} than average (-2.28 ± 0.06 MPa; t-test, P=0.003). Species differences explained 31% and 68% of the variability within our subset of Fabaceae and Lecythidaceae respectively (n=4 species for both families and 25-26 individuals; ANOVA, P=0.02 and $P<1.10^{-5}$ respectively).

Drought-tolerant species are regionally less frequent than drought-intolerant ones

Species with a more negative π_{tlp} tended to have a lower regional occupancy (Fig. 2; Spearman rank-order correlation r_s = 0.68; P=0.01). In particular, the most frequent species, *Eschweilera coriacea,* which occurred at 62/478 grid cells across Amazonia, had a less negative π_{tlp} than average (t-test, P=0.03). Conversely, the most drought-tolerant species, in terms of its π_{tlp}, *Lecythis poiteaui,* is regionally infrequent, occurring at 26/478 grid cells.

Wider range of π_{tlp} *than previously accounted for in moist tropical forests*

The mean π_{tlp} (±SE) across species in the study plots was -2.01 ± 0.02 MPa. This mean value was substantially more negative than that determined from data previously compiled for moist tropical forests during the wet season (Table 1; Fig. 1; Bartlett *et al.* 2012b; t-test, P<0.005). The most negative values we measured were below the most negative value reported for this ecosystem compilation (Table 1; Bartlett *et al.* 2012b).

Variation in mean π_{tlp} across forest plots

The π_{tlp} varied significantly across our three sites (ANOVA, P < 0.005; Fig. 1). The mean π_{tlp} at the clay-sand site was similar to that for the sandstone site (Table 1; Tukey test, P=0.54), which is also on a well-drained soil with a large sandy fraction, ca. 100 km away, and both were on average marginally more negative than that of the clay site (Table 1; Fig. 1; Tukey tests, P<0.001 and P=0.02 for comparisons with the clay-sand and sandstone sites, respectively).

Weak correlation of π_{tlp} with other functional traits

Across species, a more negative π_{tlp} was associated with lower leaf toughness (Fig. S1a; P=0.04, R^2=22%, n=19 species). Additionally, a more negative π_{tlp} was weakly associated with lower leaf thickness (Fig. S1c; $P=0.03$, $R^2=3\%$, $n=151$ individuals). We found no statistical association of π_{tlp} with other functional traits, i.e., leaf area, dry mass, dry mass per area (LMA; Fig. S1d), carbon and nitrogen concentrations per leaf mass, carbon isotope ratio ($\delta^{13}C$), sapwood density (Fig. S1b) or bark thickness.

Discussion

Leaf potential at turgor loss point primarily depends on species identity

We found strong variation in π_{tlp} among the tree species sampled in our study. Species identity was the best explanatory factor for the variation in leaf drought tolerance of trees and explained a major part of intra-family variability. Within the Lecythidaceae, *Eschweilera coriacea* had a higher (less negative) π_{tlp} than the all-species average, whereas *Lecythis poiteaui* had a more negative π_{tlp} than average. Similarly, within the Fabaceae, *Dicorynia guianensis* and *Vouacapoua americana* had π_{tlp} values that were substantially less and more negative respectively than the all-species average. Such a substantial variation in a key hydraulic trait has already been observed in another lineage (stem hydraulic vulnerability for species of *Cordia*; Choat, Sack & Holbrook 2007). However, despite such variation observed within lineages, our results are also remarkably consistent with observations of differences across genera in drought vulnerability in the long-term through-fall exclusion experiments conducted in the Brazilian Amazon (Caxiuanã, da Costa *et al.* 2010; Tapajós, Nepstad *et al.* 2007). In these experiments, some genera displayed much higher mortality than average under the drought treatment, especially the genus *Eschweilera*, which includes *Eschweilera coriacea*. In contrast, individuals belonging to genus *Protium* appeared relatively insensitive to the experimental drought. *Protium* also tends to increase in abundance in more seasonally dry forests across Amazonia (ter Steege *et al.* 2006). Consistent with these observations, *Protium* individuals included in our study had higher leaf-level drought-tolerance (lower-than-average π_{tlp}).

The above considerations suggest that π_{tlp}, measured at leaf level, is a useful integrative trait for plant-level tolerance. The π_{tlp} is a predictor of the leaf water status at which plant gas exchange declines during drought for many species, and its incorporation into photosynthetic models may allow for mechanistic predictions of the impacts of water stress on plant performance (Prentice et al. 2014). The ability to rapidly measure π_{tlp} therefore constitutes a significant step towards a better integration of tree responses to drought into vegetation models (Fisher *et al.* 2006; Smith *et al.* 2014). Future work is needed to determine for more species the correspondence of π_{tlp} with the responses of stomatal and hydraulic conductances to soil drying, and its mechanisms (Meinzer *et al.* 1990; Williams & Ehleringer 2000; Brodribb *et al.* 2003; Fisher *et al.* 2006; West *et al.* 2012).

The influence of soil parameters on both species composition and drought tolerance is a crucial question for vegetation modelling in Amazonia (Sabatier *et al.* 1997; Kursar, Engelbrecht & Tyree 2005; Quesada *et al.* 2009; Condit *et al.* 2013). We found that trees at the clay site were less drought-tolerant than trees at the two other sites in our dataset, despite similar rainfall. This pattern may result from both differences in π_{tlp} within species across environmental variation (i.e., plasticity and ecotypic variation), and/or from site differences in species composition. Indeed, even though the clay and clay-sand sites are only a few hundred meters apart, they harbour distinct tree floras, and this potential environmental filtering may be in part due to differential soil water retention ability (see also Lenz *et al.* 2006). A more exhaustive sampling across the local flora would help determine the relative extent to which site conditions, community composition and intra-species plasticity contribute to differences in π_{tlp} across geographic and environmental gradients.

Drought tolerance as predicted by π_{tlp} showed a positive trend with regional occupancy across our well-sampled species (Fig. 2). Based on this observation, we infer that drought-sensitive canopy trees are more widely distributed in the rain forests of the Guiana Shield compared to more drought-tolerant trees. If confirmed, future work is needed to determine the degree to which drought-tolerant species are confined to particular habitats. One would expect that in a more drought-prone climate, such drought-tolerant species may gain in abundance at the expense of others (Phillips *et al.* 2009, 2010; Feeley *et al.* 2011; Fauset *et al.* 2012). Further, studies to resolve the phylogenetic signal in π_{tlp} are needed to assess the evolutionary underpinnings of drought tolerance in tropical trees.

On the measurement of π_{tlp} and comparison across biomes

Our study is based on a novel approach for measuring leaf water potential at turgor loss point. It is based on the strong correlation of π_{tlp} with the osmotic potential at full hydration (π_o), easily measured with an osmometer. Previous studies suggest that this relationship stems from fundamental principles of leaf physiology, and consequently is robust to leaf type and habitat (Bartlett *et al.* 2012a, Bartlett *et al.* 2012b). Future studies can further test the robustness of this correlation and potentially refine the calibration equation by including points for more species and vegetation types. In Appendix S1, we report raw osmometer π_o values in addition to π_{tlp} values to facilitate future calibration analyses.

The π_{tlp} values in our dataset were on average more negative than those previously reported in the literature for moist tropical forests (Fig. 1). There are several possible explanations for such a pattern, one of them being that previous studies tended to be conducted during the wet season, whereas we measured π_{tlp} at the peak of the dry season. Plants often acclimate π_{tlp} during drought periods, through the accumulation of cell solutes, or osmotic adjustment. Such an adjustment results in a lowering of π_{tlp} and can contribute to drought tolerance in vegetation worldwide (Wright *et al.* 1992; Abrams & Kubiske 1994; Cao 2000; Merchant *et al.* 2007; Zhu & Cao 2009; Bartlett *et al.* 2012b, 2014). The only previous study that reported a significant osmotic adjustment in a comparable moist tropical forest found an average adjustment of ca. 0.4 MPa for five species of *Psychotria*, a genus of understory plants (Wright *et al.* 1992), similar to the 0.5 MPa difference we found. However, in other reports, some moist tropical tree species did not present any osmotic adjustment (Wright *et al.* 1992; Cao 2000; Brodribb *et al.* 2003). Thus the lower mean π_{tlp} in this study may also reflect greater drought tolerance for species of the French Guiana tree flora compared with other moist tropical forests. Indeed, North-East Amazonia dried out repeatedly during the Holocene in a region that is today known as the Roraima corridor (extending from Para, Brazil, towards the Rupununi savannahs in Guyana, and including the Sipaliwini savannah; Mayle & Power 2008). Over long time scales, such repeated droughts may have induced shifts in the floristic composition of these forests, driven by strong ecological sorting of pre-adapted species through environmental filtering (Dick *et al.* 2013). Thus at least some elements of the flora of French Guiana may be able to better accommodate drought conditions than is currently assumed in most simulation models (Freycon *et al.* 2010).

On the status of π_{tlp} in the plant economics spectrum

In the literature, high sapwood density has often been considered as associated with drought tolerance, because trees with a lower vulnerability of the water transport system to stem embolism have been found to have denser wood (Hacke *et al.* 2001; Santiago *et al.* 2004; Markesteijn *et al.* 2011a; b). However, variation in sapwood density across various habitats and lineages of Amazonian rainforests appears to be less related to hydraulic function estimated from wood vessel anatomy and more closely associated with biomechanical support as estimated by wood fibre composition (Fortunel *et al.* 2014; see also Chave *et al.* 2009; Zanne *et al.* 2010; Zieminska *et al.* 2013). The lack of a significant correlation between π_{tlp} and sapwood density in our dataset is further evidence that wood density is uncoupled from drought tolerance across phylogenetically and functionally diverse rainforest species.

The relationships between π_{tlp} and other leaf traits we found here, and in particular, the independence of π_{tlp} from leaf dry mass per area (LMA), reveal a disconnect of π_{tlp} from the leaf economics spectrum (Wright *et al.* 2004). The positive correlations between π_{tlp} and leaf toughness or thickness are at first sight counter-intuitive: they would suggest that a tougher or thicker leaf tends to be less drought tolerant. These results shed light on a long-standing controversy about the use of leaf structural traits as drought tolerance proxies. Higher values of LMA, leaf toughness and thickness as species traits have sometimes been found to be associated with drier conditions and thus proposed as potential predictors of leaf drought tolerance (e.g., Niinemets 2001; Lamont *et al.* 2002; Read & Sanson 2003; Wright *et al.* 2005; Poorter *et al.* 2009; Onoda *et al.* 2011). Although leaf toughness and thickness are associated with sclerophylly and often positively correlated with the leaf modulus of elasticity (ε), which reduces leaf shrinkage and dehydration under drought (Scoffoni *et al.* 2013), it has been recently demonstrated that neither of them play a direct role in drought tolerance globally, in particular because many drought sensitive species can have high LMA (Bartlett *et al.* 2012b). Here we confirmed that even within a given community, drought sensitive species may present either high or low LMA, and tougher and/or thicker leaves, probably in response to other evolutionary and environmental drivers, such as shade, nutrient availability or herbivory (see also Coste *et al.* 2005; Blackman *et al.* 2010; Markesteijn *et al.* 2011a). More generally, and as discussed elsewhere (Sack *et al.* 2003, 2013; Baraloto *et al.*

2010b; Reich 2014), LMA-related traits, including the leaf economics spectrum, tend to be independent of leaf- and plant hydraulic traits. In summary, soft traits commonly included in functional traits screenings and models, such as wood density and LMA, do not appear relevant to capture mechanistic drivers of tree growth response to environmental water stress and its species variability (Wagner *et al.* 2014).

We emphasize that π_{tlp} is a reasonably good proxy for a single, but key dimension of drought tolerance, i.e., maintaining gas exchange at strong transpiration rates and/or at negative soil water potentials, with a contribution to the prevention of cell shrinkage and consequent mechanical and metabolic damage. However, plants display a wide range of adaptations to delay or cope with these hazards. In particular, some species possess adaptations to delay or avoid the experience of drought in their tissues, in addition to, or instead of adaptations to maintain function during progressive drought: they mobilize stored water, develop a deep root system, limit gas exchange, or at the extreme shed leaves to stop leaf-level water exchange. Classically measured traits, such as deciduousness, already account, at least in part, for these alternative routes to drought tolerance. Future models integrating traits that reveal alternative means to drought tolerance will provide a more complete picture of plant resistance to drought and its variability.

Conclusion

Our study demonstrated strong variability in leaf drought tolerance across species, sites and environmental conditions. This variation illustrates how Amazonian plants' vulnerability to drought is poorly modelled in the plant functional types (Sitch *et al.* 2008) used by current dynamic global vegetation models (DGVMs). Such species variation is likely to be a source of discrepancy in models' simulations (Allen *et al.* 2010; Delbart *et al.* 2010; Joetzjer *et al.*

2013; Chave 2014). In particular, plant mortality is exclusively modelled through carbon balance in current DGVMs. However, plant survival should also depend on drought response and the stability of the hydraulic function (Tyree & Sperry 1989; Urli *et al.* 2013), the mobilization of non-structural carbohydrates and defence metabolism (McDowell 2011; Sevanto *et al.* 2014), all of which are poorly described (Powell *et al.* 2013; Xu *et al.* 2013). The new method we used is likely to be useful in conducting community-scale assessments of leaf-scale drought tolerance in the tropical tree flora. Our study suggests that, as already observed experimentally for relatively few species, important differences in drought tolerance are to be expected across evergreen species even in the Amazonian moist tropical forest vegetation zone, likely resulting in floristic composition changes. Our measure of drought tolerance, the leaf potential at turgor loss point (π_{tlp}), was found to be correlated weakly at best with typically used plant functional traits, and thus cannot be deduced easily from large existing plant functional trait repositories (Kattge *et al.* 2011). The integration of new trait-based information into models should shed crucial light on the still uncertain fate of the Amazon in response to climatic change. We propose that a more systematic measurement of π_{tlp}, integrated into the plant ecologist's toolkit of core plant functional traits that are routinely measured (Cornelissen *et al.* 2003), will significantly contribute to advancing this research agenda.

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Data Accessibility

All data used in this manuscript are present in the manuscript and its supporting information.

References

Abrams, M. & Kubiske, M. (1994) Synchronous changes in tissue water parameters of mature foliage from well-watered and periodically droughted tree seedlings. *Journal of Experimental Botany*, **45**, 171–177.

Abrams, M., Kubiske, M. & Steiner, K. (1990) Drought adaptations and responses in 5 genotypes of fraxinus-pennsylvanica marsh - photosynthesis, water relations and leaf morphology. *Tree Physiology*, **6**, 305–315.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (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.

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.

Baraloto, C., Timothy Paine, C.E., Patiño, S., Bonal, D., Hérault, B. & Chave, J. (2010a) Functional trait variation and sampling strategies in species-rich plant communities. *Functional Ecology*, **24**, 208–216.

Baraloto, C., Timothy Paine, C.E., Poorter, L., Beauchene, J., Bonal, D., Domenach, A.-M., Hérault, B., Patiño, S., Roggy, J.-C. & Chave, J. (2010b) Decoupled leaf and stem economics in rain forest trees. *Ecology Letters*, **13**, 1338–1347.

Bartlett, M.K., Scoffoni, C., Ardy, R., Zhang, Y., Sun, S., Cao, K. & Sack, L. (2012a) Rapid determination of comparative drought tolerance traits: using an osmometer to predict turgor loss point. *Methods in Ecology and Evolution*, **3**, 880–888.

Bartlett, M.K., Scoffoni, C. & Sack, L. (2012b) 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.

Bartlett, M.K., Zhang, Y., Kreidler, N., Sun, S., Ardy, R., Cao, K. & Sack, L. (2014) Global analysis of plasticity in turgor loss point, a key drought tolerance trait. *Ecology Letters*, **17**, 1580–1590.

Blackman, C.J., Brodribb, T.J. & Jordan, G.J. (2010) Leaf hydraulic vulnerability is related to conduit dimensions and drought resistance across a diverse range of woody angiosperms. *New Phytologist*, **188**, 1113–1123.

Blackman, C.J., Brodribb, T.J. & Jordan, G.J. (2012) Leaf hydraulic vulnerability influences species' bioclimatic limits in a diverse group of woody angiosperms. *Oecologia*, **168**, 1–10.

Bongers, F., Charles-Dominique, P., Forget, P.-M. & Thery, M. (2001) *Nouragues: Dynamics and Plant-Animal Interactions in a Neotropical Rainforest*. Kluwer Academic Publishers, Dordrecht ; Boston.

Boyce, C.K., Lee, J.-E., Feild, T.S., Brodribb, T.J. & Zwieniecki, M.A. (2010) Angiosperms Helped Put the Rain in the Rainforests: The Impact of Plant Physiological Evolution on Tropical Biodiversity1. *Annals of the Missouri Botanical Garden*, **97**, 527–540.

Brando, P.M., Nepstad, D.C., Davidson, E.A., Trumbore, S.E., Ray, D. & Camargo, P. (2008) Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: results of a throughfall reduction experiment. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363**, 1839–1848.

Brodribb, T.J., Holbrook, N.M., Edwards, E.J. & Gutiérrez, M.V. (2003) Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant, Cell & Environment*, **26**, 443–450.

Cao, K. (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.

De Castilho, C.V., Magnusson, W.E., Oliveira de Araújo, R.N., Da Costa Pereira, E. & De Souza, S.S. (2006) The use of French spikes to collect botanical vouchers in permanent plots: evaluation of potential impacts. *Biotropica*, **38**, 555–557.

Chave, J. (2014) Floristic shifts versus critical transitions in Amazonian forest systems. *Forests and Global Change* Ecological Reviews. pp. 131–159. Cambridge University Press, Cambridge, UK.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.

Cheung, Y.N.S., Tyree, M.T. & Dainty, J. (1975) Water relations parameters on single leaves obtained in a pressure bomb and some ecological interpretations. *Canadian Journal of Botany*, **53**, 1342–1346.

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.

Condit, R., Engelbrecht, B.M.J., Pino, D., Pérez, R. & Turner, B.L. (2013) Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proceedings of the National Academy of Sciences*, **110**, 5064–5068.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Steege, H. ter, Morgan, H.D., Heijden, M.G.A. van der, Pausas, J.G. & Poorter, H. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.

Da Costa, A.C.L., Galbraith, D., Almeida, S., Portela, B.T.T., da Costa, M., de Athaydes Silva Junior, J., Braga, A.P., de Gonçalves, P.H.L., de Oliveira, A.A., Fisher, R., Phillips, O.L., Metcalfe, D.B., Levy, P. & Meir, P. (2010) Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytologist*, **187**, 579–591.

Coste, S., Roggy, J.-C., Imbert, P., Born, C., Bonal, D. & Dreyer, E. (2005) Leaf photosynthetic traits of 14 tropical rain forest species in relation to leaf nitrogen concentration and shade tolerance. *Tree Physiology*, **25**, 1127–1137.

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.

Delbart, N., Ciais, P., Chave, J., Viovy, N., Malhi, Y. & Le Toan, T. (2010) Mortality as a key driver of the spatial distribution of aboveground biomass in Amazonian forest: results from a dynamic vegetation model. *Biogeosciences*, **7**, 3027–3039.

Dick, C.W., Lewis, S.L., Maslin, M. & Bermingham, E. (2013) Neogene origins and implied warmth tolerance of Amazon tree species. *Ecology and Evolution*, **3**, 162–169.

Engelbrecht, B.M.J., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L. & Hubbell, S.P. (2007) Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, **447**, 80–82.

Fauset, S., Baker, T.R., Lewis, S.L., Feldpausch, T.R., Affum-Baffoe, K., Foli, E.G., Hamer, K.C. & Swaine, M.D. (2012) Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana. *Ecology Letters*, **15**, 1120–1129.

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.

Ferry, B., Morneau, F., Bontemps, J.-D., Blanc, L. & Freycon, V. (2010) Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. *Journal of Ecology*, **98**, 106–116.

Fisher, R.A., Williams, M., Da Costa, A.L., Malhi, Y., Da Costa, R.F., Almeida, S. & Meir, P. (2007) The response of an Eastern Amazonian rain forest to drought stress: results and modelling analyses from a throughfall exclusion experiment. *Global Change Biology*, **13**, 2361–2378.

Fisher, R.A., Williams, M., Do Vale, R.L., Da Costa, A.L. & Meir, P. (2006) Evidence from Amazonian forests is consistent with isohydric control of leaf water potential. *Plant, Cell & Environment*, **29**, 151–165.

Fortunel, C., Ruelle, J., Beauchene, J., Fine, P.V.A. & Baraloto, C. (2014) Wood specific gravity and anatomy of branches and roots in 113 Amazonian rainforest tree species across environmental gradients. *New Phytologist*, **202**, 79–94.

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.

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

Good, P., Jones, C., Lowe, J., Betts, R. & Gedney, N. (2013) Comparing tropical forest projections from two generations of Hadley Centre Earth System models, HadGEM2-ES and HadCM3LC. *Journal of Climate*, **26**, 495–511.

Gourlet-Fleury, S., Guehl, J.-M. & Laroussinie, O. (2004) *Ecology and Management of a*

Neotropical Rainforest: Lessons Drawn from Paracou, a Long-Term Experimental Research Site in French Guiana. Elsevier, Paris.

Grimaldi, M. & Riéra, B. (2001) Geography and climate. *Nouragues: dynamics and plant-animal interactions in a neotropical rainforest.* pp. 9–18. Kluwer Academic Publishers, Boston.

Guyot, G., Scoffoni, C. & Sack, L. (2012) Combined impacts of irradiance and dehydration on leaf hydraulic conductance: insights into vulnerability and stomatal control. *Plant Cell and Environment*, **35**, 857–871.

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.

Harper, A., Baker, I.T., Denning, A.S., Randall, D.A., Dazlich, D. & Branson, M. (2013) Impact of evapotranspiration on dry season climate in the Amazon forest. *Journal of Climate*, **27**, 574–591.

Hilker, T., Lyapustin, A.I., Tucker, C.J., Hall, F.G., Myneni, R.B., Wang, Y., Bi, J., Moura, Y.M. de & Sellers, P.J. (2014) Vegetation dynamics and rainfall sensitivity of the Amazon. *Proceedings of the National Academy of Sciences*, 201404870.

Huntingford, C., Fisher, R.A., Mercado, L., Booth, B.B.B., Sitch, S., Harris, P.P., Cox, P.M., Jones, C.D., Betts, R.A., Malhi, Y., Harris, G.R., Collins, M. & Moorcroft, P. (2008) Towards quantifying uncertainty in predictions of Amazon 'dieback'. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363**, 1857–1864.

Huntingford, C., Zelazowski, P., Galbraith, D., Mercado, L.M., Sitch, S., Fisher, R., Lomas, M., Walker, A.P., Jones, C.D., Booth, B.B.B., Malhi, Y., Hemming, D., Kay, G., Good, P., Lewis, S.L., Phillips, O.L., Atkin, O.K., Lloyd, J., Gloor, E., Zaragoza-Castells, J., Meir, P., Betts, R., Harris, P.P., Nobre, C., Marengo, J. & Cox, P.M. (2013) Simulated resilience of tropical rainforests to CO2-induced climate change. *Nature Geoscience*, **6**, 268–273.

Jabot, F. & Chave, J. (2011) Analyzing tropical forest tree species abundance distributions using a nonneutral model and through approximate Bayesian inference. *The American Naturalist*, **178**, E37–47.

Joetzjer, E., Douville, H., Delire, C. & Ciais, P. (2013) Present-day and future Amazonian precipitation in global climate models: CMIP5 versus CMIP3. *Climate Dynamics*, **41**, 2921–2936.

Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., Harrison, S.P., Van Bodegom, P.M., Reichstein, M., Enquist, B.J., Soudzilovskaia, N.A., Ackerly, D.D., Anand, M., Atkin, O., Bahn, M., Baker, T.R., Baldocchi, D., Bekker, R., Blanco, C.C., Blonder, B., Bond, W.J., Bradstock, R., Bunker, D.E., Casanoves, F., Cavender-Bares, J., Chambers, J.Q., Chapin Iii, F.S., Chave, J., Coomes, D., Cornwell, W.K., Craine, J.M., Dobrin, B.H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W.F., Fang, J., Fernández-Méndez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G.T., Fyllas, N.M., Gallagher, R.V., Green, W.A., Gutierrez, A.G., Hickler, T., Higgins, S.I., Hodgson, J.G., Jalili, A., Jansen, S., Joly, C.A., Kerkhoff, A.J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J.M.H., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D., Lee, T.D., Leishman, M., Lens, F., Lenz, T., Lewis, S.L., Lloyd, J., Llusià, J., Louault, F., Ma, S., Mahecha, M.D., Manning, P., Massad, T., Medlyn, B.E., Messier, J., Moles, A.T., Müller, S.C., Nadrowski, K., Naeem, S., Niinemets, Ü., Nöllert, S., Nüske, A., Ogaya, R., Oleksyn, J., Onipchenko, V.G., Onoda, Y., Ordoñez, J., Overbeck, G., Ozinga, W.A., Patiño, S., Paula, S., Pausas, J.G., Peñuelas, J., Phillips, O.L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negret, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J.-F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S.J., Yguel, B., Zaehle, S., Zanne, A.E. & Wirth, C. (2011) TRY – a global database of plant traits. *Global Change Biology*, **17**, 2905–2935.

Koide, R.T., Robichaux, R.H., Morse, S.R. & Smith, C.M. (1989) Plant water status, hydraulic resistance and capacitance. *Plant Physiological Ecology* (eds R.W. Pearcy, J.R. Ehleringer, H.A. Mooney & P.W. Rundel), pp. 161–183. Springer, Netherlands.

Kursar, T.A., Engelbrecht, B.M.J., Burke, A., Tyree, M.T., El Omari, B. & Giraldo, J.P. (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. (2005) A comparison of methods for determining soil water availability in two sites in Panama with similar rainfall but distinct tree communities. *Journal of Tropical Ecology*, **21**, 297–305.

Lamont, B.B., Groom, P.K. & Cowling, R.M. (2002) High leaf mass per area of related species assemblages may reflect low rainfall and carbon isotope discrimination rather than low phosphorus and nitrogen concentrations. *Functional Ecology*, **16**, 403–412.

Lenz, T.I., Wright, I.J. & Westoby, M. (2006) Interrelations among pressure–volume curve traits across species and water availability gradients. *Physiologia Plantarum*, **127**, 423–433.

Lewis, S.L., Brando, P.M., Phillips, O.L., Heijden, G.M.F. van der & Nepstad, D. (2011) The 2010 Amazon Drought. *Science*, **331**, 554–554.

Malhi, Y., Aragão, L.E.O.C., Galbraith, D., Huntingford, C., Fisher, R., Zelazowski, P., Sitch, S., McSweeney, C. & Meir, P. (2009) Exploring the Likelihood and Mechanism of a Climate-Change-Induced Dieback of the Amazon Rainforest. *Proceedings of the National Academy of Sciences*, **106**, 20610–20615.

Malhi, Y., Roberts, J.T., Betts, R.A., Killeen, T.J., Li, W. & Nobre, C.A. (2008) Climate change, deforestation, and the fate of the Amazon. *Science*, **319**, 169–172.

Markesteijn, L., Poorter, L., Bongers, F., Paz, H. & Sack, L. (2011a) Hydraulics and life history of tropical dry forest tree species: coordination of species' drought and shade tolerance. *New Phytologist*, **191**, 480–495.

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

Mayle, F.E. & Power, M.J. (2008) Impact of a drier Early–Mid-Holocene climate upon Amazonian forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363**, 1829–1838.

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

McDowell, N.G., Fisher, R.A., Xu, C., Domec, J.C., Holtta, T., Mackay, D.S., Sperry, J.S., Boutz, A., Dickman, L., Gehres, N., Limousin, J.M., Macalady, A., Martinez-Vilalta, J., Mencuccini, M., Plaut, J.A., Ogee, J., Pangle, R.E., Rasse, D.P., Ryan, M.G., Sevanto, S., Waring, R.H., Williams, A.P., Yepez, E.A. & Pockman, W.T. (2013) Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. *New Phytologist*, **200**, 304–321.

Meinzer, F.C., Grantz, D.A., Goldstein, G. & Saliendra, N.Z. (1990) Leaf water relations and maintenance of gas exchange in coffee cultivars grown in drying soil. *Plant Physiology*, **94**, 1781–1787.

Merchant, A., Callister, A., Arndt, S., Tausz, M. & Adams, M. (2007) Contrasting physiological responses of six Eucalyptus species to water deficit. *Annals of Botany*, **100**, 1507–1515.

Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, C.E.T., Renaud, J. & Thuiller, W. (2013) Rare Species Support Vulnerable Functions in High-Diversity Ecosystems. *PLoS Biol*, **11**, e1001569.

Nepstad, D.C., Moutinho, P., Dias-Filho, M.B., Davidson, E., Cardinot, G., Markewitz, D., Figueiredo, R., Vianna, N., Chambers, J., Ray, D., Guerreiros, J.B., Lefebvre, P., Sternberg, L., Moreira, M., Barros, L., Ishida, F.Y., Tohlver, I., Belk, E., Kalif, K. & Schwalbe, K. (2002) The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest. *Journal of Geophysical Research: Atmospheres*, **107**, LBA 53–1–LBA 53–18.

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.

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

Onoda, Y., Westoby, M., Adler, P.B., Choong, A.M.F., Clissold, F.J., Cornelissen, J.H.C., Díaz, S., Dominy, N.J., Elgart, A., Enrico, L., Fine, P.V.A., Howard, J.J., Jalili, A., Kitajima, K., Kurokawa, H., McArthur, C., Lucas, P.W., Markesteijn, L., Pérez-Harguindeguy, N., Poorter, L., Richards, L., Santiago, L.S., Sosinski, E.E., Van Bael, S.A., Warton, D.I., Wright, I.J., Joseph Wright, S. & Yamashita, N. (2011) Global patterns of leaf mechanical properties. *Ecology Letters*, **14**, 301–312.

Phillips, O.L., Aragao, L.E.O.C., Lewis, L.S., Fisher, J.B., Lloyd, J., Lopez-Gonzalez, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., Heijden, G.V.D., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Banki, O., Blanc, L. & al, et. (2009) Drought sensitivity of the Amazon rainforest. *Science*, **323**, 1344–1347.

Phillips, O.L., van der Heijden, G., Lewis, S.L., López-González, G., Aragão, L.E.O.C., Lloyd, J., Malhi, Y., Monteagudo, A., Almeida, S., Dávila, E.A., Amaral, I., Andelman, S., Andrade, A., Arroyo, L., Aymard, G., Baker, T.R., Blanc, L., Bonal, D., de Oliveira, Á.C.A., Chao, K.-J., Cardozo, N.D., da Costa, L., Feldpausch, T.R., Fisher, J.B., Fyllas, N.M., Freitas, M.A., Galbraith, D., Gloor, E., Higuchi, N., Honorio, E., Jiménez, E., Keeling, H., Killeen, T.J., Lovett, J.C., Meir, P., Mendoza, C., Morel, A., Vargas, P.N., Patiño, S., Peh, K.S.-H., Cruz, A.P., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez, H., Rudas, A., Salamão, R., Schwarz, M., Silva, J., Silveira, M., Ferry Slik, J.W., Sonké, B., Thomas, A.S., Stropp, J., Taplin, J.R.D., Vásquez, R. & Vilanova, E. (2010) Drought-mortality relationships for tropical forests. *New Phytologist*, **187**, 631–646.

Poorter, H., Niinemets, Ü., 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.

Powell, T.L., Galbraith, D.R., Christoffersen, B.O., Harper, A., Imbuzeiro, H.M.A., Rowland, L., Almeida, S., Brando, P.M., da Costa, A.C.L., Costa, M.H., Levine, N.M., Malhi, Y., Saleska, S.R., Sotta, E., Williams, M., Meir, P. & Moorcroft, P.R. (2013) Confronting model predictions of carbon fluxes with measurements of Amazon forests subjected to experimental drought. *New Phytologist*, **200**, 350–365.

Quesada, C.A., Lloyd, J., Schwarz, M., Baker, T.R., Phillips, O.L., Patiño, S., Czimczik, C., Hodnett, M.G., Herrera, R., Arneth, A., Lloyd, G., Malhi, Y., Dezzeo, N., Luizão, F.J., Santos, A.J.B., Schmerler, J., Arroyo, L., Silveira, M., Priante Filho, N., Jimenez, E.M., Paiva, R., Vieira, I., Neill, D.A., Silva, N., Peñuela, M.C., Monteagudo, A., Vásquez, R., Prieto, A., Rudas, A., Almeida, S., Higuchi, N., Lezama, A.T., López-González, G., Peacock, J., Fyllas, N.M., Alvarez Dávila, E., Erwin, T., di Fiore, A., Chao, K.J., Honorio, E., Killeen, T., Peña Cruz, A., Pitman, N., Núñez Vargas, P., Salomão, R., Terborgh, J. & Ramírez, H. (2009) Regional and large-scale patterns in Amazon forest structure and function are mediated by variations in soil physical and chemical properties. *Biogeosciences Discussions*, **6**, 3993–4057.

R Core Team. (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Read, J. & Sanson, G.D. (2003) Characterizing sclerophylly: the mechanical properties of a diverse range of leaf types. *New Phytologist*, **160**, 81–99.

Reich, P.B. (2014) The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *Journal of Ecology*, **102**, 275–301.

Saatchi, S., Asefi-Najafabady, S., Malhi, Y., Aragão, L.E.O.C., Anderson, L.O., Myneni, R.B. & Nemani, R. (2013) Persistent effects of a severe drought on Amazonian forest canopy. *Proceedings of the National Academy of Sciences*, **110**, 565–570.

Saatchi, S.S., Harris, N.L., Brown, S., Lefsky, M., Mitchard, E.T.A., Salas, W., Zutta, B.R., Buermann, W., Lewis, S.L., Hagen, S., Petrova, S., White, L., Silman, M. & Morel, A. (2011) Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences*, **108**, 9899–9904.

Sabatier, D., Grimaldi, M., Prévost, M.-F., Guillaume, J., Godron, M., Dosso, M. & Curmi, P. (1997) The influence of soil cover organization on the floristic and structural heterogeneity of a Guianan rain forest. *Plant Ecology*, **131**, 81–108.

Sack, L., Cowan, P.D., Jaikumar, N. & Holbrook, N.M. (2003) The 'hydrology' of leaves: co-ordination of structure and function in temperate woody species. *Plant, Cell & Environment*, **26**, 1343–1356.

Sack, L., Scoffoni, C., John, G.P., Poorter, H., Mason, C.M., Mendez-Alonzo, R. & Donovan, L.A. (2013) How do leaf veins influence the worldwide leaf economic spectrum? Review and synthesis. *Journal of Experimental Botany*, **64**, 4053–4080.

Santiago, L.S., Goldstein, G., Meinzer, F.C., Fisher, J.B., Machado, K., Woodruff, D. & Jones, T. (2004) Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia*, **140**, 543–550.

Scoffoni, C., Rawls, M., McKown, A., Cochard, H. & Sack, L. (2011) Decline of leaf hydraulic conductance with dehydration: relationship to leaf size and venation architecture. *Plant Physiology*, **156**, 832–843.

Scoffoni, C., Vuong, C., Diep, S., Cochard, H. & Sack, L. (2013) Leaf shrinkage with dehydration: coordination with hydraulic vulnerability and drought tolerance. *Plant Physiology*, pp.113.221424.

Sevanto, S., Mcdowell, N.G., Dickman, L.T., Pangle, R. & Pockman, W.T. (2014) How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant, Cell & Environment*, **37**, 153–161.

Sitch, S., Huntingford, C., Gedney, N., Levy, P.E., Lomas, M., Piao, S.L., Betts, R., Ciais, P., Cox, P., Friedlingstein, P., Jones, C.D., Prentice, I.C. & Woodward, F.I. (2008) Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Global Change Biology*, **14**, 2015–2039.

Smith, N.G., Rodgers, V.L., Brzostek, E.R., Kulmatiski, A., Avolio, M.L., Hoover, D.L., Koerner, S.E., Grant, K., Jentsch, A., Fatichi, S. & Niyogi, D. (2014) Toward a better integration of biological data from precipitation manipulation experiments into Earth system models. *Reviews of Geophysics*, 2014RG000458.

Sokal, R.R. & Rohlf, F.J. (1987) *Introduction to Biostatistics*, 2nd ed. Freeman, New York.

Ter Steege, H., Pitman, N.C.A., Phillips, O.L., Chave, J., Sabatier, D., Duque, A., Molino, J.-F., Prévost, M.-F., Spichiger, R., Castellanos, H., von Hildebrand, P. & Vásquez, R. (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature*, **443**, 444–447.

Tyree, M.T. & Sperry, J.S. (1989) Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Plant Molecular Biology*, **40**, 19–36.

Urli, M., Porté, A.J., Cochard, H., Guengant, Y., Burlett, R. & Delzon, S. (2013) Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiology*, **33**, 672–683.

Wagner, F., Rossi, V., Baraloto, C., Bonal, D., Stahl, C. & Hérault, B. (2014) Are commonly measured functional traits involved in tropical tree responses to climate? *International Journal of Ecology*, **2014**, e389409.

West, A.G., Dawson, T.E., February, E.C., Midgley, G.F., Bond, W.J. & Aston, T.L. (2012) Diverse functional responses to drought in a Mediterranean-type shrubland in South Africa. *New Phytologist*, **195**, 396–407.

Williams, D.G. & Ehleringer, J.R. (2000) Intra- and interspecific variation for summer precipitation use in pinyon–juniper woodlands. *Ecological Monographs*, **70**, 517–537.

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.

Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K., Lee, W., Lusk, C.H., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Warton, D.I. & Westoby, M. (2005) Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography*, **14**, 411–421.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.

Xu, C., McDowell, N.G., Sevanto, S. & Fisher, R.A. (2013) Our limited ability to predict vegetation dynamics under water stress. *New Phytologist*, **200**, 298–300.

Zanne, A.E., Westoby, M., Falster, D.S., Ackerly, D.D., Loarie, S.R., Arnold, S.E.J. & Coomes, D.A. (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.

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.

Zieminska, K., Butler, D.W., Gleason, S.M., Wright, I.J. & Westoby, M. (2013) Fibre wall and lumen fractions drive wood density variation across 24 Australian angiosperms. *Aob Plants*, **5**, plt046.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Dataset of estimated π_{osm} and π_{tlp} values for 165 trees in forests French Guiana

Figure S1. Correlation between leaf drought tolerance (π_{tlp}, in MPa) and several structural soft traits

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Figures

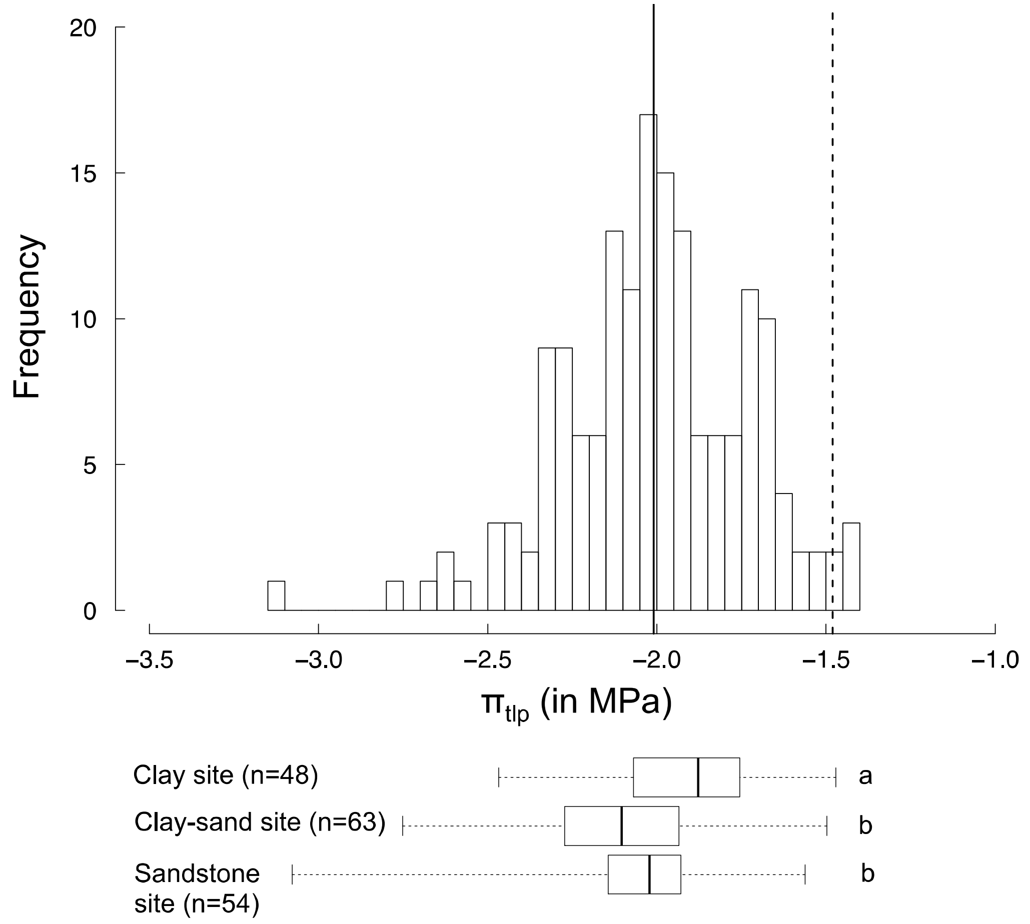

Figure 1. Diversity of leaf drought tolerance across 71 species in a tropical forest. Upper panel: histogram of leaf-level water potential at turgor loss point (π_{tlp}, in MPa) in our dataset (n=165 individuals). Solid and dashed lines indicate mean of π_{tlp} values in our dataset and in Bartlett *et al.* (2012b) dataset, respectively. Lower panel: boxplots for the three study plots in

French Guiana (with 33, 40 and 19 species from the clay, clay-sand and sandstone sites, respectively, and 6 species sampled in the three sites). Different lower case letters indicate a significant difference between sites π_{tlp} means (Tukey test: $P<0.05$).

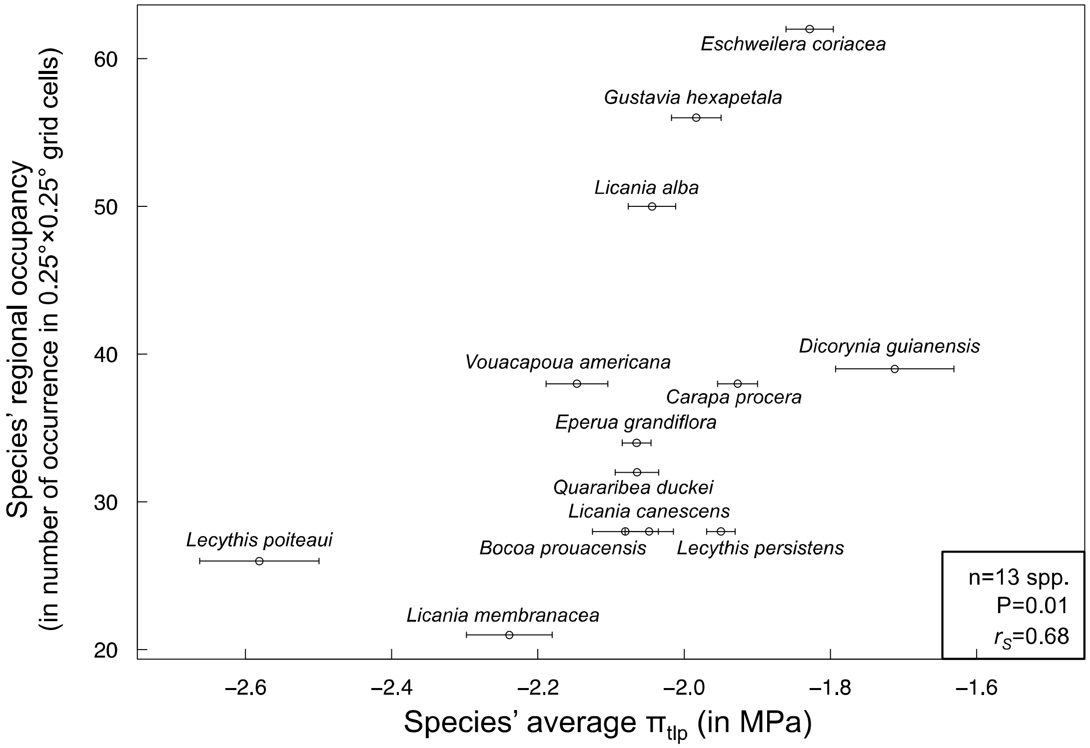

Figure 2. Relationship between species regional occupancy and species' average leaf turgor loss points (π_{tlp}, in MPa), for species for which we sampled at least five individuals. Regional occupancies were estimated as the number of occurrences in 478 0.25°×0.25° grid cells within the Guiana Shield. Whisker plots indicate standard errors of the mean.

Tables

Table 1. Mean and standard error (SE) and range of π_{tlp} values at the three sites, and comparison with literature values

Site	Number of individuals	Mean ± SE (MPa)	Min (MPa)	Max (MPa)
sandstone site	54	-2.03 ± 0.04	-3.15	-1.51
clay-sand site	63	-2.09 ± 0.04	-2.80	-1.44
clay site	48	-1.89 ± 0.03	-2.49	-1.41
Total	165	-2.01 ± 0.02	-3.15	-1.41
Bartlett *et al.* (2012b) data*	50	-1.48 ± 0.06	-2.56	-0.43

*Data for trees of moist tropical forests during the wet season from Bartlett *et al.* (2012b).