

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_o) is tightly correlated with π_{tlp} . Estimating π_{tlp} from osmometer measurements of π_o 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 data set 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

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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 savanna-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; Joetzer *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, 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. 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, Kubeske & Steiner 1990; Brodribb *et al.* 2003; Bartlett, Scoffoni & Sack 2012b; Guyot, Scoffoni & Sack 2012). Thus, a more negative value for π_{tlp} contributes to greater leaf-level drought tolerance 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 (Koidé *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, Wright & Westoby 2006; Blackman, Brodribb & Jordan 2010; Scoffoni *et al.* 2011; Bartlett, Scoffoni & Sack 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 rain forest 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 data set 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 (i) as 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; (ii) π_{tlp} depends on local environmental conditions, and thus, individuals growing in soils with a lower water retention capacity are more drought tolerant; and (iii) 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 ca. 3000 mm year⁻¹ rainfall, with significant seasonal and interannual variation due to the movement of the Intertropical 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 month⁻¹.

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 ($\delta^{13}\text{C}$), 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 data set. 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, USA) (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 (LN₂) for at least 2 min, 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 <40 s 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-min 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:

$$\pi_{\text{osm}} = \frac{2.5}{1000} \times c_0 \quad \text{eqn 1}$$

where the numerator of the first term represents $R \times T = 2.5 \text{ L MPa mol}^{-1}$ 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, $R^2 = 86\%$, $P < 2 \cdot 10^{-12}$, π_{osm}

range = (−3.03, −0.64) MPa and π_{tlp} range = (−3.00, −1.02) MPa; Bartlett *et al.* 2012a];

$$\pi_{\text{tlp}} = 0.832 \times \pi_{\text{osm}} - 0.631 \quad \text{eqn 2}$$

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 rain forest (Bartlett *et al.* 2012a). The fit of eqn 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 data set encompassed the full range of the π_{osm} values measured in this study [π_{osm} range = (−3.02, −0.94) MPa]. When this correlation data set was restricted to the tropical rain forest 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, 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, Scoffoni & Sack 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 four sampled species for which at least five 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, $\delta^{13}\text{C}$, 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 intracanopy variability within individuals. For this second set of analyses, we included only species for which trait values had been measured for at least three 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

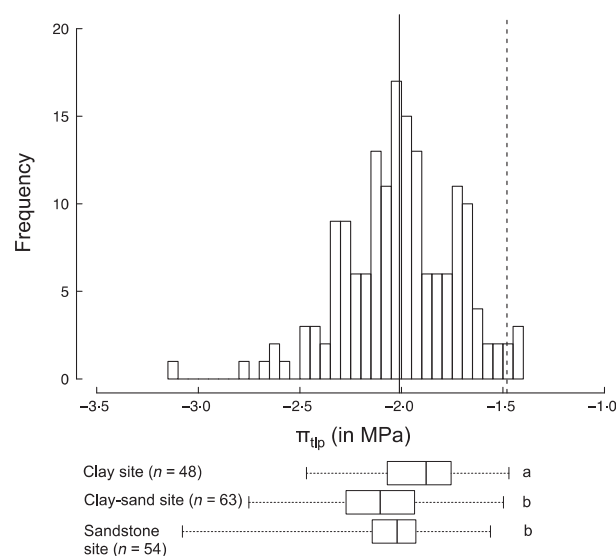


Fig. 1. Diversity of leaf drought tolerance across 71 species in a tropical forest. Upper panel: histogram of leaf-level water potential at turgor loss point (π_{tlp} , in MPa) in our data set ($n = 165$ individuals). Solid and dashed lines indicate mean of π_{tlp} values in our data set and in Bartlett, Scoffoni & Sack (2012b) data set, respectively. Lower panel: box plots 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: $P < 0.05$).

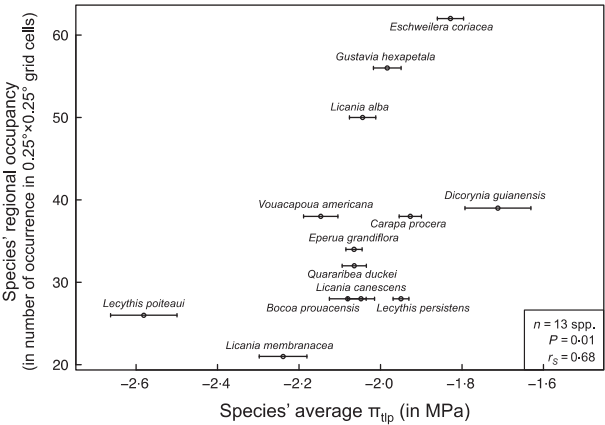


Fig. 2. Relationship between species regional occupancy and species' average leaf turgor loss points (π_{tlp} , in MPa), for species for which we sampled at least five individuals. Regional occupancies were estimated as the number of occurrences in 478 0.25° × 0.25° grid cells within the Guiana Shield.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

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} (\pm 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, Scoffoni & Sack 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, Scoffoni & Sack 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

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 \pm 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, Scoffoni & Sack (2012b) data*	50	-1.48 ± 0.06	–2.56	–0.43

*Data for trees of moist tropical forests during the wet season from Bartlett, Scoffoni & Sack (2012b).

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, Supporting information; $P = 0.04$, $R^2 = 22\%$, $n = 19$ species). Additionally, a more negative π_{tlp} was weakly associated with lower leaf thickness (Fig. S1c, Supporting information; $P = 0.03$, $R^2 = 3\%$, $n = 151$ individuals). We found no statistical association of π_{tlp} with other functional traits, that is leaf area, dry mass, dry mass per area (LMA; Fig. S1d, Supporting information), carbon and nitrogen concentrations per leaf mass, carbon isotope ratio ($\delta^{13}\text{C}$), sapwood density (Fig. S1b, Supporting information) 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 intrafamily 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 data set, 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 metres 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, Wright & Westoby 2006). A more exhaustive sampling across the local flora would help to determine the relative extent to which site conditions, community composition and intraspecific plasticity contribute to differences in π_{tlp} across geographical 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_{TLF} 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, Scoffoni & Sack 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 (Supporting information), we report raw osmometer π_o values in addition to π_{tlp} values to facilitate future calibration analyses.

The π_{tlp} values in our data set 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 world-wide (Wright *et al.* 1992; Abrams & Kubiske 1994; Cao 2000; Merchant *et al.* 2007; Zhu & Cao 2009; Bartlett, Scoffoni & Sack 2012b; Bartlett *et al.* 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 understorey 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 savannas in Guyana, and including the Sipaliwini savanna; 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_{TLF} 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 rain forests

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 data set is further evidence that wood density is uncoupled from drought tolerance across phylogenetically and functionally diverse rain forest 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, Groom & Cowling 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, Scoffoni & Sack 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, Brodribb & Jordan 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, that is 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; Joetjzer *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; Urii *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.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

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

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