

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

Isabelle Maréchaux<sup>\*,1,2</sup>, Megan K. Bartlett<sup>3</sup>, Lawren Sack<sup>3</sup>, Christopher Baraloto<sup>4</sup>, Julien Engel<sup>5</sup>, Emilie Joetzer<sup>6</sup> and Jérôme Chave<sup>1</sup>

<sup>1</sup>CNRS, Université Paul Sabatier, ENFA; UMR5174 EDB (Laboratoire Evolution et Diversité Biologique), 118 route de Narbonne, Toulouse F-31062, France; <sup>2</sup>AgroParisTech-ENGREF, 19 avenue du Maine, Paris F-75015, France; <sup>3</sup>Department of Ecology and Evolution, University of California Los Angeles, 621 Charles E. Young Drive South, Los Angeles, CA 90095, USA; <sup>4</sup>International Center for Tropical Botany, Department of Biological Sciences, Florida International University, Miami, FL 33199, USA; <sup>5</sup>INRA, UMR 'Ecologie des Forêts de Guyane', 97387 Kourou Cedex, French Guiana; and <sup>6</sup>CNRM-GAME – URA1357, 42 avenue G. Coriolis, Toulouse 31057, France

## 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 ( $\pi_{tlp}$ ) 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 ( $\pi_o$ ) is tightly correlated with  $\pi_{tlp}$ . Estimating  $\pi_{tlp}$  from osmometer measurements of  $\pi_o$  is much faster than the standard pressure–volume curve approach of  $\pi_{tlp}$  determination. We used this technique to estimate  $\pi_{tlp}$  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,  $\pi_{tlp}$  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  $\pi_{tlp}$  (i.e. with greater leaf-level drought tolerance) occurred less frequently across the region than drought-sensitive species.

5. Across individuals,  $\pi_{tlp}$  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  $\pi_{tlp}$  among species indicates a potential for highly diverse species responses to drought within given forest communities. Given the weak correlations between  $\pi_{tlp}$  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

\*Correspondence author. E-mail: isabelle.mj.marechaux@gmail.com

## 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; Joetjzer *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, Brodrribb & 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  $\pi_{\text{tlp}}$ ) 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  $\pi_{\text{tlp}}$  (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; Brodrribb *et al.* 2003; Bartlett, Scoffoni & Sack 2012b; Guyot, Scoffoni & Sack 2012). Thus, a more negative value for  $\pi_{\text{tlp}}$  contributes to greater leaf-level drought tolerance and therefore also plant-level drought tolerance.

Previously,  $\pi_{\text{tlp}}$  has been estimated from pressure–volume curves, which measure the decline of leaf water potential as the leaf dehydrates. This standard method of  $\pi_{\text{tlp}}$  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 ( $\pi_{\text{o}}$ ), was repeatedly found to be an excellent correlate for  $\pi_{\text{tlp}}$  (Sack *et al.* 2003; Lenz, Wright & Westoby 2006; Blackman, Brodrribb & 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  $\pi_{\text{tlp}}$  from osmometer measurements of  $\pi_{\text{o}}$ . The  $\pi_{\text{o}}-\pi_{\text{tlp}}$  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  $\pi_{\text{tlp}}$  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  $\pi_{\text{tlp}}$ , 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,  $\pi_{\text{tlp}}$  would correlate negatively with species rarity; (ii)  $\pi_{\text{tlp}}$  depends on local environmental conditions, and thus, individuals growing in soils with a lower water retention capacity are more drought tolerant; and (iii)  $\pi_{\text{tlp}}$  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<sup>-1</sup> 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<sup>-1</sup>.

In 2007 and 2008, the three 1-ha plots were fully censused for trees  $\geq 10$  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  $\geq 10$  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; Marksteijn *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 $\pi_{\text{TLp}}$ VALUES

We assessed the leaf turgor loss point,  $\pi_{\text{tlp}}$ , from a previously established linear relationship with the osmotic potential at full hydration ( $\pi_0$ ), 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 (LN<sub>2</sub>) 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  $\mu\text{L}$  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<sup>-1</sup>) was recorded from the osmometer when the difference between consecutive 2-min measurements fell below 5 mmol kg<sup>-1</sup>. This value was converted to  $\pi_0$  values from the osmometer ( $\pi_{\text{osm}}$ ) 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  $\pi_{\text{tlp}}$  was estimated from  $\pi_{\text{osm}}$  using the previously published regression equation relating  $\pi_{\text{osm}}$  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,  $R^2 = 86\%$ ,  $P < 2 \cdot 10^{-12}$ ,  $\pi_{\text{osm}}$

range =  $(-3.03, -0.64)$  MPa and  $\pi_{\text{tlp}}$  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  $\pi_o$  values ( $\pi_{\text{osm}}$ ) and  $\pi_{\text{tlp}}$  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  $\pi_{\text{osm}}$  range of the correlation data set encompassed the full range of the  $\pi_{\text{osm}}$  values measured in this study [ $\pi_{\text{osm}}$  range =  $(-3.02, -0.94)$  MPa]. When this correlation data set was restricted to the tropical rain forest species group only, the  $\pi_{\text{osm}}$  range [ $\pi_{\text{osm}}$  range =  $(-1.70, -0.70)$  MPa; Bartlett *et al.* 2012a] encompassed 86% of the range of our measured  $\pi_{\text{osm}}$  values. All  $\pi_{\text{osm}}$  and  $\pi_{\text{tlp}}$  data are available (see Appendix S1, Supporting information).

#### DATA ANALYSIS

We compared the  $\pi_{\text{tlp}}$  values for the measured trees with a published compilation of  $\pi_{\text{tlp}}$  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  $\pi_{\text{tlp}}$  for a subset of 13 species for which at least 5 individuals were sampled ( $n = 82$  individuals). We also tested for species differences in  $\pi_{\text{tlp}}$  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  $\pi_{\text{tlp}}$  variability was quantified with variance partitioning (Sokal & Rohlf 1987).

To test the significance of the variation of  $\pi_{\text{tlp}}$  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  $\pi_{\text{tlp}}$  and regional occupancy, estimated as the number of occurrences across  $478\ 0.25^\circ \times 0.25^\circ$  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  $\pi_{\text{tlp}}$  and regional occupancy.

We tested correlations between  $\pi_{\text{tlp}}$  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  $\pi_{\text{tlp}}$  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 intracopy 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  $\pi_{\text{tlp}}$  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).

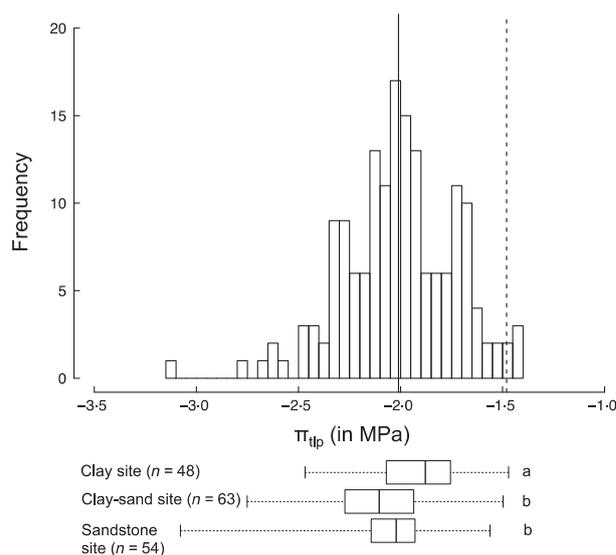
## Results

#### VARIATION IN MEAN $\pi_{\text{TLP}}$ ACROSS SPECIES

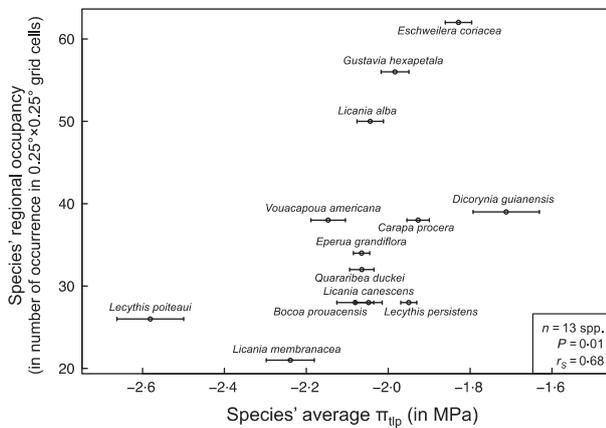
The  $\pi_{\text{tlp}}$  varied strongly across species (Fig. 1; ANOVA,  $P < 1 \cdot 10^{-6}$ ), with 40% of the variance in  $\pi_{\text{tlp}}$  associated with species differences ( $n = 13$  species and 82 individuals). Strong species differences were exemplified by *Dicorynia guianensis* (Fabaceae) and *Eschweilera coriacea* (Lecythidaceae), which had less negative  $\pi_{\text{tlp}}$  values than the average ( $-1.71 \pm 0.16$  MPa and  $-1.83 \pm 0.06$  MPa, respectively) and *Lecythis poiteaui* (Lecythidaceae), which had a more negative  $\pi_{\text{tlp}}$  than average ( $-2.58 \pm 0.16$  MPa). *Protium* (Burseraceae) individuals also had significantly more negative  $\pi_{\text{tlp}}$  than average ( $-2.28 \pm 0.06$  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  $P < 1 \cdot 10^{-5}$ , respectively).

#### DROUGHT-TOLERANT SPECIES ARE REGIONALLY LESS FREQUENT THAN DROUGHT-INTOLERANT ONES

Species with a more negative  $\pi_{\text{tlp}}$  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 ( $\pi_{\text{tlp}}$ , in MPa) in our data set ( $n = 165$  individuals). Solid and dashed lines indicate mean of  $\pi_{\text{tlp}}$  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  $\pi_{\text{tlp}}$  means (Tukey test:  $P < 0.05$ ).



**Fig. 2.** Relationship between species regional occupancy and species' average leaf turgor loss points ( $\pi_{\text{tlp}}$ , in MPa), for species for which we sampled at least five individuals. Regional occupancies were estimated as the number of occurrences in 478  $0.25^\circ \times 0.25^\circ$  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  $\pi_{\text{tlp}}$  than average ( $t$ -test,  $P = 0.03$ ). Conversely, the most drought-tolerant species, in terms of its  $\pi_{\text{tlp}}$ , *Lecythis poiteaui*, is regionally infrequent, occurring at 26/478 grid cells.

#### WIDER RANGE OF $\pi_{\text{TLP}}$ THAN PREVIOUSLY ACCOUNTED FOR IN MOIST TROPICAL FORESTS

The mean  $\pi_{\text{tlp}}$  ( $\pm$ SE) across species in the study plots was  $-2.01 \pm 0.02$  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 $\pi_{\text{TLP}}$ ACROSS FOREST PLOTS

The  $\pi_{\text{tlp}}$  varied significantly across our three sites (ANOVA,  $P < 0.005$ ; Fig. 1). The mean  $\pi_{\text{tlp}}$  at the clay–sand site was

**Table 1.** Mean and standard error (SE) and range of  $\pi_{\text{tlp}}$  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	$-2.03 \pm 0.04$	-3.15	-1.51
Clay–sand site	63	$-2.09 \pm 0.04$	-2.80	-1.44
Clay site	48	$-1.89 \pm 0.03$	-2.49	-1.41
Total	165	$-2.01 \pm 0.02$	-3.15	-1.41
Bartlett, Scoffoni & Sack (2012b) data*	50	$-1.48 \pm 0.06$	-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 $\pi_{\text{TLP}}$ WITH OTHER FUNCTIONAL TRAITS

Across species, a more negative  $\pi_{\text{tlp}}$  was associated with lower leaf toughness (Fig. S1a, Supporting information;  $P = 0.04$ ,  $R^2 = 22\%$ ,  $n = 19$  species). Additionally, a more negative  $\pi_{\text{tlp}}$  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  $\pi_{\text{tlp}}$  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  $\pi_{\text{tlp}}$  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)  $\pi_{\text{tlp}}$  than the all-species average, whereas *Lecythis poiteaui* had a more negative  $\pi_{\text{tlp}}$  than average. Similarly, within the Fabaceae, *Dicorynia guianensis* and *Vouacapoua americana* had  $\pi_{\text{tlp}}$  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  $\pi_{\text{tlp}}$ ).

The above considerations suggest that  $\pi_{\text{tlp}}$ , measured at leaf level, is a useful integrative trait for plant-level tolerance. The  $\pi_{\text{tlp}}$  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  $\pi_{\text{tlp}}$  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  $\pi_{\text{tlp}}$  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  $\pi_{\text{tlp}}$  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  $\pi_{\text{tlp}}$  across geographical and environmental gradients.

Drought tolerance as predicted by  $\pi_{\text{tlp}}$  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  $\pi_{\text{tlp}}$  are needed to assess the evolutionary underpinnings of drought tolerance in tropical trees.

#### ON THE MEASUREMENT OF $\pi_{\text{TLF}}$ 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  $\pi_{\text{tlp}}$  with the osmotic potential at full

hydration ( $\pi_{\text{o}}$ ), 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  $\pi_{\text{o}}$  values in addition to  $\pi_{\text{tlp}}$  values to facilitate future calibration analyses.

The  $\pi_{\text{tlp}}$  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  $\pi_{\text{tlp}}$  at the peak of the dry season. Plants often acclimate  $\pi_{\text{tlp}}$  during drought periods, through the accumulation of cell solutes, or osmotic adjustment. Such an adjustment results in a lowering of  $\pi_{\text{tlp}}$  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  $\pi_{\text{tlp}}$  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 $\pi_{\text{TLF}}$ 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  $\pi_{\text{tlp}}$  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  $\pi_{\text{tlp}}$  and other leaf traits we found here, and in particular, the independence of  $\pi_{\text{tlp}}$  from leaf dry mass per area (LMA), reveal a disconnect of  $\pi_{\text{tlp}}$  from the leaf economics spectrum (Wright *et al.* 2004). The positive correlations between  $\pi_{\text{tlp}}$  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 ( $\epsilon$ ), 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, Brodrigg & 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  $\pi_{\text{tlp}}$  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; 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; 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 ( $\pi_{\text{tlp}}$ ), 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  $\pi_{\text{tlp}}$ , 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.

## Acknowledgements

We thank V. Alt and P. Gaucher for their help in tree climbing. This work has benefited from 'Investissement d'Avenir' grants managed by the French Agence Nationale de la Recherche (CEBA, ref. ANR-10-LABX-25-01 and TULIP, ref. ANR-10-LABX-0041; ANAEE-France: ANR-11-INBS-0001) and from an additional ANR grant (BRIDGE project) and funds from CNRS.

## 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. *et al.* (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.
- Baltzer, J.L., Davies, S.J., Bunyavechewin, 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. *et al.* (2010b) Decoupled leaf and stem economics in rain forest trees. *Ecology Letters*, **13**, 1338–1347.
- 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., Scoffoni, C., Ardy, R., Zhang, Y., Sun, S., Cao, K. *et al.* (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., Zhang, Y., Kreedler, N., Sun, S., Ardy, R., Cao, K. *et al.* (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 biodiversity. *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 and 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.
- Chave, J. (2014) Floristic shifts vs. critical transitions in Amazonian forest systems. *Forests and Global Change* (eds D.A. Coomes, D.F.R.P. Burslem & W.D. Simonson), 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. *et al.* (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.
- 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.
- Da Costa, A.C.L., Galbraith, D., Almeida, S., Portela, B.T.T., da Costa, M., de Athaydes Silva Junior, J. *et al.* (2010) Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytologist*, **187**, 579–591.
- 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.
- Delbart, N., Ciais, P., Chave, J., Viovy, N., Malhi, Y. & Le Toan, T. (2010) Mortality as a key driver of the spatial distribution of above-ground 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. *et al.* (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. *et al.* (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., 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 and Environment*, **29**, 151–165.
- Fisher, R.A., Williams, M., Da Costa, A.L., Malhi, Y., Da Costa, R.F., Almeida, S. *et al.* (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.
- 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* (ed F. Bongers), 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. *et al.* (2014) Vegetation dynamics and rainfall sensitivity of the Amazon. *Proceedings of the National Academy of Sciences*, **111**, 16041–16046.
- Huntingford, C., Fisher, R.A., Mercado, L., Booth, B.B.B., Sitch, S., Harris, P.P. *et al.* (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. *et al.* (2013) Simulated resilience of tropical rainforests to CO<sub>2</sub>-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. *American Naturalist*, **178**, E37–E47.
- Joetzier, E., Douville, H., Delire, C. & Ciais, P. (2013) Present-day and future Amazonian precipitation in global climate models: CMIP5 vs. CMIP3. *Climate Dynamics*, **41**, 2921–2936.
- Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönišch, G. *et al.* (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. & 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.
- 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.
- 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.L., 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., van der Heijden, G.M.F. & Nepstad, D. (2011) The 2010 Amazon drought. *Science*, **331**, 554.
- 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.
- Malhi, Y., Aragão, L.E.O.C., Galbraith, D., Huntingford, C., Fisher, R., Zelazowski, P. *et al.* (2009) Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proceedings of the National Academy of Sciences*, **106**, 20610–20615.
- Marksteijn, 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.
- Marksteijn, 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., Holttta, T., Mackay, D.S. *et al.* (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.
- Moullot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M. *et al.* (2013) Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biology*, **11**, e1001569.
- Nepstad, D.C., Moutinho, P., Dias-Filho, M.B., Davidson, E., Cardinot, G., Markewitz, D. *et al.* (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. *et al.* (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. *et al.* (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. *et al.* (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. *et al.* (2013) Confronting model predictions of carbon fluxes with measurements of Amazon forests subjected to experimental drought. *New Phytologist*, **200**, 350–365.
- Prentice, I.C., Dong, N., Gleason, S.M., Maire, V. & Wright, I.J. (2014) Balancing the costs of carbon gain and water transport: testing a new theoretical framework for plant functional ecology. *Ecology Letters*, **17**, 82–91.
- Quesada, C.A., Lloyd, J., Schwarz, M., Baker, T.R., Phillips, O.L., Patiño, S. *et al.* (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.S., Harris, N.L., Brown, S., Lefsky, M., Mitchard, E.T.A., Salas, W. *et al.* (2011) Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences*, **108**, 9899–9904.
- Saatchi, S., Asefi-Najafabady, S., Malhi, Y., Aragão, L.E.O.C., Anderson, L.O., Myneni, R.B. *et al.* (2013) Persistent effects of a severe drought on Amazonian forest canopy. *Proceedings of the National Academy of Sciences*, **110**, 565–570.
- Sabatier, D., Grimaldi, M., Prévost, M.-F., Guillaume, J., Godron, M., Dosso, M. *et al.* (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., Jaikummar, N. & Holbrook, N.M. (2003) The 'hydrology' of leaves: co-ordination of structure and function in temperate woody species. *Plant, Cell and Environment*, **26**, 1343–1356.
- Sack, L., Scoffoni, C., John, G.P., Poorter, H., Mason, C.M., Mendez-Alonzo, R. *et al.* (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. *et al.* (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*, **164**, 1772–1788.
- 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. *et al.* (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. *et al.* (2014) Toward a better integration of biological data from precipitation manipulation experiments into Earth system models. *Reviews of Geophysics*, **54**, 2014RG000458.
- Sokal, R.R. & Rohlf, F.J. (1987) *Introduction to Biostatistics*, 2nd edn. Freeman, New York.
- Ter Steege, H., Pitman, N.C.A., Phillips, O.L., Chave, J., Sabatier, D., Duque, A. *et al.* (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., Burrell, 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., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.
- Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K. *et al.* (2005) Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography*, **14**, 411–421.
- 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. *et al.* (2010) Angiosperm wood structure: global patterns in vessel anatomy and their relation to wood density and potential conductivity. *American Journal of Botany*, **97**, 207–215.
- 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.

Received 3 July 2014; accepted 27 March 2015

Handling Editor: Kaoru Kitajima

## Supporting Information

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

**Appendix S1.** Data set of estimated  $\pi_{\text{osm}}$  and  $\pi_{\text{tlp}}$  values for 165 trees in forests French Guiana.

**Fig. S1.** Correlation between leaf drought tolerance ( $\pi_{\text{tlp}}$ , in MPa) and several structural soft traits.