[1]Tree intraspecific adjustment of hydraulic traits explain changes in abundance from a clay to a sand soil forest savannah (Cerrado) in southwest Brazil

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ABSTRACT

Tree intraspecific adjustment of hydraulic traits explain changes in abundance from a clay to a sand soil forest savannah (Cerrado) in southwest Brazil

Plants occupy all of Earth is overwater surfaces. This is only possible because of the wide range of functional strategies they evolved to deal with different levels of conditions, resource availabilities and stresses. Arguably, the key axis of plant functioning is their water relations, as all other axis depends on this one. Thus, if we want to predict changes in vegetation formation and its consequent ecosystem process we need to understand how plants adapt their strategies to different environments. In this work, I study adjustment of hydraulic traits of seven Brazilian forest savannahs tree species that occur with different abundances in two contrasting soils a few kilometers apart only: a drier and nutrient poorer sand soil site and a wetter, nutrient richer clay soil site. I test the hypothesis that 1) tree species adjust hydraulic traits to be more drought resistant in the sand soil than in the clay soil site and 2) the level of adjustment of tree species to the sand soil in relation to the clay soil site determine their change in dominance in the sites. To test the hypothesis, I study three hydraulic traits that integrate water demand control (minimum foliar conductance, g_{min}), water demand to water supply (leaf area to sapwood area, LX) carbon and water transport (phloem area to xylem area, PX). I find a large diversity in the studied traits, with g_{min} varying 7 to 8 times. There was no directional adjustment of hydraulic traits to the clay or sand soil sites, rather the direction of adjustment of PX explained the change in dominance of each species from one site to another. I discuss consequences of adjustment at species level and why PX is possible an important integrator of plant hydraulic functioning.

Introduction

Despite the huge variability of terrestrial ecosystem environments plants colonized all latitudes and longitudes where overwater surfaces occurs. This was only possible due to the high diversity of functional strategies plants evolved to deal with different levels of resource availabilities and stresses. By covering much of terrestrial surfaces plants became key factors modulating the planet is biogeochemistry, mainly through their effects on hydrological regimes (Jasechko *et al.* 2013; Bloom *et al.* 2016). With a large portion of the earth surface altered by mankind and global changes forecasted to intensify thermal and drought stresses (Lawrence & Vandecar 2014; Donat *et al.* 2016), to predict the consequences to earth systems and anticipate social and economical impacts we need to understand how plants adapt to different environments (Matheny *et al.* 2016).

The most important functional axis plants have to adapt to occur in different environments is their water relations as all other axis depends on this one. Carbon assimilation requires the plant to lose huge quantities of water in leaves which must be readily transported from roots in the soil though the plant water supply system in the xylem to prevent leaf desiccation (Sperry *et al.* 2002). Despite more than a hundred years of research, there are still many things we do not know about how plants transport water. We know that water is transported under tension, with liquid water inside leaves being pulled by the dry atmosphere, causing transpiration, and the pull being transmitted through the plant water column until the water bonded to soil particles, which are then pulled to leaves and replace the lost water (Cruiziat *et al.* 2002). As water is bonded to soil particles, they also pull the water column towards it making soil water availability strongly affect plants. Water in the plant is thus like a rope in a tug-of-war, being pulled on one side by the atmosphere and on the other by the soil. As a rope, it can also break, causing hydraulic failure (Tyree 2003). Although we know the general processes, we do not have a good knowledge of how plants water relations are adapted to different environments.

Plant water relation strategies occur at different levels. Morphological and allometric changes in leaf area in relation to root and stem areas can change water

demand and supply relations (Mencuccini & Bonosi 2001). Anatomical traits like stomata size and density can change plant control over transpiration (Fanourakis *et al*. 2015). Xylem conduits traits can reduce or increase water supply capacity and the tensioning of the plant water column plants can withstand (Cruiziat *et al*. 2002). Physiological traits, like cuticle composition can change how much plants can uncouple the leaf from the atmosphere Burghardt (2003) and modulation of xylem water composition may also change water supply capacity (Nardini *et al*. 2012). Plants have to modulate and integrate those three levels of function to match their water relations to the environment.

In this work, I study how tree species adjust their traits to occur in different environments and how this affect their abundance. I evaluate three traits that modulate plant hydraulic water and carbon functioning: leaf area to xylem area (LS), phloem to xylem area (PX) and minimum foliar conductance (g_{min}). LS is a proxy of plant water demand in the leaves and plant water supply through the xylem; although plant carbon transport is not well understood, it does occur through the phloem and PX is thus an indicator of investment in carbon transport in relation to water transport. g_{min} is the minimum conductance a plant can achieve, or, in other words, the maximum control it has over transpiration and determines unavoidable transpiration. g_{min} is determined by leakages in closed stomata and cuticular conductance. I study how those three traits changes in the same forest savannah species in two contrasting soil types only a few kilometers apart: a sand, nutrient poor site and a clay nutrient rich site and with more water holding capacity than the sand site.

I test the following hypothesis with the following predictions: 1) Tree species adjust their hydraulic traits to be more drought resistant in the sand soil than in the clay soil site. I predict PX and G_{min} will be lower and PX higher in the sand soil than in the clay soil site. 2) Species that adjust their hydraulic systems to be more drought resistant in the sand soil than in the clay soil site also increase in abundance in the sand soil. I predict that species adjustment in PX, G_{min} and LS from the clay site to the sand soil explain their different abundance in the two sites.

Material and Methods

Study site - I studied two forest savannahs (Cerradão) in Horto Florestal de Itirapina (22º15'10"S 47º49'22"W), southwest Brazil, municipality of Itirapina, that occurs 3 kilometers apart from each other. Meteorological data from a Instituto Nacional de Meteorologia weather station (2008-2016 period) in the neighbor city of São Carlos indicates mean annual air temperature of $20.7 \pm 4.6\ ^{o}C$ (mean ± standard deviation), relative humidity of 69.6 ± 18.9 % and incident solar radiation of 1395 ± 1072 kJ m^{-2} (Fig. 1 a-c). Mean total annual rainfall is 1506 with 69% of it occurring from November to March and a dry period from May to September where monthly rainfall is less than 60mm (Fig. 1d). Frost may occur in the winter.

In both sites surveys of trees with more than 10 cm perimeter at ground level are conducted annually since 2010 using the quadrant method (Bryant *et al*. 2004) with 100 quadrants per area (Martins & Santos, unpublished data). The clay soil forest savannah (Vermelhão) has 348 individuals per hectare, tree basal area 2.25 m^2 ha^{-1} and tree height of 5.4±3.0 m with canopy occurring approximately at 10 m height. The sand soil forest savannah (Valério) has 280 individuals per hectare, tree basal area 2.41 m^2 ha^{-1} and tree height of 4.4±3.1 m with canopy occurring approximately at 8 m height. The clay soil site has 161 species from 51 families while the sand soil site has 103 species from 36 families. Despite the high diversity, 15 species represent 61% and 86% of tree basal area in the clay and sand soil sites, respectively.

Species used and plant material collection - I selected seven tree species from different families that occur in both the clay and sand soil sites but with different relative dominances (Table 1). Relative dominances (i.e. percentage basal area of each species in relation to total tree basal area per hectare) were calculated using the 2010-2017 surveys pooled together and excluding quadrants that were less than 35 meters from the forest border due to difference in composition at border. The relative dominance is thus based on a 1960 individual trees survey per site.

For each species in each site I selected five individuals with similar perimeter and height and the same canopy position (Table 2). From each individual I collected in the

days 29th and 30th January 2017 terminal branches of first or second order, counting from top to bottom, with approximately 4-7mm diameter and with all their leaves. All terminal branches were kept in a moist plastic bag to avoid desiccation, transported to laboratory and processed on the day of collection.

Minimum foliar conductance - To ensure stomata of leaves in collected terminal branches were closed, I dehydrated branches for one hour in the shade at ambient conditions and then I stored them again in plastic bags. The one hour desiccation time was chosen to allow for stomatal closure without drying to much leaves and affecting leaf area measurements. I measured minimum foliar conductance (g_{min}; $\mu mol\ m^2\ s^{-1}$) in abaxial and adaxial surfaces of two leaves per branch using an infra-red gas analyzer (Licor 6400) in the dark, at room conditions (air temperature and relative humidity of 28-32 ^{o}C and 40-55%) and with a CO^2 supply of 400ppm. I carefully calibrated the equipment and matched reference and sample infrared gas analyzers after each individual was measured to ensure accuracy of the low foliar conductance measured with closed stomata. Conductances measured with closed chamber and without leaves were approximately $\pm\ 2\mu mol\ m^2\ s^{-1}$.

Leaf to sapwood area and phloem to xylem - After I measured g_{min}, I photographed all leaves distal do the terminal branch with a regular camera (Sony a6000) together with a ruler to set scale. I flattened curved leaves and set camera horizontally above the leaves to ensure no distortion of areas on the photos. I used ImageJ image analyzer (Schneider *et al*. 2012) to threshold leaves by color and then measure their area. To measure pit, xylem and phloem areas I made a fine transversal cut of the basal stem of the terminal branches with a sharp razor. I placed the transversal cut in a stereomicroscope and used a digital caliber (0.01mm precision) to measure pit diameter, pit plus xylem diameter, and pit plus xylem plus phloem diameters. I used the diameters to calculate the xylem and phloem areas by subtracting pit area for the xylem area and pit and xylem area for the phloem area. There was no heartwood in any of the branches. Leaf to sapwood area (LX; mm^2 mm^{-2}) was calculated dividing one sided leaf area by xylem area in the branch base and

phloem to xylem area (PX; mm^2 mm^{-2}) was calculated dividing phloem area by xylem area.

Analysis - I processed and analysed all data using R environment with base packages (R Core Team 2014). For each species in each area I calculated mean and standard deviations using the five individual analyzed. I checked for correlations between the studied variables using Pearson correlations. To test hypothesis 1) predictions I used paired T-tests of species mean g_{min}, LX and PX with site as factor. To test hypothesis 2) predictions, first I calculated the change in relative dominance, g_{min}, LX and PX (ΔRD, Δg_{min}, ΔLX and ΔPX, respectively) of the species in the clay site in relation to the sand site as:

1) $\Delta X = -(X_{clay} - X_{sand})$

Where X stands for the analyzed variable and the subscripts indicate the area. The minus sign outside the parenthesis is used to facilitate comprehension of the values. A ΔX of 0 indicates the variable has not changed between the two areas; ΔX higher than 0 indicates the variable has increased from the clay to the sand soil; and ΔX lower than 0 indicate the variable has decreased from the clay to the sand soil. I tested hypothesis 2) predictions using linear regressions with ΔRD as the response variable and Δg_{min}, ΔLX and ΔPX as predictors.

Results

We found a high variation in the analyzed traits (Table 2). Species LX was 6019 ± 2032 mm^2 of leaves per mm^{-2} of xylem and was highest in *X. aromatica* (9519 ± 2037 mm^2 mm^{-2}) and lowest in *O. pulchella* (3601 ± 1325 mm^2 mm^{-2}). Species PX was 0.74 ± 0.29 mm^2 of phloem per mm^2 of xylem and was highest in *X. aromatica* (1.27 ± 0.52 mm^2 mm^{-2}) and lowest in *S. guianensis* (0.44 ± 0.10 mm^2 mm^{-2}).

g_{min} of *X. aromatica* and *D. miscolobium* was 5 to 10 times higher than other species and, following a desiccation test I did, kept decreasing after further desiccation, indicating that the species were still with open stomata (Fig. 2). Those two species had similar conductance in abaxial and adaxial faces, indicating they have stomata in both faces. As we could accurately measure g_{min} of those two species we discarded them from further analysis of g_{min}. For all other species, g_{min} in the abaxial and adaxial faces were strongly related ($F_{(1,49)} = 1024$; $r^2 = 0.95$; $p < 0.001$; regression forcing intercept to zero) and we then only used g_{min} of leaf abaxial surfaces in further analysis. g_{min} ranged from 5.1 to 38.3 μmol m^2 s^{-1}, being highest in *Q. grandiflora* (27.2 ± 20.9) and lowest in *P. glabrata* (10.6 ± 5.8).

Clay and sand soil effect on traits - Clay and sand soils had no effect on species g_{min} (paired T-test t = -0.87; df = 4; p = 0.44), on LX (paired T-test t = -0.08; df = 6; p = 0.94) and on PX (paired T-test t = -1.10; df = 6; p = 0.32; Fig. 3).

Trait adjustment effect on relative dominance - Adjustment of species g_{min} from clay soil site to sand soil site (Δg_{min}) did not explain changes in species relative dominance from clay soil site to sand soil site (ΔRD; $F_{(1,3)} = 0.84$; p = 0.43; Fig. 4). ΔLX also did not explain changes in ΔRD ($F_{(1,5)} = 3.1$; p = 0.14) however, when not considering *X. aromatica* ΔLX strongly explained ΔRD ($F_{(1,4)} = 13.0$; $r^2 = 0.77$; p = 0.022). ΔPX explained much of ΔRD variation ($F_{(1,5)} = 34.8$; $r^2 = 0.88$; p = 0.002). As species PX variation is not determined by xylem area ($F_{(1,12)} = 1.8$; p = 0.20) but in a large part by phloem area ($F_{(1,12)} = 9.6$; $r^2 = 0.45$; p = 0.009), we can assume most of the variation in PX is due to phloem variation and ΔPX explaining ΔRD is mostly because of phloem area adjustments.

Discussion

   I have found substantial functional diversity of the studied traits in seven species analyzed. Despite the contrasting sites with clay and sand soils, there was no trait selection by the two sites at the species level. Rather than a trait selection, the direction that each species adjusts their traits explained how much their relative abundance changed between the clay and sand soil sites.

Diversity of minimum foliar conductance - Hydraulic failure of plants water transport system occurs when tension in xylem conduits exceed the maximum tension that conduit can withstand (Cruiziat *et al*. 2002). This can happen because of soil water stress, atmospheric water stress and their combinations (Sperry & Love 2015). Soil water stress is avoidable if plants can have access to deeper soils with higher water content. Atmospheric water stress is only avoidable in as much as plants can uncouple themselves from the atmosphere. I have shown that g_{min}, the minimum conductance plants can have or, in other words, the maximum control over transpiration they can have, can vary 8 times from the species with most control *P. glabrata*, to the one with the least, *Q. grandiflora*. This effectively implies that unavoidable transpiration per leaf area in *Q. grandiflora* is 8 times higher than *P. glabrata*. Very few studies have studied hydraulic failure in terms of how much a plant can uncouple itself from the atmosphere and at which conditions control of transpiration fails. My data shows g_{min} can vary significantly between species and seems to be driven mainly by leafcuticle properties, given the almost perfect correlation between adaxial and abaxial g_{min}. g_{min} and cuticle traits may be important trait, together with other forms of transpiration control like changes in leaf angle and leaf area, determining failure of transpiration control.

Soil type does direct intraspecific trait adjustment, but direction of trait adjustment explains changes in relative dominance between soil types - I have found no relationship between any of the analyzed traits, which are proxies of water supply, water demand and demand control, and the type of soil in the same species. This leads me to reject my hypothesis 1), that there is a directional adaptation to more drought resistant hydraulic

systems in sand soils, although it is still possible that adaptations at physiological and anatomical levels may be occurring. It will be interesting to check if directional adaptation occurs at the genus or family level, as higher genetic diversity may allow for more variability in traits.

My data however shows that, at the same species level at least, the direction each species adjust their traits explains how much its dominance changes between the clay and sand soils. Species that kept the same PX did not change in dominance between sites while those that increase PX from clay to sand decreased in dominance and those that decreased PX increased in dominance (Fig. 4c). However the same pattern was not found considering g_{min}, suggesting cuticle properties may be much more conserved or less important to determine dominance (Fig. 4a) and was only found for LX when *X. aromatica* was excluded from the analysis (Fig. 4b). Following those results I accept partially my hypothesis 2), thus, adjustment of some hydraulic traits, and not all of them, to increase drought resistance drive increase in dominance from the clay to the sand soi.

According to my data, PX strongly explained changes in dominance of the studied species and PX is driven mostly by phloem area changes. My result thus shows that higher abundance in sand sites was related to adjustments diminishing phloem area and/or increasing xylem area. Phloem has a myriad of not well understood functions (Savage *et al.* 2016), but is known to coordinate with shade tolerance (Zhang *et al.* 2016). As much as 20 to 50% of all carbon assimilates by plants are transported to roots so plants that assimilate much carbon have to transport much carbon (Epron *et al.* 2012). Carbon transport outside of the leaf is considered as one of the limiting factors of photosynthesis because transport of carbon outside the leaf has to match carbon assimilation (Savage *et al.* 2016). My result seems them to suggest carbon transport is less important than water transport in the sand soil site than in the clay soil site and species that decreased investment in carbon transport while maintaining or increasing investment in water transport increased in dominance in the sand soil site.

Why ΔPX was significant and ΔLX not is intriguing. The fact that ΔLX explained almost equally well ΔRD as ΔPX after removal of *X. aromatica* indicate either a limitation of the low number of samples or a limitation of LX as an indicator of leaf water supply and demand relations. My measurements were carried out during the wet

season, when water limitation does not occur, I wonder whether LX values would be much different where I to measure LX during the dry season, when reduction in leaf area possible occurs. While changes in leaf area may lead to variation in LX during the year, PX probably does not vary so much during the year and the phloem area may be a better integrator of year around leaf area, transpiration and carbon assimilation. It will be very important to test how plants coordinate leaf, phloem and xylem area though the year and which functions phloem area integrate.

Conclusion - Soil type leads to different water and nutrient resource availability. Although there is a diversity of interespecific hydraulic trait variability, dryer and poorer sand soil is not selecting more drought resistant hydraulic traits than wetter and richer clay soils at the intraspecific level. A diversity of directions or absence of changes in hydraulic traits is occurring. Species that can adjust to have lower phloem area to xylem area become more dominant in the sand site than in the clay site. Finding out which functions phloem area and xylem area integrate or coordinate may be important next steps the limits of species distribution.

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Tables

Table 1. Relative dominance (%), mean perimeter at soil height (m) and mean height (m) of the studied species accoding to the 2010-2017 surveys. C indicates the clay soil site and S the sand soil site.

Species	Family	Relative dominance (%)		Perimeter (m)		Height (m)	
		C	S	C	S	C	S
Amaioua guianensis	rubiaceae	1.9	2.2	0.22	0.32	5.4	5.6
Dalbergia miscolobium	fabaceae	2.2	7.5	0.13	0.53	2.9	7.9
Ocotea pulchella	lauraceae	1.9	3.3	0.29	0.21	7	3.6
Pera glabrata	peraceae	4.7	2.2	0.31	0.31	6.9	6.9
Qualea grandiflora	vochysiaceae	0.8	3.4	0.26	0.42	4.1	6.6
Siparuna guianensis	siparunaceae	4.7	0.3	0.13	0.14	4.7	4.8
Xylopia aromatica	annonaceae	1.1	8.9	0.18	0.22	4.1	4.8

Table 2. Perimeter at soil height (PSH, m), height (m) minimum foliar conductances (g_{min} µmol m^2 s^{-1}) of abaxial and adaxial leaf surfaces, leaf area to xylem area (LX, mm^2 mm^{-2}) and phloem to xylem area (PX, mm^2 mm^{-2}) of the seven studied sites at the clay and sand soil sites.

Species	PSH (m) Clay	PSH (m) Sand	Height (m) Clay	Height (m) Sand	Gmin abaxial (µmol m^2 s^{-1}) Clay	Gmin abaxial (µmol m^2 s^{-1}) Sand	g_{min} adaxial (µmol m^2 s^{-1}) Clay	g_{min} adaxial (µmol m^2 s^{-1}) Sand	LX (mm^2 mm^{-2}) Clay	LX (mm^2 mm^{-2}) Sand	PX (mm^2 mm^{-2}) Clay	PX (mm^2 mm^{-2}) Sand
Amaioua guianensis	0.23 ± 0.05	0.36 ± 0.08	7.7 ± 0.8	7.4 ± 1.3	15.7 ± 5.1	13.6 ± 5.7	16.6 ± 5.5	13.7 ± 4.4	5603 ± 1592	4007 ± 1074	0.52 ± 0.19	0.53 ± 0.19
Dalbergia miscolobium	0.49 ± 0.14	0.37 ± 0.07	8.6 ± 1.3	8.3 ± 1.9	108.8 ± 47.2	184.1 ± 50.9	112.5 ± 47	174.4 ± 51.5	3713 ± 1669	6586 ± 2470	0.95 ± 0.32	0.88 ± 0.29
Ocotea pulchella	0.44 ± 0.17	0.49 ± 0.08	7.8 ± 1.5	9.1 ± 1	12.5 ± 7.6	15.1 ± 4.6	11.4 ± 6.2	13 ± 3.1	3391 ± 1165	3812 ± 1575	0.56 ± 0.08	0.58 ± 0.09
Pera glabrata	0.73 ± 0.22	0.56 ± 0.15	12.3 ± 1	11.8 ± 2.2	11.6 ± 8.3	9.5 ± 1.7	10.3 ± 5.8	9.1 ± 1.6	6783 ± 2359	6532 ± 958	0.64 ± 0.17	0.61 ± 0.25
Qualea grandiflora	0.55 ± 0.05	0.42 ± 0.08	10 ± 1.6	7.5 ± 1.3	30.8 ± 29.5	23.5 ± 8.6	39.6 ± 37.1	27.7 ± 10.1	4661 ± 1379	5763 ± 1567	0.87 ± 0.5	0.75 ± 0.19
Siparuna guianensis	0.08 ± 0.01	0.1 ± 0.02	4.9 ± 0.4	3.9 ± 0.7	10.6 ± 2.3	11.9 ± 3.7	10.2 ± 3.8	11.6 ± 3.4	8192 ± 2551	6184 ± 1345	0.38 ± 0.09	0.5 ± 0.07
Xylopia aromatica	0.17 ± 0.06	0.25 ± 0.04	6.2 ± 2.1	8.3 ± 1	75.8 ± 41.5	76.5 ± 35.4	78.5 ± 42.6	99.3 ± 71.1	9607 ± 1442	9430 ± 2689	1.45 ± 0.47	1.09 ± 0.56

Figures

Figure 1. Regional climate for the 2008-2017 period. a) Hourly air temperature (^{o}C); b) hourly relative humidity (%); c) hourly incident solar radiation (kJ m^2); and d) monthly total rainfall (mm).

Figure 2. Relationship between minimum foliar conductances (G$_{min}$; μmol m^2 s^{-1}) of abaxial and adaxial leaf surfaces of the studie species. The dashed red line separates values that are considered as correctly measured bellow it from the ones where G$_{min}$ was not correctly measured above. The black line is the linear regression with 0 intercept of the data bellow the dashed red line. Red and blue data points indicate data from the clay and sand soil sites, respectively. Letters indicate the species of the datum: A – *Amaioua guianensis*, D – *Dalbergia miscolobium*, O – *Ocotea pulchella*, P – *Pera glabrata*, Q – *Qualea grandiflora*, S – *Siparuna guianensis* and X – *Xylopia aromatica*.

Figure 3. Paired species comparisons of the analysed traits between the clay and sand soil sites. a) minimum foliar conductance (G$_{min}$; μmol m^2 s^{-1}); b) leaf area to xylem area (LX; mm^2 mm^{-2}); and c) phloem area to xylem area (PX; mm^2 mm^{-2}). Letters indicate the species of the datum: A – *Amaioua guianensis*, D – *Dalbergia miscolobium*, O – *Ocotea pulchella*, P – *Pera glabrata*, Q – *Qualea grandiflora*, S – *Siparuna guianensis* and X – *Xylopia aromatica*.

Figure 4. Change in relative dominance (ΔRD, %) as a function of adjustment of species hydraulic traits from the clay to the sand soil site. a) ΔRD as a function of minimum foliar conductance (G$_{min}$; μmol m^2 s^{-1}); b) ΔRD as a function of leaf area to xylem area (LX; mm^2 mm^{-2}); and c) ΔRD as a function of phloem area to xylem area (PX; mm^2 mm^{-2}). Red dashed lines indicate 0 values for y and x axis, i.e. data over red lines have not changed ΔRD or adjusted hydraulic traits from clay to sand soil sites. Black line is the best fit linear regression. Letters indicate the species of the datum: A – *Amaioua guianensis*, D – *Dalbergia miscolobium*, O – *Ocotea pulchella*, P – *Pera glabrata*, Q – *Qualea grandiflora*, S – *Siparuna guianensis* and X – *Xylopia aromatica*.