Sensitivity of tropical trees to drought stress and the implications of the responses of tropical forest to climate change

Thesis submitted towards the partial fulfilment of BS-MS Dual degree programme

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Certificate

This is to certify that this dissertation entitled “Sensitivity of tropical trees to drought stress and the implications of the responses of tropical forest to climate change” towards the partial fulfillment of the BS-MS dual degree programme at the Indian Institute of Science Education and Research (IISER), Pune represents the study/work carried out by Kausal A K at IISER Pune and Kerala Forest Research Institute (KFRI), Peechi under the Co-supervision of Dr. Deepak Barua, Associate professor, Biology department, IISER Pune, and Dr. Sreejith K A, Senior scientist, Forest Ecology department, KFRI Peechi, during the academic year 2019-2020.

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Declaration

I hereby declare that the matter embodied in the report entitled "Sensitivity of tropical trees to drought stress and the implications of the responses of tropical forest to climate change" are the results of the work carried out by me at the Department of Biology, Indian Institute of Science Education and Research (IISER), Pune and Forest Ecology department of Kerala Forest Research Institute (KFRI), Peechi under the co-supervision of Dr. Deepak Barua, associate professor, Biology department, IISER Pune, and Dr. Sreejith K A, Senior Scientist, Forest Ecology department, KFRI Peechi. The same has not been submitted elsewhere for any other degree.

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Contents

P.no

Abstract

Tropical Species are expected to be adversely affected by the increased frequency in drought due to climate change.While being a hotspot for biodiversity as well as impact of climate change, the flora of tropical India is underrepresented in the literature and not much is known about its response to drought stress to understand and predict the sensitivity to future changes in climate. In this study stem and leaf hydraulic traits of 20 tree species from a moist deciduous forest in south western ghats were measured. Xylem vulnerability to embolism agreed with reports from studies on similar ecosystems across the world, if not slightly shifted towards higher resistance to embolism. Leaf and stem hydraulic traits showed a broad range.While xylem vulnerability to cavitation and leaf rehydration capacity had a positive correlation with leaf and wood functional traits like Leaf mass per area (LMA), Leaf dry matter content (LDMC) and Wood density (WD), with more resistant species having a higher structural investment, species with a resistant chlorophyll response to drought showed lower structural investment. Both these observations are in agreement with the existing leaf economy and slow-fast resource acquisition spectrum. Xylem vulnerability analysis also hinted at the contribution of non structural features like presence of latex and resin to resist embolism formation in xylem.

List of Figures

Acknowledgements

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Introduction

Forest ecosystems cover approximately 30.6 % (3999 million ha) of earth's land surface area (FAO. 2015), of which more than half the canopy cover belongs to the tropical systems (Song et al., 2018). Tropical forests, housing more than 50% of the earth's biodiversity, play the most important role in maintaining the biosphere functions that sustain life on this planet. Tropical forests act as sinks for sequestering carbon in the form of biomass and keeps the carbon cycle balanced while keeping ecosystem productivity high (Malhi et al., 2000 ; Lewis et al., 2019).

The global climate changes, accelerated by events including anthropological intervention, is predicted to bring about a 1 to 4 ^{o}C increment in global surface temperature by the twenty second century. Other predicted events include increased drought, heat wave frequencies , rainfall anomalies, and have already been recorded for the past couple of decades (IPCC, 2014). Increased magnitude of precipitation (Trenberth et al., 2003) and reduced frequency of rainfall (Sun et al., 2007) can increase the runoff - precipitation ratio. Increased surface air temperature and radiative heating can lead to a higher atmospheric demand for moisture. Coupling both the runoff-precipitation ratio and atmospheric demand, the soil moisture will remain low even if the precipitation increases due to higher temperature, and will result in severe droughts (Dai, 2010). Such drought events have resulted in increased observations of tree mortality across the world (Allen et al., 2010; Peng et al., 2011; Allen et al., 2015; Fettig et al., 2019).

Flora, having a sessile lifestyle, get the bitter end of the stick as they cannot (unlike fauna) actively search out for a different micro or macro habitat with favourable extremes. Trees and plants of the tropics are under greater threat due to the lack of existence of significant seasonal variability, resulting in the organisms evolutionarily confined to a narrow tolerance range (Stevens,1989). Indian tropical forests account for 11% of the world's flora (Chitale et al., 2014), but are seriously underrepresented in the scientific literature and are waiting to be explored. Tropical wet deciduous forests (37% of total forest cover) and tropical dry deciduous forests (28.6% of total forest cover) are the two major forest ecosystems in India (National Wasteland Development Board, 1988).

Understanding the underlying mechanisms and patterns of plant response to heat and drought stress is important to model and mitigate the situation. As stated before, the Flora of Indian subcontinent is underrepresented in the global data models while the tropical-subtropical spatial range is expected to be adversely affected by climate changes. Hence a tropical moist deciduous forest of south- western ghats (Chandrasekharan, 1962) were chosen as the study system to understand their susceptibility to changing climate conditions with focus on drought.

Drought is a climate extreme characterised by below normal precipitation over a period of time (Sun et al., 2007), resulting in a fall in soil moisture content. Drought affects stomatal conductance (Irvine et al.1998), dark respiration (Gimeno et al., 2010), photosynthesis (Pinheiro et al., 2010) etc. Two hypotheses prevail about the response that is the key player in drought induced tree mortality : a) hydraulic failure and b) carbon starvation (Sala et al., 2010). While the evidence for carbon starvation is not universal, hydraulic failure due to xylem embolism has emerged as the primary reason for mortality from experimental data (Adams et al., 2017).

A xylem vulnerability curve traces the relation between embolism formation (change in hydraulic conductance)with respect to xylem water potential (P_x). Embolised air is sucked out from defined branches across varying water potentials. In a healthy plant, air exists inside the xylem vessels, pulled in through pores in the pit membrane, in the form of nano bubbles. During a drought, when the molecular water availability decreases, P_x becomes more negative causing the air bubbles to break within the xylem and create large air pockets i.e., embolism, disrupting the continuous root to shoot water column (Pereira et al., 2016; Adams et al., 2017). Hence water potential at which 50% of xylem vessels are embolized (50% loss of conductance), P_{50} , can be used as a hydraulic trait to compare the drought tolerance between two plant/tree species(Pereira et al., 2016).

It is important to understand the present P_{50} values of the dominant tree species in an ecosystem to figure out the range and fundamental niche of the individual species as well as the ecosystem average. Hydraulic safety margin, HSM , is the difference between the observed P_{50} value and the minimum water potential, P_{min} experienced by the given species in its habitat (Delzon and Cochard, 2014). The breadth of the margin can give insights into future tree mortality(narrow margin ,the greater risk to individual species)(Anderegg et al.,2016) as well as identify existing drought tolerators and at risk groups(negative HSM). Twenty dominant tree species belonging to the moist deciduous ecosystem of south western ghats were chosen to address the above questions.

Drought tolerant species exhibit tissue rehydration capabilities to an extent (Salleo et al.,1997). Such a trait is the ability of leaf rehydration capacity (Oppenheimer et al.,1963). Leaf rehydration capacity decreases as Relative Water Content (RWC), the amount of cellular water present in a leaf falls from 100% to 0%. A complete irreversible loss of rehydration capacity occurs at lower RWCs (Oppenheimer et al.,1966). Limiting cellular water content also affects the photochemistry of the leaf, creating oxidative stress within chloroplast resulting in irreversible loss of photosystem functionality (Lima et al., 2002). Chlorophyll fluorescence, measured as variable to maximum fluorescence ratio : Fv/Fm (Valladares and Pearcy,1997 ; Baker, 2008 ; Buchner, 2017) is a direct measure of efficiency for photosystem II photochemistry (Maxwell and Johnson,2000).

RWC at which the rehydration capability drops by 50% (Percentage Loss of Rehydration Capacity; PLRC) and chlorophyll fluorescence drops by 50% (Percentage Loss of Chlorophyll Fluorescence; PLCF) from that of a healthy leaf, abbreviated as RWC_{PLRC50} and RWC_{PLCF50} respectively in this document, is used to compare species based on how tolerant their leaf photochemical system and conductive vasculature is to drought. RWC_{PLRC50} and RWC_{PLCF50} along with analysing long term drought tolerance are also helpful in analysing the resistance to spontaneous events like a heatwave or a heat burst that affects leaf tissues adversely within a short period. Same twenty species chosen for hydraulic trait measurement were considered for the experiment.

Leaf functional traits like leaf mass per area (LMA) and leaf dry matter content (LDMC) reflects structural carbon investment in leaf tissues and is helpful in identifying the location of a given species in the slow-fast resource acquisition and utilization spectrum (Wilson et al.,1999; Wright et al.,2005). LMA and LDMC are expected to show a positive correlation to stress tolerance as higher LMA and LDMC species have a greater structural investment and longer leaf lifespan (Wright et al.,2005). Wood density (WD) is another functional trait that determines the structural investment resulting in a fast growing vs higher lifespan tradeoff (King et al., 2006). A positive correlation between WD and resistance to cavitation may exist(Wang et al. 2003) or can be dependent on other conditions like climate, genetics and geography(Corcuera et al., 2011)

Thus the study aims to measure the P_{50} , identify and compare the range of observed P_{50} values with different sites across the world, and calculate the hydraulic safety margins to understand the direction in which the ecosystem changes with respect to the predicted climate change models. It also aims to measure RWC_{PLRC50} and RWC_{PLCF50} values, identify and compare the range with different sites across the world if published data exist. Whether these traits are correlated to the measured leaf and wood functional traits will give an insight to their present strategy and how the future changes may affect the ecosystem functions.

Materials and methods

Study site and sample description

Twenty tree species were sampled from the moist deciduous forest around KFRI-Peechi campus(10°53'N and 76°34'E) lying in the outskirts of Peechi-Vazhani wildlife sanctuary (between latitudes 10°26'N - 10°40'N and longitudes 76°15'E - 76°28'E) in Thrissur District of Kerala State, India . Mean annual precipitation of the region is 3,000mm (Iqbal et al., 2016).The mean maximum monthly temperature ranges from 32°C (August) to 38°C (April) and the minimum from 2O°C (January) to 23.5°C (April). The area has a warm humid climate with rainfall from May to October followed by a generally dry spell from November to April (Mohan Kumar & Deepu, 1992). Dry summer season lasts 3-4 months from January to April. The impact of climate change from the past couple of years over this region is still unclear and under investigation. *Xylia xylocarpa and Terminalia paniculata* exhibit very high dominance in the region leaving other species far behind in relative density studies in the area. Vegetation analysis by Menon et al., 2010 , puts the relative density of *Xylia xylocarpa* at 23.11 and of *Terminalia paniculata* 10.68 over their study area of Peechi-Vazhani. Existing lab data of Peechi from previously laid hundred quadrats of 10x10m size was used, data collected on all individuals having more than 10 cm in diameter. Dominant species were listed out.

Fully elongated mature leaf and stem samples were collected from mature individuals at dusk to minimize native embolism and were water saturated overnight (12-16 h) in opaque airtight containers made of water buckets and black bin bags, maintaining a constant vapour pressure inside.

Xylem Vulnerability

The methodology for generation of xylem vulnerability curve developed by (Pereira et al.,2016) was followed. Overnight water saturated branches were cut at one end, making the sample length roughly around 30 cm, leaks sealed with glue. All this was done with minimized exposure of the branch to the atmosphere, inside an opaque bag with a wet towel to maintain a constant vapour pressure. The cut end of the branch was attached to a three way stop cork which in turn was attached to a pneumatic apparatus to measure the xylem conductance. The pneumatic apparatus consist of a defined vacuum/negative pressure source applied to the cut end of the branch. Once connected, change in pressure in the source was measured for a standard time of 2:30 min. The air discharge from the branch (change in negative pressure) was measured using a pressure sensor connected to a voltmeter output, which will be proportional to the embolism present in the xylem which in turn is inversely proportional to xylem conductance. Simultaneously the water potential, P_x of the branch was measured using a PMS pressure chamber model 615 D. For this an excised leaf from the same branch is inserted into the pressure chamber with the petiole sticking out. When the pressure inside the chamber equates to the current value of P_x ,Free water is pushed out through the vasculature in the petiole, and is made visible with the help of a hand lens or a portable microscope. Once this pressure is recorded for a given P_x , the branches are then bench dried progressively in increasing time intervals. Air discharge values are measured for the respective (falling) values of P_x for the given interval of drying, till a constant value of air discharge is observed from the branch (completely dried and embolized). One hour our equilibration under constant vapour pressure is given for the branch between each interval such that the leaf and xylem water potential reach an equilibrium after each session of drying. Percentage air discharge (PAD) is plotted against P_x , with a sigmoidal curve fitting as in Pereira et al.,2016. The equation $PAD=100/(1+\exp((a/25)(P_x–P_{50}))$ is fitted in the basic R package. Water potential P_{50} and P_{88} at 50% and 88% air discharge (half the value of upper asymptote) is extrapolated.

Percentage loss of Chlorophyll Fluorescence

Methodology followed as of (Trueba et al., 2019). From the overnight water saturated branches, healthy, mature and fully turgid leaves were selected and excised including the petiole for the assay. The fresh weight (Wf) of the leaves were weighed immediately after picking and each leaf was assigned and bench dried for a certain period of time (0,1,2,3,6,....108 hours). At the given hour, the dehydrated weight (Wde) of the leaf assigned to that hour is measured along with its chlorophyll fluorescence value Fv/Fm. Fluorescence measurements were done using Handy PEA, Hansatech instruments. Each chlorophyll measurement was taken after thirty minutes of dark adaptation using leaf clips and pouches. After Fv/Fm measurements, the leaves were oven dried for 72 hours and dry weight (Wd) were measured. Relative water content of each dehydrated leaf was calculated as

RWCde = 100 x [(Wde - Wd)/(Ws-Wd)]

Fv/Fm was plotted against RWCde using the dose response curve package (drc) in R. A 5 parameter drc was fitted to the plots and RWC at 50% fall in Fv/Fm (Half the value of upper asymptote) is extrapolated as $RWC_{fv/fm50}$.

Percentage loss of Rehydration Capacity

Methodology followed as of (Trueba et al., 2019). From the overnight water saturated branches, healthy, mature and fully turgid leaves were picked, excised at the petiole for the assay. The fresh weight (Wf) of the leaves were weighed immediately after picking and each leaf was assigned and bench dried for a certain period of time (0,1,2,3,6,....108 hours). At the given hour, the dehydrated weight (Wde) of the leaf assigned to that hour is measured and the leaf is inserted into a centrifuge tube with water for rehydration such that only the petiole is immersed. The tubes were kept inside an air tight - water saturated zip lock bag under constant vapour pressure and was covered by an opaque bag. After 24 hours of rehydration, Rehydrated weights were measured (Wre) and leaves were oven dried for 72 hrs to measure the dry weight (Wd).

Saturated water content of a fresh leaf is :

SWC f = (Wf - Wd)/Wd

Saturated water content of a rehydrated leaf is

SWC re = (Wre- Wd)/Wd

Percentage loss of Rehydration capacity was calculated as :

PLRC = 100 x [1 - (SWC re/SWC s)]

Relative water content of each dehydrated leaf was calculated as :

RWCde = 100 x [(Wde - Wd)/(Ws-Wd)]

PLRC was plotted against RWCde using the dose response curve package (drc) in R. A 5 parameter drc was fitted to the plots and RWC at 50% fall in rehydration capacity (half the value of upper asymptote) is extrapolated as RWC_{PLRC50} .

Leaf area was scanned using Canon CanoScan LiDE 400 flatbed scanner and measured using ImageJ software. Leaf mass per area, LMA was calculated as the ratio of leaf dry weight to leaf area. Leaf dry matter content, LDMC was calculated as the ratio of leaf dry weight to fresh weight. Wood density, wood mass to volume ratio, was calculated using wood immersion method in water (volume of wood immersed equals weight of water displaced upon immersion)

For statistical analysis, data was normalised where possible and to check the correlation between all individual traits under consideration, Pearson and Spearman correlation tests were used. Both the tests were run using the package ‘PerformanceAnalytics’ in R.

Results

From the xylem vulnerability curve (Figure 1, appendix Figure.S1) data, P_{50} ranges from -5.28 for *Aporosa cardiosperma* to -0.80 for *Wrightia tinctoria* (Figure 2) . The mean (non-dominance weighted) P_{50} for the ecosystem is -2.89 (+/- 1.12 SD). The three most dominant tree species of the ecosystem according to Menon et al., 2010: *Xylia xylocarpa* , *Terminalia paniculata* and *Grewia Tiliifolia* have a P_{50} of -3.93, -2.93 and -3.31 respectively. P_{88} , which is strongly correlated to P_{50} (0.96, both Spearman, r_s and Pearson, r_p coefficients , Figure 8,9.), follows a similar trend as it ranges from -8.45 for *Aporosa cardiosperma* to -1.11 for *Wrightia tinctoria*. *Xylia xylocarpa* , *Terminalia paniculata* and *Grewia Tiliifolia* have a P_{88} of -5.58, -4.80 and -5.21 respectively. P_{50} and P_{88} displays a weak linear inverse correlation with LDMC ($-0.40 < r_s, r_p < -0.50$). P_{50} has a very weak positive correlation with inverse log of wood density ($r_s = 0.42$, $r_p = 0.39$). P_{50} and P_{88} show a weak positive correlation to RWC_{PLRC50} ($0.39 <= r_s < 50$).

Leaf $RWC_{fv/fm50}$ values (Figure 3, appendix Figure.S2) range from 6.77% for *Tabernaemontana alternifolia* to 24.82% for *Macaranga peltata* (Figure 4). Non-normalised $RWC_{fv/fm50}$ displays a moderate positive correlation to log LA (r_s= 0.61), LDMC (r_s= 0.54) and a weak correlation to LMA (r_s= 0.48) (Figure 9) .

Leaf RWC_{PLRC50} values (Figure 5, appendix Figure.S3) have a broad range from 19.00% for *Pongamia pinnata* to 60.90% for *Dalbergia Lanceolaria* (Figure 6). RWC_{PLRC50} displays a moderate linear positive correlation with

log^{-1}(WD) (r_s =0.66 , r_p=0.56). LMA shows a linear positive correlation with LDMC (r_p =0.45) and LA (r_s =0.54 , r_p=0.46) (Figure 8 , 9).

Discussion

Very strong observation of a positive linear correlation between P_{50} and P_{88} shows that all the species under consideration is following the same method of mitigation to prevent further embolism formation of xylem from 50% to 88%, if any such method exists. There is no special case where the complete xylem closedown is somehow delayed or accelerated for a certain species.

LDMC represents the carbon investment of the plant. The inverse correlation represented here , higher the LDMC , the more negative the P_{50} , P_{88} values implies that the fundamental structural investment traits can play an important role in providing xylem resistance to embolism (Ying and Wang , 2016). Species at the slow growing end of the economic spectrum will show more resistance to extremes , in this case drought.

Weak positive correlation of P_{50} with inverse logarithm of wood density implies more or less the same as the relation with LDMC. But specifically in terms of secondary xylem elements, it is the mechanical investment and thereby the strength of xylem that determines the wood density. The thicker, stronger and closely packed the individual xylem walls are, there is less chance of air seeding into the xylem and subsequent embolism formation (Hoffmann et al., 2011)

While Trueba et al., 2019 discuss the relation between rehydration capacity associated trait (RWC_{PLRC50}) and drought sensitivity traits such as leaf hydraulic vulnerability and turgor loss point, it would be reasonable to extend the relation to stem- xylem vulnerability traits as it is the same kind of xylem vessels that runs through the leaves as well as the stem. Cavities in xylem can hamper movement of water through petioles and veins preventing rehydration of the leaf. Greater the resistance to embolism formation greater the rehydration capability in future. This correlation can also arise from the fact that we are ultimately measuring leaf water potential as a proxy for stem water potential under equilibrium.
Of the twenty species considered, the four lowest resistant species are *Wrightia tinctoria, Tabernaemontana alternifolia, Macaranga peltata & Alstonia scholaris.* Of the four, *Macaranga peltata* is characterised for its dark viscous resin that is used commercially. The other three belong to the same genus Apocynaceae , which is characterised for milky latex production that solidifies on air contact. These plants may be able to plug their vessels (Sangsing et al., 2004) on dehydration and prevent further embolism, even before P_{50} is reached. Since we are measuring air discharge, air pulled out will asymptote at a lower P with no new embolism formation due to xylem plugging. If these substances are water soluble, the trees will be able to unplug the xylem when water status restores.

Some studies across the world on tropical seasonal forests are as follows

Venezuela : P_{50} range -3.82 to -1.48, mean = - 2.28 (Sobrado 1996, Sobrado 1997)

Brazil : P_{50} range -3.40 to -1.48, mean = -2.35 (Bucci et al., 2006; Hao et al., 2008 ; Zhang et al., 2009)

Panama : P_{50} range -2.1 to -1.38, mean = -1.68 (Tyree et al., 1998; Meinzer et al., 2003)

Costa Rica : P_{50} range -3.60 to -1.00, mean = -2.56 (Brodribb et al., 2003; Choat et al., 2007)

China : P_{50} range -2.32 to -1.14, mean = -1.83 (Chen et al ., 2009)

Within the country data from two sites are available :

Bhimashankar : P_{50} range -3.65 to -0.43, mean = -1.71 (unpublished)

Sirsi : P_{50} range -2.64 to -0.22, mean = -1.71(unpublished)

In comparison, Peechi has the broadest range of P_{50} : -5.8 to -0.80 and a mean of -2.89 (+/- 1.12 SD) . The standard deviation of 1.12 validates the spread of the data. With this high value of P_{50} around -3.0, on a moist deciduous forest with mean average precipitation of 3000mm, a positive hydraulic safety margin is being expected at the community level. HSM is measured during the summer months, and with respect to this work, is scheduled during the April month of 2020, will provide more insights into the above assumption as well as whether the individual species are drought tolerators with -ve HSM values or drought resistant with a positive HSM.

The P_{50} value of Peechi is in agreement with the values from seasonal tropical forests of Brazil, Costa Rica and Venezuela. Panama, having a stable and wet equatorial climate can be the reason for a narrow range for P_{50} and a higher average of -1.68. In the case of China, the experiment was focused on the euphorbiaceae shrub family alone and not on mature trees. Sirsi is a tropical evergreen forest (Kumara and Singh, 2004) expecting less fluctuations in soil moisture due to abundant rainfall as well as retention by leaf litter. This could be the reason for a smaller P_{50} Value. Moist deciduous forests like Peechi, due to high mean annual precipitation along with existing seasonality, is a mix of both evergreen and deciduous species when compared with purely evergreen or deciduous forests, which may be the reason for a broader P_{50} range. Bhimashankar is a mixed type seasonal forest, higher seasonality, still with the lower mean P_{50} and range than Peechi. This peculiarity is reported, and may be explained by the variation in strategies adopted by the plants in either embolism recovery or avoidance.

$RWC_{fv/fm50}$ values are in agreement with Trueba et al., 2019 , which showed the values fall at very low and lethal RWC of less than 20%. Only three species of the twenty showed $RWC_{fv/fm50}$ values greater than (*Dalbergia lanceolaria* at 22.42 *, Cinnamomum malabatrum* at 20.76 *and Macaranga peltata at* 24.87*)*, but are still close to 20%. Since RWC of 20 is already a lethal value, $RWC_{fv/fm50}$ cannot be used as a direct measure for tree mortality during drought. Nevertheless, it provides insights into the efficiency of the photosynthetic machinery of the given species.

$RWC_{fv/fm50}$ will be lower for plants that are able to maintain the photochemical activity with the increasing oxidative stress from unavailability of water (Lima et al., 2002). More investment in the photochemical components puts the species at the fast growing side of the leaf economic spectrum. Hence the positive correlation of $RWC_{fv/fm50}$ with leaf functional traits like LA, LMA and LDMC validates the tradeoffs of the slow - fast resource acquisition - resource use strategies (Wright et al., 2005; Wilson et al.,1999).

RWC_{PLRC50} unlike its chlorophyll counterpart can be used as an index of tree mortality. Depending on the ecosystem and the species, leaves either wilts or gets irreversibly damaged between 75% to 25% RWC. The broad range from 19.00% for *Pongamia pinnata* to 60.90% for *Dalbergia Lanceolaria* indicates some species will indeed do well during a severe to moderate drought in terms of rehydration capacity alone. The time taken for individual species to reach the given RWC is not considered here and a trade-off may exist where the morphology of the leaf may delay the fall in RWC with respect to the duration of drought.

As discussed above a higher WD reflects a higher structural investment on the vascular tissue including xylem. Hence, the xylem vessels of these species will not collapse under negative pressure caused by water scarcity compared to those with a lower wood density (Hacke et al., 2001). This will be reflected in the leaf vasculature as well, resulting in a better rehydration capability for those with a higher WD even after dehydration to lower water levels. This can be reflected in the moderate linear positive correlation between $\log^{-1}$(WD) and RWC_{PLRC50} .

Species with higher LMA will have a higher carbon investment and hence will have a higher dry matter content and surface area of leaf.

Conclusion

Moist deciduous forest of Peechi has a broader range and average P_{50} than other similar ecosystems considered in this study. It could be the difference in seasonality, rainfall pattern, niche division or even due to the unique warm and constant whirlwinds that blow through the Palakkad hill pass during the months of December to February(Jayanarayanan, 2001). A more detailed comparative study of the ecosystems is required. Correlations between Xylem resistance to cavitation, Leaf rehydration capacity and structural leaf and wood traits like LDMC and WD suggests that the slow growing structural investing species will have lesser chance of mortality due to hydraulic failure. Morphological characteristics like presence of resin or latex may help tolerate the drought by having a chemical investment than a structural one.The broad range of rehydration capacity could indicate the existence of both stress avoiding and tolerant species.Still a temporal dimension for reaching a critical dehydration value needs to be added to fully understand how the species ends up being a stress tolerator or avoider. Chlorophyll fluorescence, even though drops after lethal levels of relative water content, can provide information about the efficiency of the photosystem to dehydration stress. This efficiency is higher, unlike in hydraulic traits, with the fast growing species. Operating relative water content calculation and minimum water potential measurement is scheduled for the nearest summer month of april for comparison with existing rehydration capacity and P_{50} , which will help finding the respective safety margins and the response of the ecosystem to predicted climate change in future

Figures and Tables

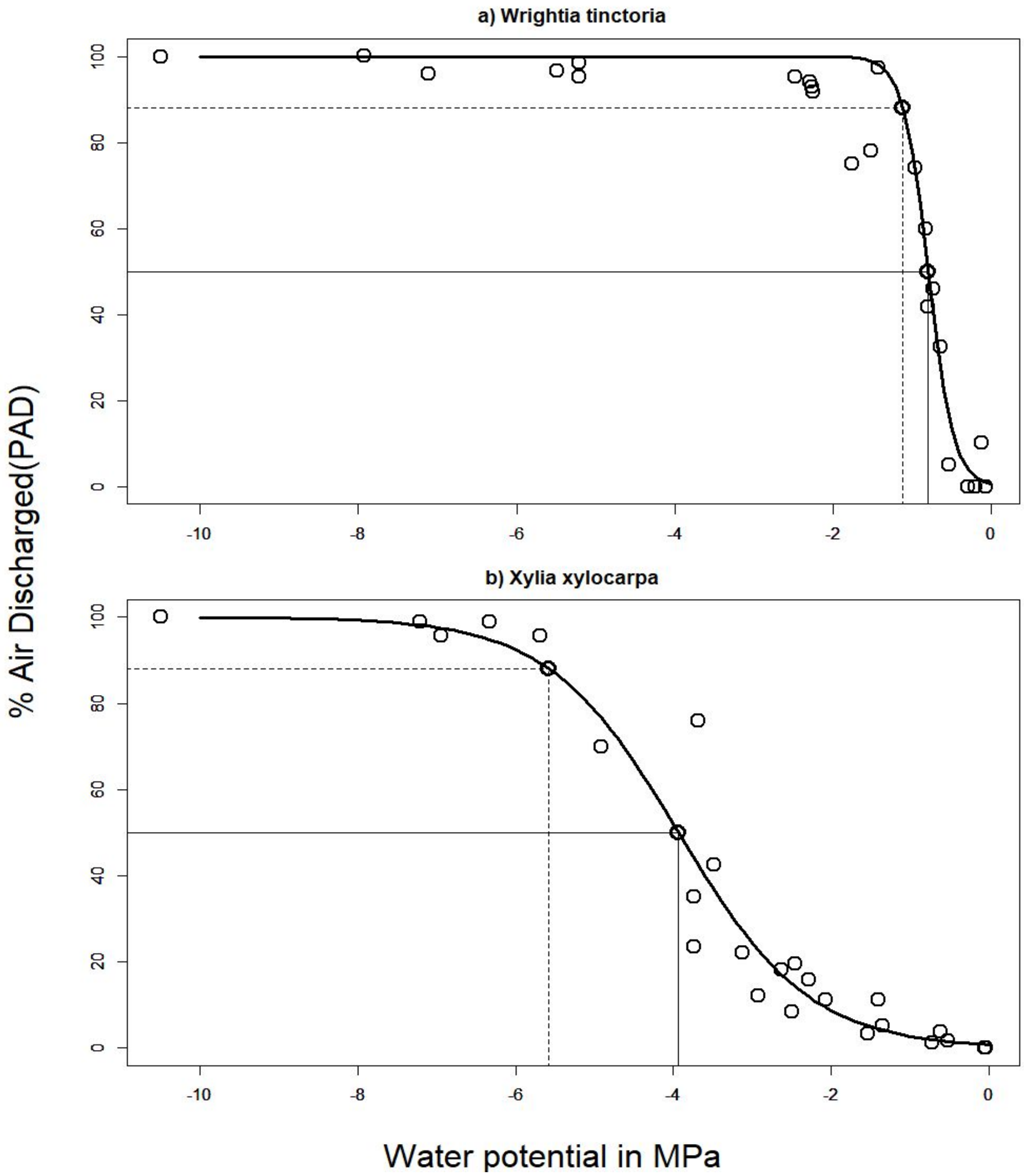

Figure.1 : Representative Xylem vulnerability curves (VC). a) VC of an individual species with low resistance to xylem cavitation, *Wrightia tinctoria* and b) an individual species with high resistance to xylem cavitation, *Xylia xylocarpa.* The stem water potential plotted on x axis and y axis, the percentage of air drawn out of the embolized branch.

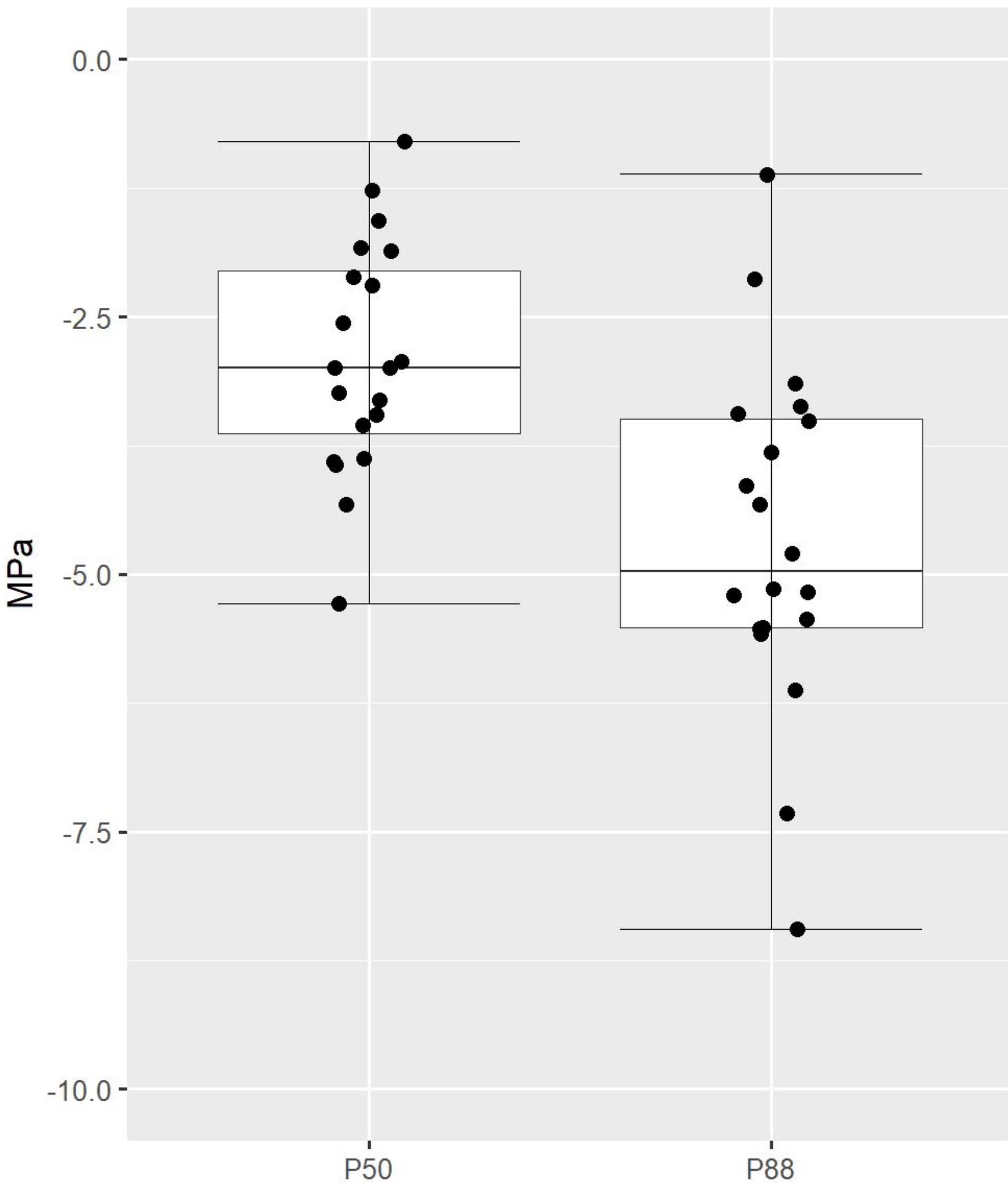

Figure 2 : Range of P_{50} and P_{88} . Each box plot represents the distribution of the respective hydraulic trait within the ecosystem. Data collected from twenty tree species.

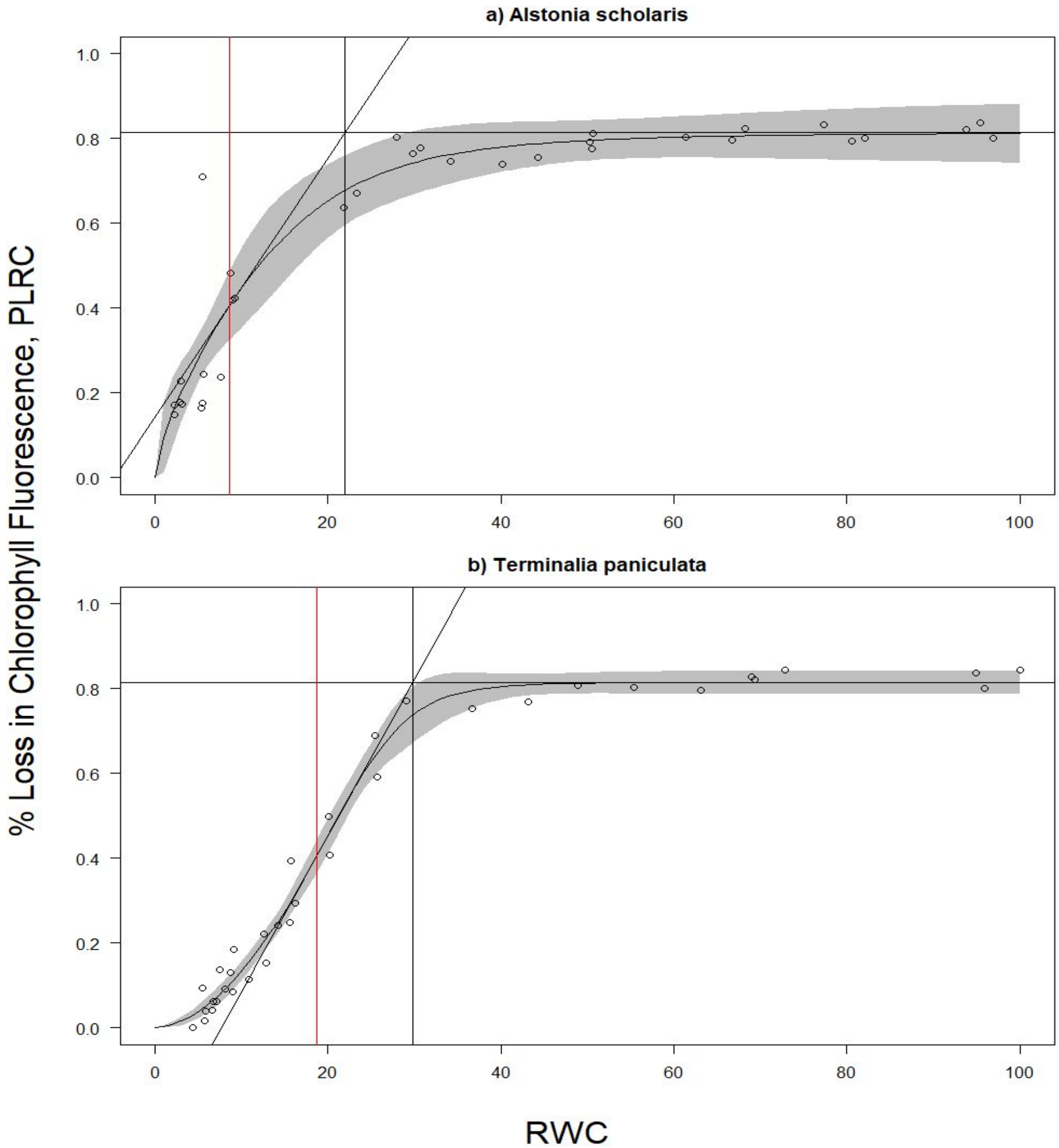

Figure 3 : Representative drought response curves for PSII functionality. a) A species with a higher photosynthetic tolerance to drought, *Alstonia scholaris* and b) one a weaker chlorophyll tolerance to drought, *Terminalia paniculata.* The x axis shows leaf relative water content , RWC and y axis the Fv/Fm value, maximum quantum yield of PSII photochemistry. Shaded region represents standard error. Red line is RWC at 50% fv/fm , Black horizontal line RWC at fv/fm break point.

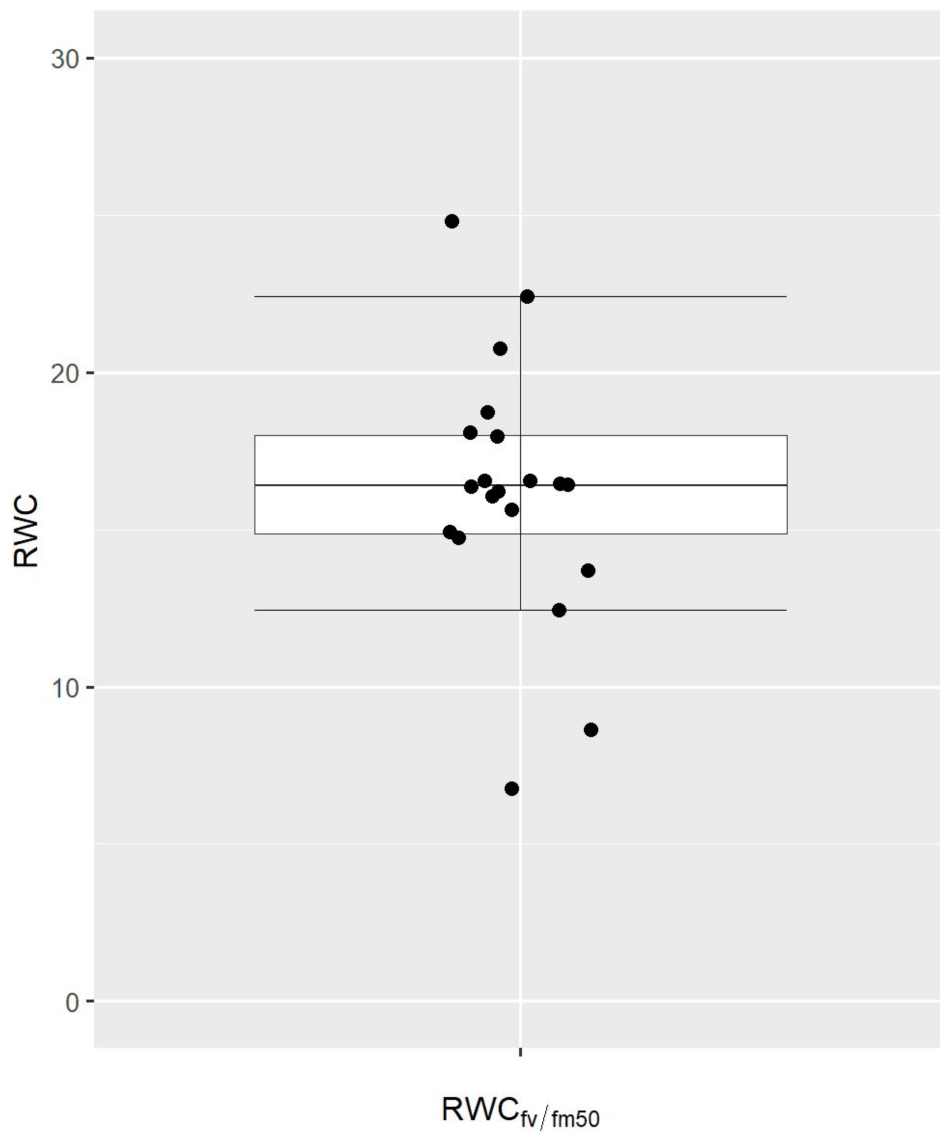

Figure 4 : Range of $RWC_{fv/fm50}$. The box plot represents distribution of the RWC in the ecosystem where the maximum quantum yield falls by half. Data collected from twenty tree species.

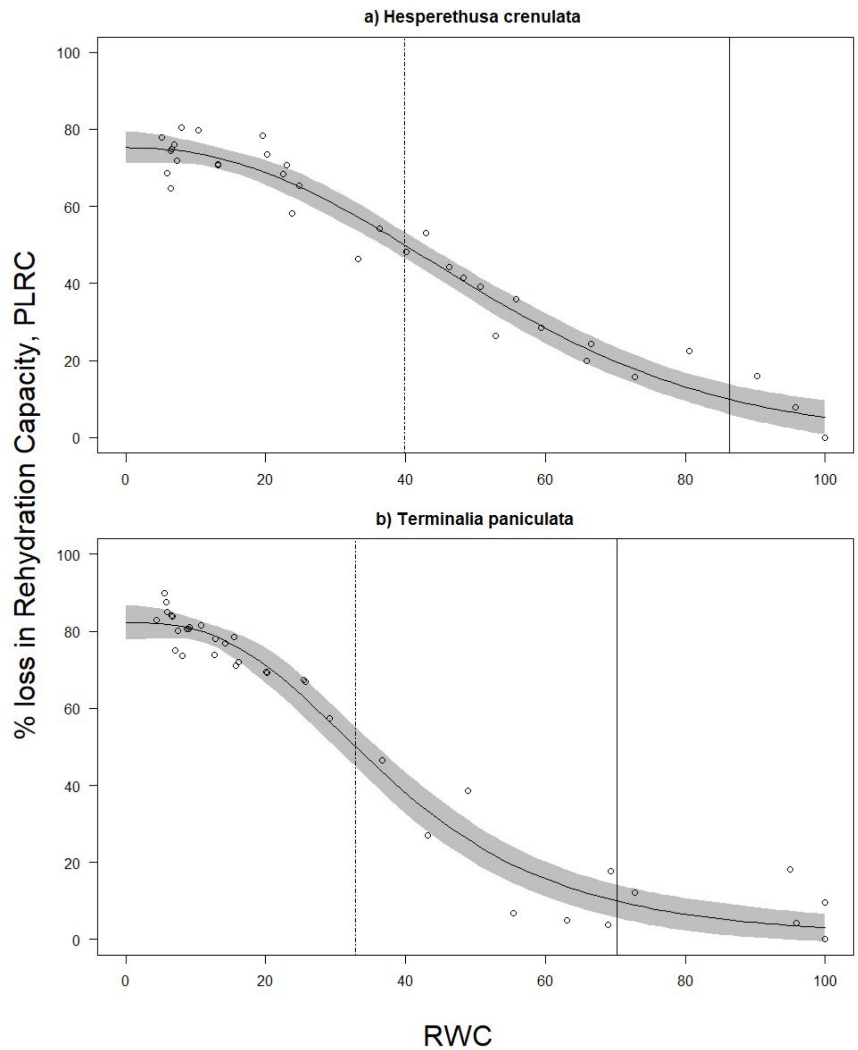

Figure 5 : Representative drought response curves for loss of leaf rehydration capacity. a) A species which loses rehydration capacity at lower drought levels, *Hesperethusa crenulata* and b) A species which keeps the rehydration capacity at lower drought levels, *Terminalia paniculata.* The x axis shows leaf relative water content and y axis percentage loss of rehydration capacity. Shaded region represents standard error. Solid line shows 10% loss and dotted line 50% loss of rehydration capacity.

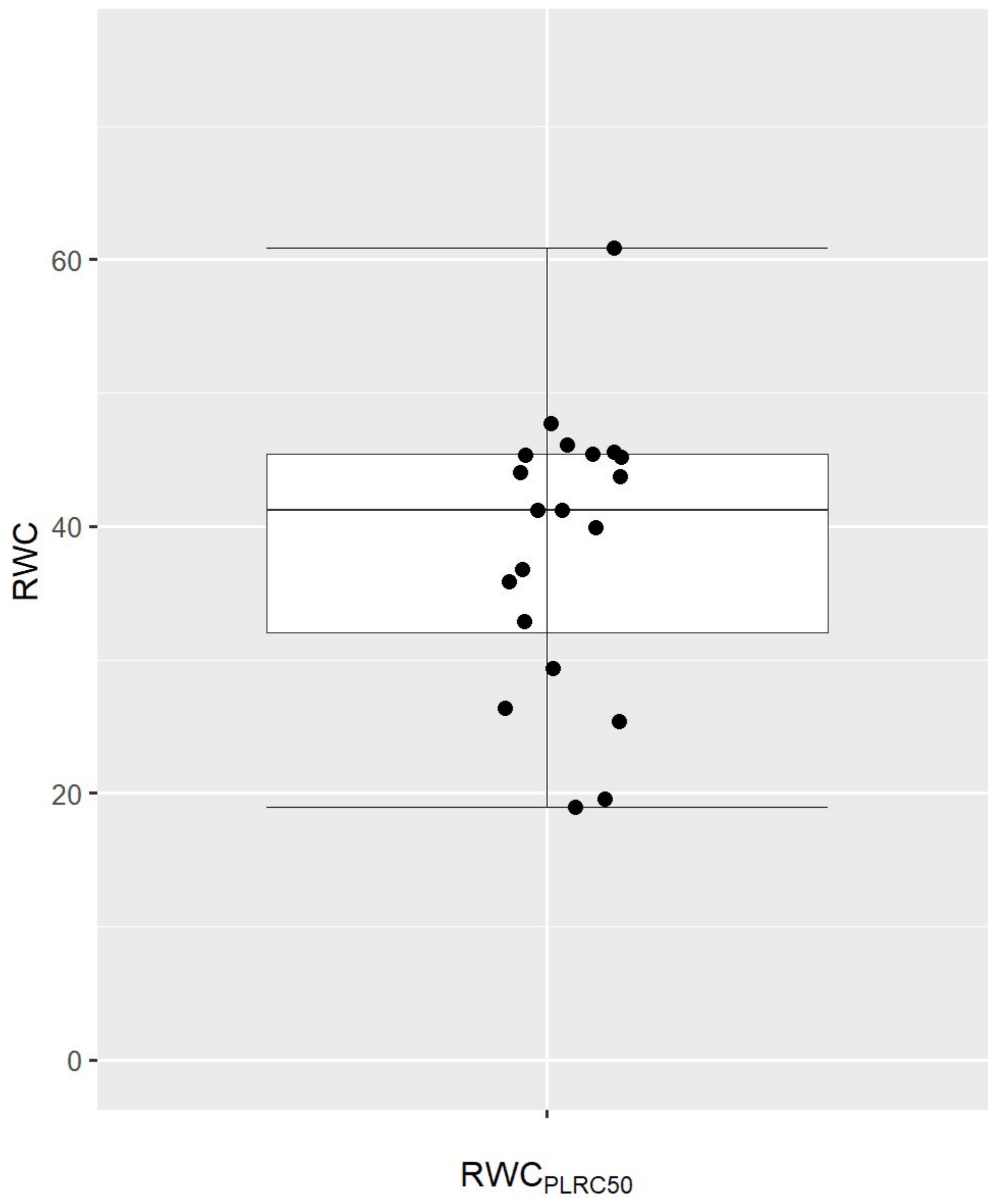

Figure 6 : Range of RWC_{PLRC50} . The box plot represents distribution of the RWC in the ecosystem where the leaf rehydration capacity falls by half. Data collected from twenty tree species.

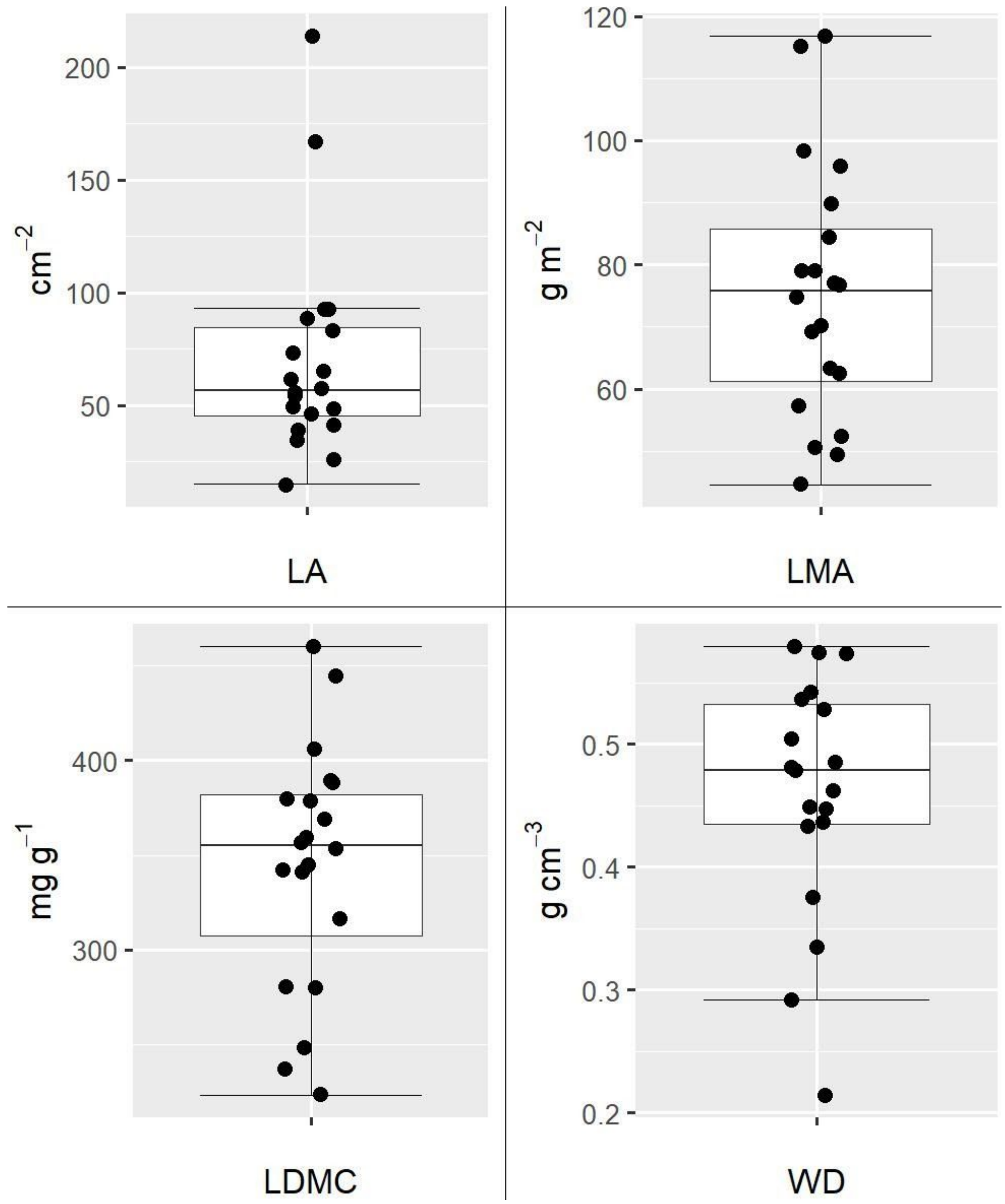

Figure 7 : Range of Leaf and wood functional traits . The box plots represent distribution leaf traits LA, LMA , LDMC and wood trait WD in the ecosystem. Data collected from twenty tree species.

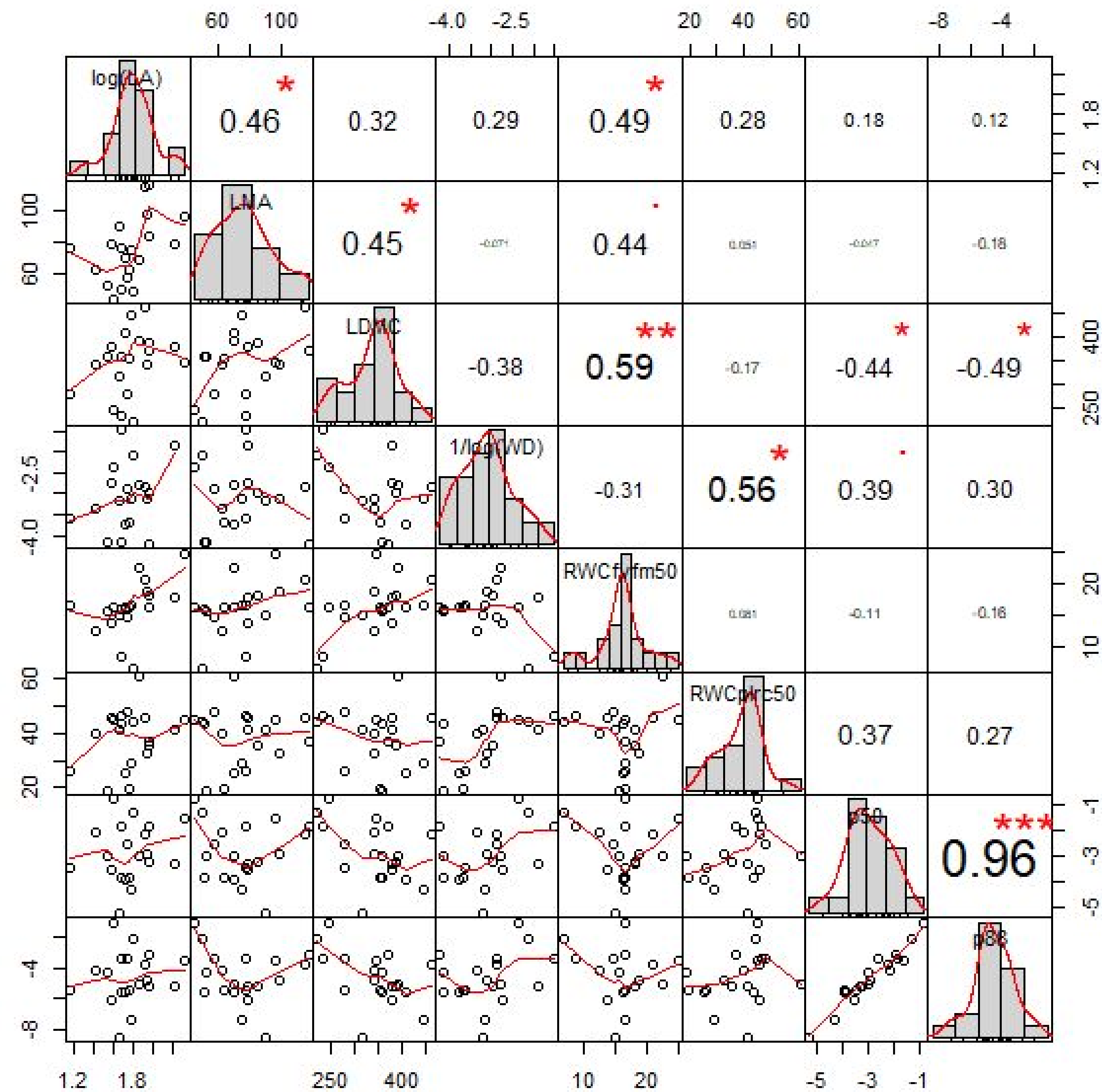

Figure 8 : Pearson correlation matrix for all traits under consideration. Weak, moderate and strong correlations for absolute values of r are defined as in intervals 0.40-0.59, 0.60-0.79 and 0.80-1.0 respectively. Corresponding p-values (<0, <0.001,< 0.01) maps to symbols (***, **, *).

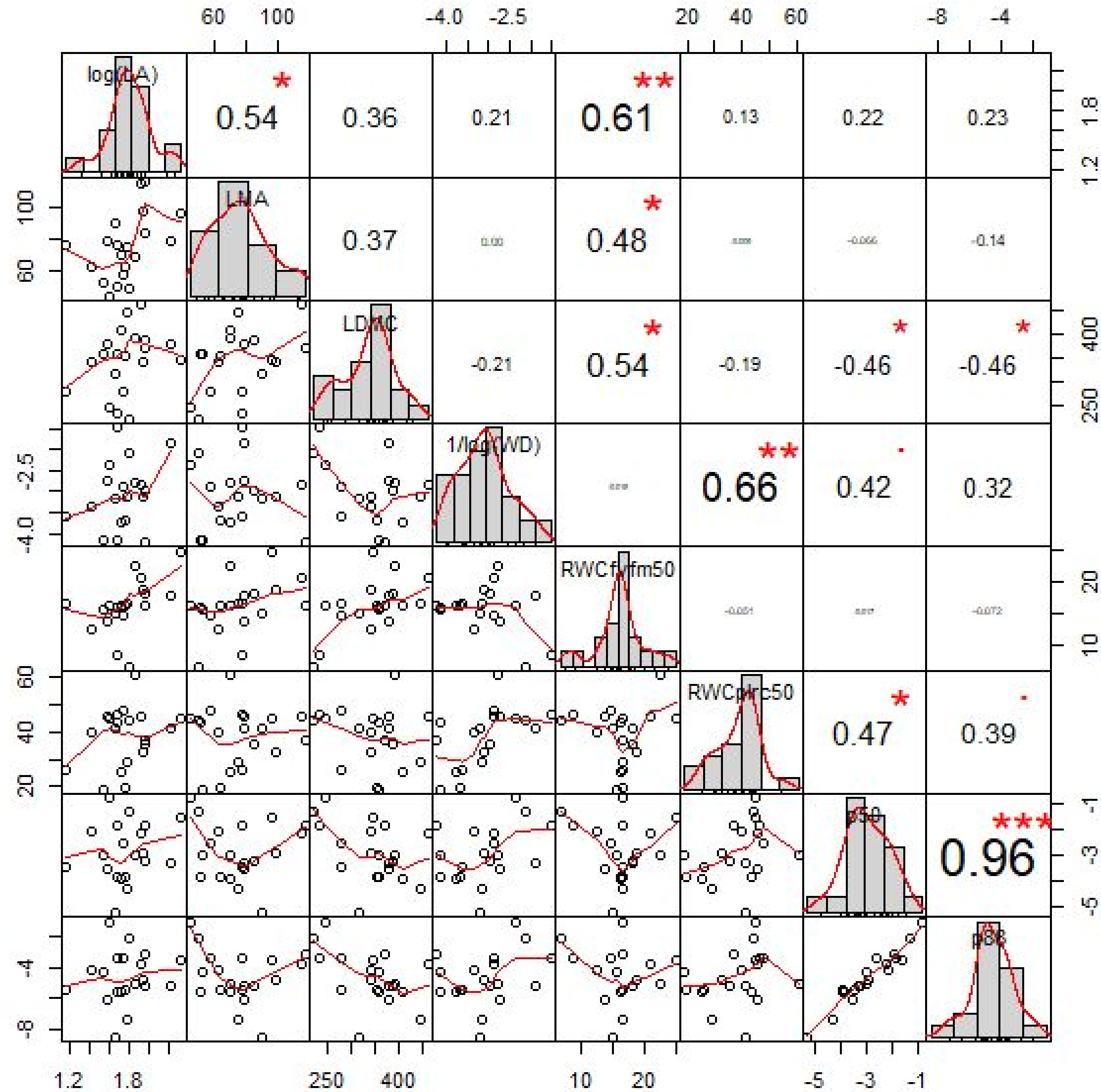

Figure 9 : Spearman correlation matrix for all traits under consideration. Weak, moderate and strong correlations for absolute values of r are defined as in intervals 0.40-0.59, 0.60-0.79 and 0.80-1.0 respectively. Corresponding p-values (0, <0.001, <0.01) maps to symbols (***, **, *).

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Appendix

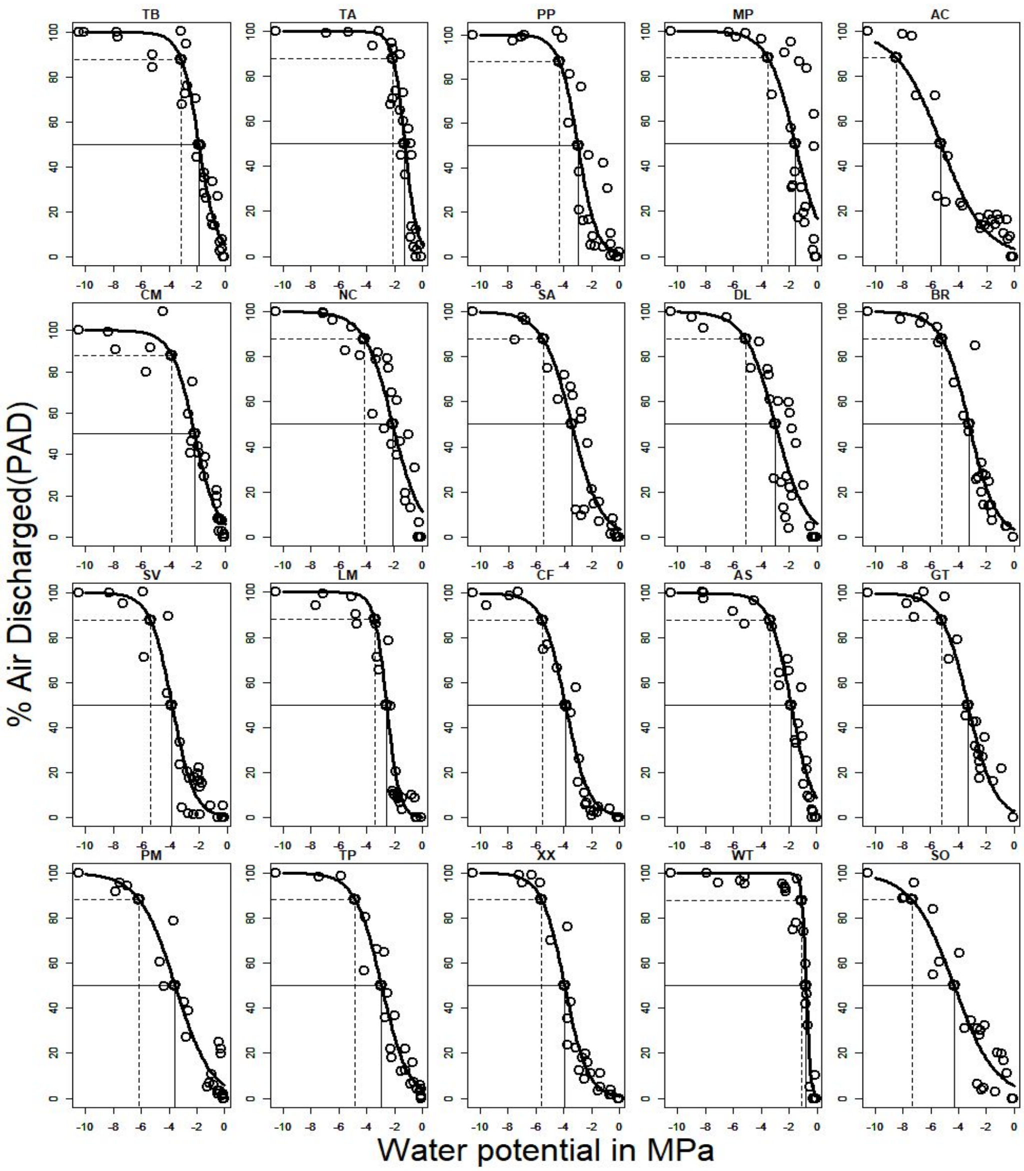

Figure. S1 : Xylem VC plots for 20 species, The stem water potential plotted on x axis and y axis, the percentage of air drawn out of the embolized branch. Dashed lines correspond to water potential at PAD 88 and solid lines at PAD 50 .

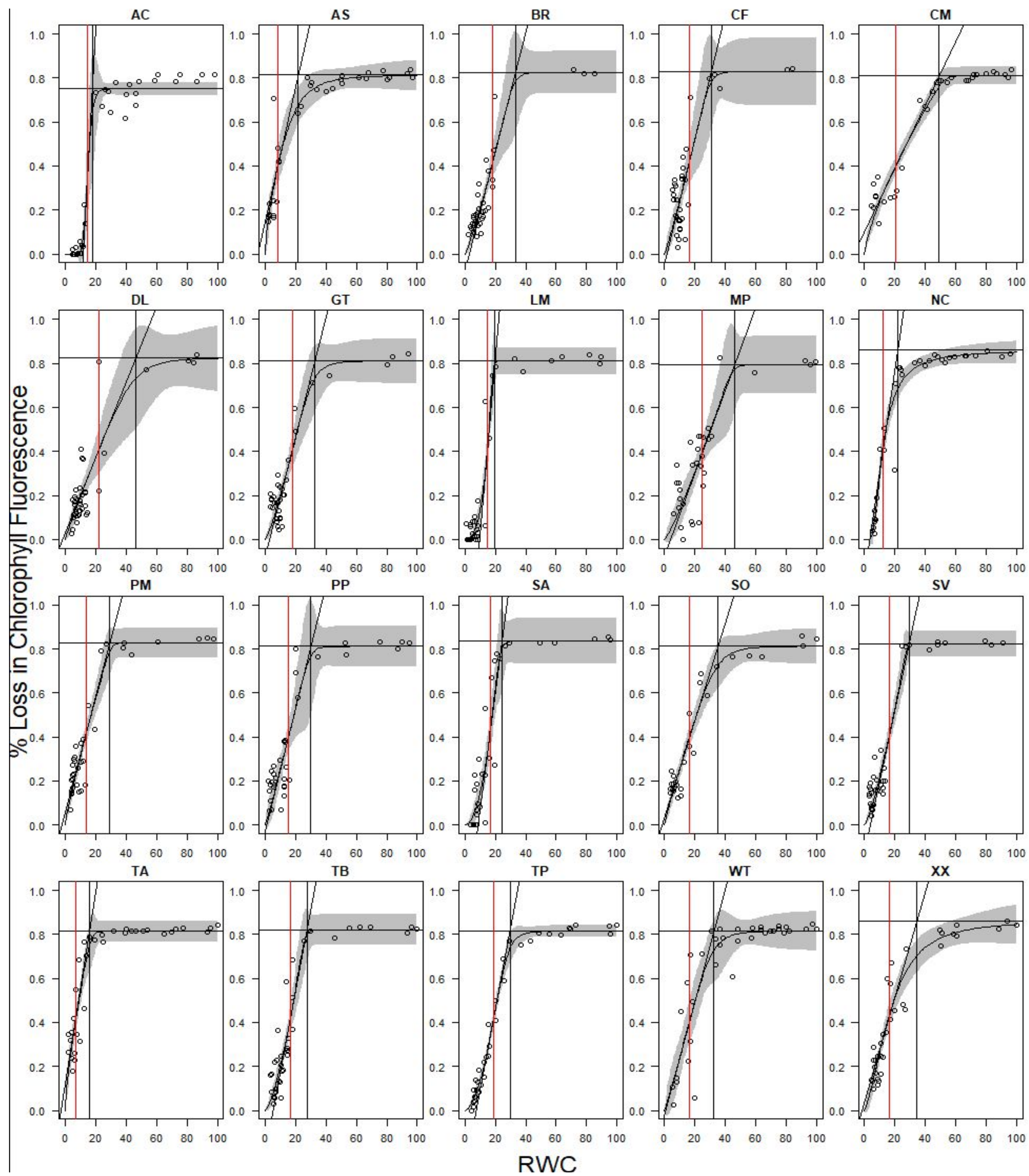

Figure. S2: Twenty species drought response curves for PSII functionality. The x axis shows leaf relative water content , RWC and y axis the Fv/Fm value, maximum quantum yield of PSII photochemistry. Shaded region represents standard error. Red line is RWC at 50% fv/fm , Black horizontal line is RWC at fv/fm break point.

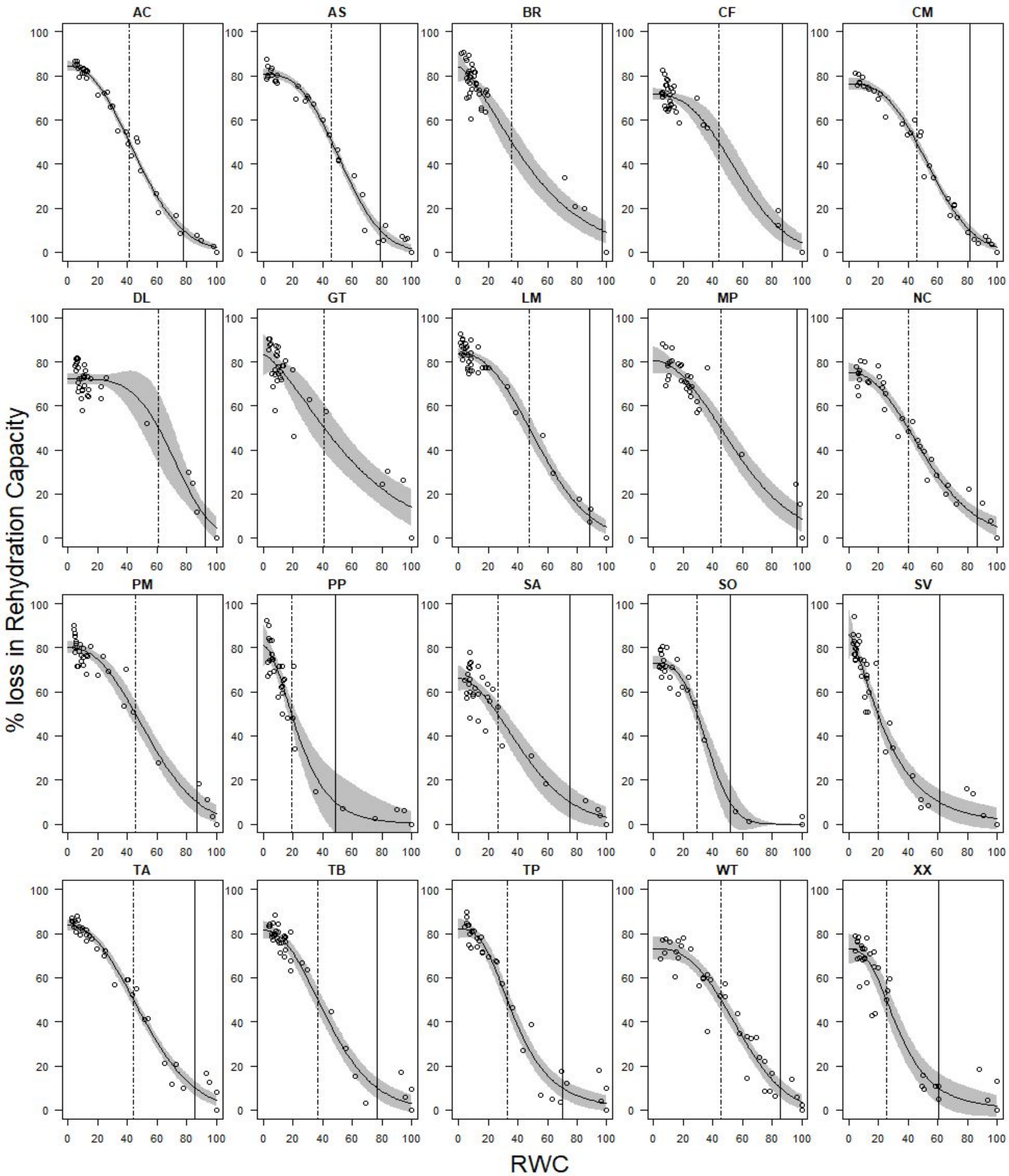

Figure. S3: 20 species drought response curves for loss of rehydration capacity. The x axis shows leaf relative water content , The x axis shows leaf relative water content and y axis percentage loss of rehydration capacity. Shaded region represents standard error. Solid line shows 10% loss and dotted line 50% loss of rehydration capacity.

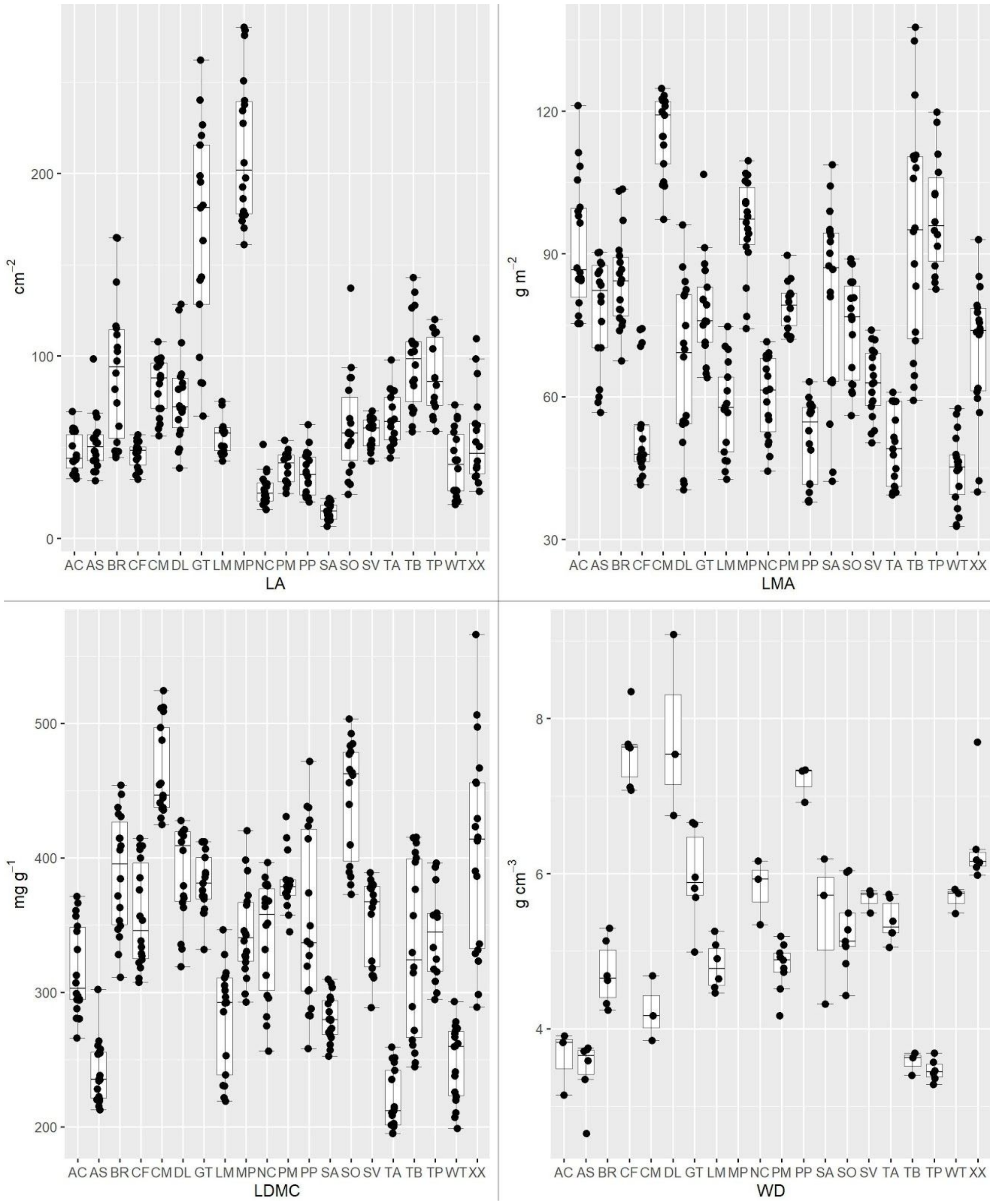

Figure. S4: 20 species box plots ; Leaf Area, Leaf Mass per Area, Leaf Dry Matter Content and Wood Density

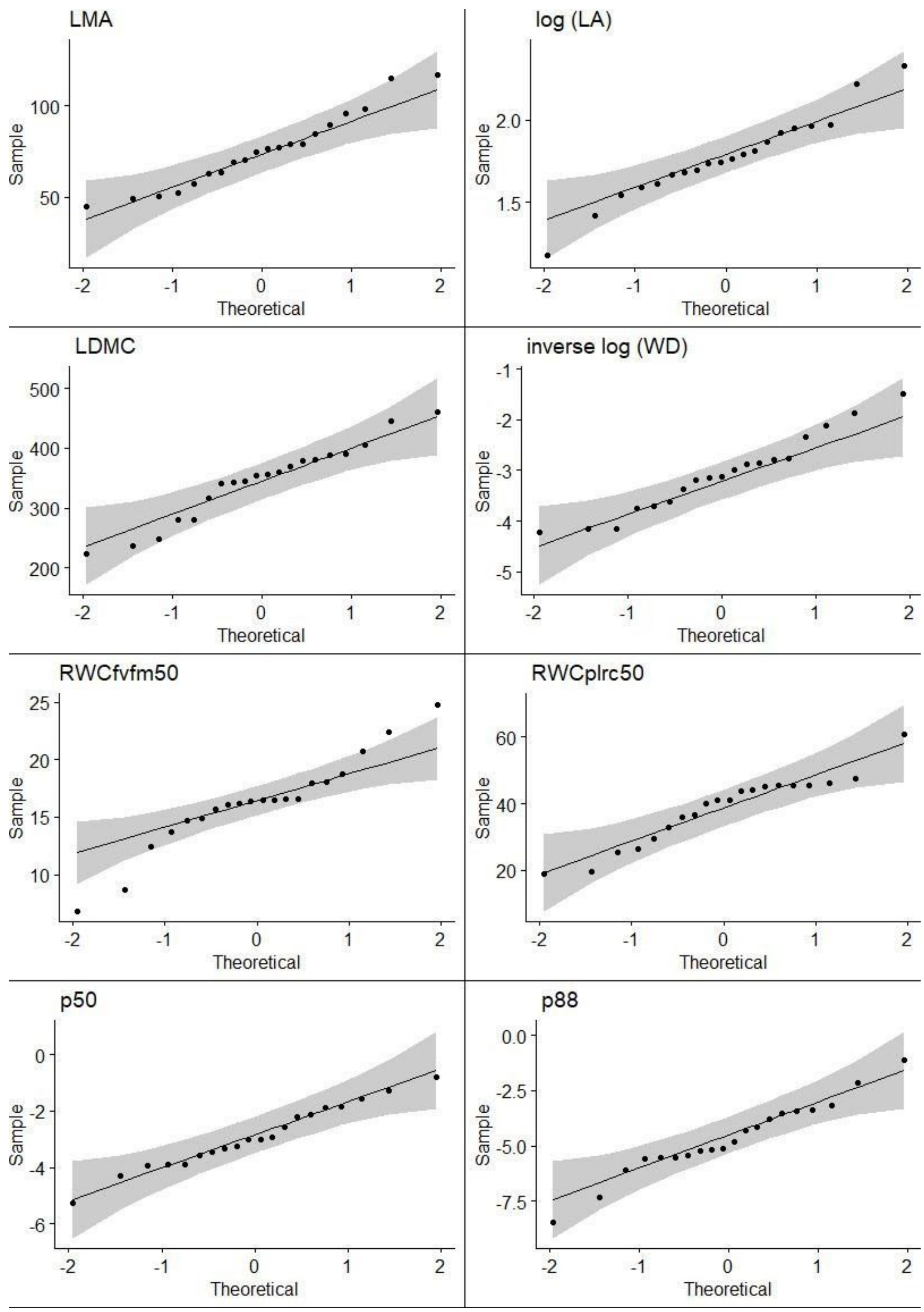

Figure. S5: Standard Normal Quantile-Quantile plots for all the traits considered. Failed to normalise $RWC_{fvfm50.}$

Table. S1 :

Summary of twenty tree species sampled, Tree dimensions height and girth at breast height (GBH) averaged over three individuals of each species.

Sl	Species	Abb.	Genus	Family	Height in m	SD	GBH	SD
1	*Aporosa cardiosperma (Gaertn.) Merr.*	AC	Aporosa	Phyllanthaceae	15.0	0.0	61.3	3.5
2	*Alstonia scholaris (L.) R. Br.*	AS	Alstonia	Apocynaceae	28.3	5.8	212.7	8.7
3	*Bridelia retusa (L.) A.Juss.*	BR	Bridelia	Phyllanthaceae	26.7	7.6	151.7	20.8
4	*Cassia fistula L.*	CF	Cassia	Leguminosae	16.7	5.8	86.0	18.3
5	*Cinnamomum malabatrum (Burm. f.) J. Presl*	CM	Cinnamomum	Lauraceae	20.0	0.0	64.0	10.6
6	*Dalbergia lanceolaria L.f.*	DL	Dalbergia	Leguminosae	21.7	2.9	133.7	11.9
7	*Grewia tiliifolia Vahl*	GT	Grewia	Malvaceae	27.7	10.8	154.0	50.2
8	*Lagerstroemia lanceolata Wall.*	LM	Lagerstroemia	Lythraceae	30.0	0.0	183.7	40.9
9	*Macaranga peltata (Roxb.) Müll.Arg.*	MP	Macaranga	Euphorbiaceae	13.3	2.9	79.3	5.5
10	*Hesperethusa crenulata (Roxb.) M. Roem.*	NC	Hesperethusa	Rutaceae	7.0	0.0	60.3	7.5
11	*Pterocarpus marsupium Roxb.*	PM	Pterocarpus	Leguminosae	38.3	2.9	271.7	2.9
12	*Pongamia pinnata (L.) Pierre*	PP	Pongamia	Leguminosae	12.3	6.8	74.7	34.2
13	*Santalum album L.*	SA	Santalum	Santalaceae	11.7	2.9	45.3	7.6
14	*Schleichera oleosa (Lour.) Merr.*	SO	Schleichera	Sapindaceae	11.7	11.5	102.0	102.2
15	*Strychnos nux-vomica L.*	SV	Strychnos	Loganiaceae	11.0	3.6	86.3	43.2
16	*Tabernaemontana alternifolia L*	TA	Tabernaemontana	Apocynaceae	7.3	2.5	39.7	12.5
17	*Terminalia bellirica (Gaertn.) Roxb.*	TB	Terminalia	Combretaceae	33.3	5.8	345.0	113.0
18	*Terminalia paniculata Roth.*	TP	Terminalia	Combretaceae	25.0	8.7	161.0	64.0
19	*Wrightia tinctoria R.Br.*	WT	Wrightia	Apocynaceae	11.7	2.9	84.7	6.8
20	*Xylia xylocarpa (Roxb.) Taub.*	XX	Xylia	Leguminosae	15.0	0.0	142.7	13.7

Table. S2 :

Summary of Shapiro-Wilks normality test for all traits considered, Tree dimensions height and girth at breast height (GBH) averaged over three individuals of each species. All W > 0.9, P > 0.05. Null hypothesis that for all traits ,sample is taken from a normal distribution is accepted , including for $RWC_{fv/fm50}$.

Trait	W value	P value
Log(LA)	0.97179	0.97179
LMA	0.95536	0.4558
LDMC	0.95595	0.4664
1/log(WD)	0.96418	0.657
RWCfv/fv50	0.93795	0.2192
RWCplrc50	0.93353	0.1805
P50	0.98453	0.9786
P88	0.97431	0.8419