Photosynthetic and water transport strategies of plants along a tropical forest aridity gradient: a test of optimality theory

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Summary

(1) The research conducted, including the rationale

The direct effect of aridity on photosynthetic and water-transport strategies is not easy to discern in global analyses because of large-scale correlations between precipitation and temperature. We analyze tree traits collected along an aridity gradient in Ghana, West Africa, that shows little temperature variation, in an attempt to disentangle thermal and hydraulic influences on plant traits.

(2) Methods

Predictions derived from optimality theory of the variation of key plant traits along the gradient are tested with field measurements.

(3) Results

Most photosynthetic traits show trends consistent with optimality-theory predictions, including higher photosynthetic rates in the drier sites, and an association of higher photosynthetic rates with greater respiration rates and greater water transport. Leaf economic and hydraulic traits show less consistency with theory or global-scale pattern, especially predictions based on xylem efficiency-sfatety trafeoff. Nonetheless, the link between photosynthesis and water transport still holds: species (predominantly deciduous species found in drier sites) with both higher sapwood-to-leaf area ratio (AS/AL) and potential hydraulic conductivity (Kp), implying higher transpiration, tend to have both higher photosynthetic capacity, and lower leaf-internal CO_2.

(4) Conclusions

These results indicate that aridity is an independent driver of spatial patterns of photosynthetic traits, while plants show a diversity of water-transport strategies along the aridity gradient.

Plain language summary: Along an aridity gradient in Ghana, West-Africa, we used optimality theory to explain why higher photosynthetic rates should be found at drier places and how plants arrange water transportation to support quicker photosynthesis at the drier site. We also reported surprising data-theory inconsistency for some hydraulic traits along the aridity gradient where further research is needed.

Introduction

Three key photosynthetic processes are frequently considered when seeking to understand plants photosynthesis strategies: light availability and electron transport; aridity and water transport; and CO_2 concentration and carboxylation (Farquhar et al., 2001). Plants capacities in these processes vary considerably along environmental gradients (Wang *et al.*, 2017a; Bahar *et al.*, 2017; Yang *et al.*, 2019; Oliveras *et al.*, 2020). Recently, many efforts have been made to propose universal rules to explain worldwide plant photosynthetic strategies, frequently cited as 'optimality theories', which could serve as a basic theoretical framework for vegetation carbon modelling and enable quantitative predictions of key photosynthetic traits (Franklin *et al.*, 2020; Harrison *et al.*, 2021).

One of the main challenges confronting these universal theories is to explain the 'pure' effect of aridity on photosynthesis (Rogers *et al.*, 2017). Such challenges become particularly pressing in the context of climate as greater atmospheric dryness (water vapour deficit, VPD) is predicted for most places (Neelin *et al.*, 2006; Grossiord *et al.*, 2020a; Bauman *et al.*, 2022), which may strongly influence photosynthesis and hence the carbon cycle (Canadell *et al.*, 2021). However, the theoretical expectation for the impact of aridity on plant traits based on optimality theories has not been summarized and tested. Most current earth systems models predict a negative relationship between photosynthesis (denoted by CO_2 assimilation rate per leaf area, A_{area}) and VPD simply due to the closing of stomata without incorporating the dynamics of photosynthetic capacity (denoted by electron-transport capacity, J_{max25} and Rubisco carboxylation capacity standardized to 25 degree celsius, V_{cmax25}) (Wang *et al.*, 2017a; Green *et al.*, 2020). On the contrary, a study focusing on Amazonia argued that higher VPD increases photosynthetic capacity which

counteracts the reduced conductivity, leading to higher photosynthesis under drier climates (Restrepo-Coupe *et al.*, 2013; Green *et al.*, 2020). However, a global study found the above pattern only exists in wet ecosystems and higher VPD reduces photosynthesis overall (Fu *et al.*, 2022) although globally higher V_{cmax25} was indeed found for plants grown in drier sites (Peng *et al.*, 2021). Under experimental conditions, CO_2 assimilation was found to be lower under high VPD (Long & Woolhouse, 1978; Dai *et al.*, 1992; Cunningham, 2005).

With such mixed evidence in the literature, the stand-alone effect of aridity on photosynthesis still remains unclear. There are two particular challenges. First, on a large spatial scale, aridity can be confounded with temperature (especially when VPD is used as a metric of aridity). Temperature is a stronger driver of photosynthesis than aridity (Smith *et al.*, 2019; Peng *et al.*, 2021), but few studies try to disentangle aridity from temperature (Grossiord *et al.*, 2020a). Second, the effect of VPD can be confounded with soil water availability. Optimality theory predicted higher Vcmax and A_{area} under higher VPD (Smith *et al.*, 2019) but it is unclear how plants in drier environments arrange water transportation to support higher $A_{area.}$ A comprehensive theoretical framework is lacking to incorporate the effect of VPD on all leaf-level photosynthesis processes (light, water and CO_2) with full consideration of water delivery to leaves (Mencuccini *et al.*, 2019a).

Here, we examine a dataset of detailed traits measurements along an aridity gradient in West African forests to disentangle the effect of aridity on photosynthesis from temperature and to explain the effect with optimality theory. The key questions we address are: (1) do drier environments have higher photosynthesis rates and how do aridity and photosynthesis interact? (2) If photosynthetic rates are higher in arid environments, as predicted by optimality theory, how do plants arrange greater water transportation, given greater water stress in drier places? To answer these questions, we adopted a theory-data comparison approach where we first review the expectation of recent 'universal' theories and deduced 16 testable predictions (some of which have previously been tested but with confounding results). We then examined the consistency between each prediction and field measurement along the aridity gradient (Table 1). Consistency would give field-observed patterns a mechanistic explanation and reinforce the stand-alone impact of aridity on the corresponding trait, while inconsistency would imply weakness of the theory and possible confounding interactions between aridity and other climate variables. Before closing the

paper, we summarize the consistency and inconsistency with an integrated theoretical framework to address and explore the 'pure' effect of aridity on photosynthesis.

Description of theory and hypotheses development

'Optimality theory' was developed recently with the assumption that plants can optimize photosynthesis and minimize maintenance costs according to their living environments by optimizing investment in the above processes, which provides a universal explanation of the variation of photosynthetic strategies under different growing environments (Prentice *et al.*, 2014; Wang *et al.*, 2017b; Mencuccini *et al.*, 2019a; Stocker *et al.*, 2020; Xu *et al.*, 2021). Although the above-cited studies have tested the theories on global scales and along elevation gradients, discussion and validation of these theories along other abiotic gradients, such as aridity gradients, are still lacking. Therefore, we first review the implication of such theories on plants photosynthetic strategies along aridity gradients.

In drier sites, higher VPD increases potential transpiration per unit leaf area. As predicted by the 'least-cost hypothesis' (Wright *et al.*, 2001, 2003; Medlyn *et al.*, 2011; Prentice *et al.*, 2014), plants can compensate for high water costs in dry climates by keeping stomata relatively closed. Thus, in drier sites, plants are expected to have lower leaf internal CO_2 concentration (c_i), lower internal-to-external CO_2 ratio (c_i/c_a) and lower stomatal conductance (g_s). The 'coordination hypothesis' (Beerling & Quick, 1995; Maire *et al.*, 2012; Walker *et al.*, 2014) assumes equilibrium between Rubisco-limited photosynthesis rates (A_C) (depending on V_{cmax25} and c_i) and electron transport-limited photosynthesis rates (A_J) (depending on J_{max25} and leaf absorbed PPFD) (see the quantitative expression in (Wang *et al.*, 2017b; Smith *et al.*, 2019; Stocker *et al.*, 2020)). To maintain such an equilibrium, plants in drier sites are expected to have larger V_{cmax25} to compensate for the lower c_i. Otherwise, A_C would be lower than A_J resulting in unused capacity for electron transport (J_{max25}). To sum up, lower c_i but higher V_{cmax25} is expected toward drier sites if J_{max25} stays constant (in which case A_J would be slightly lower due to smaller c_i).

In reality, toward drier sites, it is common to see higher leaf absorbed photosynthetic photon flux density (I_{abs}) because of less cloud cover and more open canopies. Considering an additional optimality criterion that J_{max25} is acclimated to I_{abs} (Smith *et al.*, 2019), supported by multiple

experiments (Björkman, 1981; Ögren, 1993), we would expect higher J_{max25} in drier sites, which further encourages higher V_{cmax25} (see above paragraph). Higher J_{max25} and V_{cmax25} would give rise to higher A_C and A_J. All the above would lead to higher leaf photosynthetic protein cost, hence higher leaf dark respiration (Rd), and higher transpiration stream maintenance cost, hence higher stem respiration per leaf area (Rs) (Prentice *et al.*, 2014). Note that R_s is stem respiration per leaf area (R_{stem_leaf} hereafter), different from the commonly reported stem respiration per stem area (R_{stem_stem}). Some of the above predictions have been seen on global scale; for example, higher R_d has been found in drier sites (Wright *et al.*, 2001; Atkin *et al.*, 2015) and higher assimilation rate has been reported from drier sites (Maire *et al.*, 2015).

It is worth noting that V_{cmax25}, g_s and c_i here are discussed as an overall value for a forest stand, disregarding diurnal variation and intraspecific variation (Stangl *et al.*, 2019; Han *et al.*, 2022). At the species or individual scales, there is a positive correlation between A_{sat} (light-saturated assimilation rate at 400 ppm), V_{cmax25}, g_s and c_i (Wright *et al.*, 2003; Prentice *et al.*, 2014), instead of the opposite trend of V_{cmax25} and c_i/c_a as discussed above regarding spatial variation only.

Photosynthesis strategies predicted by the optimality theory above can be linked with xylem water transportation strategies via stomatal behaviour, as given by Fick's law,

$$g_s = A_{area} / (ca - ci) \quad (1)$$

Where g_s is stomatal conductance (umol CO_2 m-2 s-1), A_{area} is CO_2 assimilation rate per leaf area (umol CO2 m2 s-1), and leaf internal (ci, ppm) and external (ca, ppm) CO_2 concentration

We focus on daytime conditions that produce maximum rates of transpiration and photosynthesis, when water loss through stomata must equal water transport through xylem (Brodribb *et al.*, 2002; Xu *et al.*, 2021):

$$E = 1.6\ gs\ VPD / Patm = Ks\ \Delta\Psi max\ AS/AL\ / h \quad (2)$$

Where Patm is atmospheric pressure (Mpa), KS is the sapwood-specific hydraulic conductivity (mol m–1s–1 MPa–1); AS/AL is the ratio of sapwood to leaf area (m2m–2) ΔΨmax is the

maximum decrease in water potential from soil to leaves (MPa) h is the transpiration stream pathlength (m), roughly equivalent to plant height, and E is the transpiration rate (mol m–2s–1),

Combining the above two equations we obtain a link between water transportation and photosynthesis:

$$Ks \ \Delta\Psi max \ AS/AL \ / \ h = 1.6 \ VPD \ A_{area} / (ca - ci) / Patm = E \quad (3)$$

Note that here we focus on forest-stand scale as an average across time. Relationships could be very different at other scales (Mencuccini *et al.*, 2019a).

In drier sites with higher VPD, despite less open stomata (less gs and less ci), there should inevitably be a larger E (Granier *et al.*, 1996) and more negative ΔΨmax (Gleason *et al.*, 2013); therefore smaller maximum tree height, and more negative turgor loss point (TLP, Mpa) in drier sites to increase hydraulic resistance (note that TLP must be more negative than ΔΨmax) (Ryan & Yoder, 1997; Bartlett *et al.*, 2012). Equation 3 implies that in drier sites with high VPD, plants require a larger AS/AL and/or larger Ks in order to support the same amount of photosynthesis with enhanced transpiration. Following the xylem safety–efficiency trade-off (Manzoni *et al.*, 2013; Gleason *et al.*, 2016; Bittencourt *et al.*, 2016; Grossiord *et al.*, 2020b) (although arguments against this trade-off exist, here we present testable hypotheses expected by the trade-off), plants at drier sites would be expected to have lower hydraulic efficiency and lower hydraulic conductivity. Lower hydraulic conductivity is often associated with smaller vessel diameter, higher vessel density and higher wood density (Poorter *et al.*, 2010; Schuldt *et al.*, 2013; Hoeber *et al.*, 2014). Such patterns have been observed along an Australian aridity gradient (Gleason *et al.*, 2013; Pfautsch *et al.*, 2016), but no effect of aridity on vessel diameter was reported (Olson & Rosell, 2013; Olson *et al.*, 2014). Plants in drier sites should have increased hydraulic safety - more negative TLP and more negative P50 (Hacke *et al.*, 2001; Martínez-Vilalta *et al.*, 2009; Gleason *et al.*, 2013; Togashi *et al.*, 2015; Liu *et al.*, 2019; López *et al.*, 2021). In short, toward drier sites, we would expect to see, higher AS/AL and more negative TLP. The safety-efficiency trade-off implies lower Ks, smaller vessel diameter, higher vessel density and higher wood density.

The trade-off between Ks and AS/AL is also embedded in the variance of traits in equation 3. Ks and AS/AL could vary by two orders of magnitude (100-fold variation) (Mencuccini *et al.*, 2019b) on a global scale, while ci/ca and A_{area} vary much less (ci/ca: 2 fold; A_{area}: 10 fold) (Wright *et al.*, 2004; Wang *et al.*, 2017b). This leads to a trade-off between Ks and AS/AL (i.e. KS x AS/AL should vary less than either of them). However, given that there are also variations of ci/ca, A_{area}, h and $\Delta\Psi max$, it is possible that different species range along a spectrum from high A_{area} and E to low A_{area} and E while always satisfying equation 3 (Prentice *et al.*, 2014).

In short, the above review leads to an integrated hypothesis that plants in drier (normally also brighter) sites tend to develop a photosynthesis strategy with less stomatal conductance and hence lower ci, stronger photosynthetic capacities (larger V_{cmax25}, J_{max25} and A_{area}) with more maintenance cost (higher Rd and Rs), higher maximum carbon assimilation rate and larger maximum evapotranspiration which the water transport system would adjust to with higher AS/AL, lower Ks, lower tree height and more negative TLP. Information on leaf economic traits is provided in Appendix 3. We break the above prediction down into 16 testable hypotheses (Table 1) and test each of them along a forest aridity gradient.

Materials and Methods

Study sites - the aridity gradient

This study presents and analyses physiological traits data collected from seven one-hectare forest and savanna plots distributed along a wet to dry rainfall gradient across three sites, Ankasa (ANK, moist rainforest), Bobiri (BOB, semi-deciduous forest) and Kogyae (KOG, dry forest and mesic savanna), in Ghana, West Africa (Figure S1 S2) (Moore *et al.*, 2018; Oliveras *et al.*, 2020), as part of the Global Ecosystem Monitoring (GEM) network (Malhi *et al.*, 2021). These sites share very similar mean annual temperature but span a steep gradient of aridity (Figure 1), which provided a "natural laboratory" to disentangle the hydraulic aspect of plant traits variation from temperature.

Although one-hectare plots (e.g. BOB-02) within the same site (e.g. BOB) share very similar air temperature and precipitation, they can differ in terms of soil moisture supply due to small-scale variations in soil properties and topography (Table S1). Along the aridity gradient, there are also variations in soil and vegetation type, with vegetation seasonality and deciduousness increasing considerably towards drier sites (Moore *et al.*, 2018). More information about the soil properties and climate of all three sites can be found in (Domingues *et al.*, 2010; Chiti *et al.*, 2010; Moore *et al.*, 2018). Moreover, the swampy rainforest (ANK03) is partly inundated during the wet season unlike ANK01, which is located on a hill and never inundated. From KOG02 (dry forest), KOG04 to KOG05 (savanna), forest plots become more deciduous with a smaller number of trees. Within any site, there are many common species between plots but species composition (e.g., top five abundant species) could still be very different. There is almost no common abundant species between the three sites (ANK, BOB and KOG).

Aridity index and soil moisture stress

At site scales, we calculated an aridity index as the ratio of annual potential evapotranspiration (PET) to mean annual precipitation (MAP). To understand soil moisture stress experienced by plants, we reported not only measured surface (12 cm depth) soil volumetric water content, but also hydraulic simulations on plot scales with SPLASH v2.0 (Sandoval & Prentice, 2020). This model requires three sets of input data: (1) field observed climate data at site scale during 2011-2016 (2) soil properties measured following the RAINFOR protocols (Quesada *et al.*, 2010); (3) terrain data: root zone was assumed 2m, while upslope drainage area, slope inclination and orientation were extracted from (Yamazaki *et al.*, 2019). We considered two modelled indices: the relative soil moisture saturation (Θ) was defined as the volumetric water content (θ) normalized by the volumetric water content at saturation (θ_{SAT}); a vegetation water stress index (α) was estimated as the ratio of annual actual evapotranspiration (AET) to PET.

Functional trait data measurements

Leaf traits field campaigns to measure leaf traits were conducted using a standardized protocol between October 2015 and September 2016 in all plots (Oliveras *et al.*, 2020), covering both dry and wet seasons (see Appendix 1 for sampling protocol). To ensure consistent comparison along the aridity gradient, only sun leaves were sampled. Sampled leaves were chosen from individuals that correspond to the most dominant species in each plot. To determine the target species, species contributing to up to 80% of the total basal area of the plot were ranked by basal area. As equation 3 focuses on daytime conditions with maximum transpiration, we use Kp (potential specific hydraulic conductivity) as a proxy of Ks and plant stature (H_{max}) as a proxy of path length (h). Kp was calculated from vessel density and vessel diameter following (Poorter *et al.*, 2010).

Following (Prentice *et al.*, 2014), we calculated stem respiration per leaf area (Rs_leaf) instead of the commonly presented Rs_stem, as a 'maintenance cost of photosynthesis' (See Appendix 1). To our knowledge, Rs_leaf has not previously been presented with in-situ data in the literature. Here we argue the importance to understand stem respiration from per leaf area perspectives because (1) higher stem respiration per stem area has been found in wetter sites (Yang *et al.*, 2016), contradictory to theoretical expectation (Prentice *et al.*, 2014) (2) consistency with photosynthetic traits which were commonly reported per leaf area.

All data reported in this study were field-measured except for wood density, which was obtained from a global species database (Zanne *et al.*, 2009). Global scale sapwood-to-leaf-area ratio in Figure 3 is sourced from (Mencuccini *et al.*, 2019b). Global scale vessel diameter in Figure S4 is sourced from (Choat *et al.*, 2012).

Statistical analysis

Hypotheses 1-14 (Table 1) were tested by significant differences between wet and dry sites. Principal component analysis (PCA) and standardized major axis regression are used to understand the relationship between Ks, As/AL and photosynthesis traits (Hypothesis 15-16).

We performed a plot-to-plot comparison in answering Hypotheses 1 to 14 as follows: (1) The distribution was visually inspected with histograms and transformations were applied if necessary.

(2) Outliers were checked with the R package *outliers::scores*, 'iqr' method with threshold 1.5. This removed leaves/trees with extreme values but made the community-weighted mean a better representation of the whole plot. (3) Community-weighted means were calculated based on the basal area of each species. Standard error was calculated with the same weights (Madansky & Alexander, 2017). (4) Significance of differences in plot-to-plot community-weighted means were then tested with *lm*(), *glht*(), and *cld*(). (See Rscript *community_weighted_mean_Ghana_log_YS.R* for a full description). In testing Hypotheses 1-14, a hypothesis was accepted if KOG (dry region) was significantly different to ANK (wet region) while BOB (middle aridity) sat in between (Figure 1). (5) Variance partitioning was done with *vegan::varpart()*, following the 'RDA' method with the expression: *varpart* (Trait, ~ Plot, ~ Species, data = Trait). Variance partitioning reveals whether the change of traits along the aridity gradient was driven by intraspecific or interspecific variation. Variance partitioning is also used to diagnose whether the intra-specific variation or measurement errors are overwhelming. To double-check the impact of intraspecific variation, we recalculated a community-weighted mean by assuming that the same species share the same value of trait (i.e. remove intraspecific variation) and extrapolated traits value to forest plots without trait measurements (Appendix 5)

For hypothesis 16, we applied Principal Component Analysis (PCA) with *FactoMineR::PCA*(), (See Rscript ~/link_hydraulic_photosynthesis/PCA.R). Asat, Kp, AS/AL and V_{cmax25} were log10 transformed. We avoid standardization by setting 'scale.unit' as False in function PCA() so that the variance of a trait was reflected by the length of an arrow in Figure 2. Trait-trait correlations (bivariate plot) were calculated (Rscript *Compare_with_Others.R*). For hypothesis 15, the slopes and significance of correlation were calculated using Standard Major Axis Regression (*function smatr::sma*()), which is preferable to ordinary least squares regression in summarizing the relationship between two plant traits (Wright *et al.*, 2005; Warton *et al.*, 2012) as it considers uncertainties of both axes. All analyses were done at the species level (i.e. each point in Figure 2 represents a species) to compare with other studies and join among datasets. Hypothesis 15 was also tested at the global scale because Ks was reported to negatively correlate with AS/AL but there is no report on the global correlation between Kp and AS/AL (Appendix 4).

Results

Aridity gradient

The values of the aridity index (PET/MAP) (site scale) revealed a clear aridity gradient from ANK (moist rainforest site) to BOB (mid) and KOG (dry) (Appendix 2). The same order could be arrived at with VPD or maximum cumulative water deficit (MCWD). The standard deviation of monthly VPD also suggested that the seasonality was weaker in ANK and increased towards KOG.

On the other hand, the simulations of relative soil moisture saturation (Θ) and vegetation water stress index (α) (plot scale) showed that BOB was the least soil moisture stressed site, followed by ANK and KOG. BOB-02 had the highest values in these two metrics. The model reported the highest runoff at ANK-03, capturing to some degree the seasonal flooding, as also observed in the field. The different patterns of Θ (or α) to aridity index along the aridity gradient were caused by the soil characteristics which in turn define water holding capacity (WHC) and hydraulic conductivity; for example, the plots in BOB were atmospherically drier (higher PET/MAP) than in ANK but they could hold more water (higher Θ). Especially in BOB-02, the infiltration rate was strongly reduced (60 mm/hr, less than half of ANK plots), and hence water can stay more time in the root zone while percolating. This acts as a buffer against the evaporative demand, maintaining water availability during dry months. The hydrological modelling outputs also matched with field observation of plot vegetation characteristics (see Methods).

For presentation (Figure 1), we rank sites by aridity index and then plots within sites by soil moisture stress.

The effect of aridity on traits

From a photosynthesis perspective, along the aridity gradient, we saw consistency between theoretical prediction and field measurements (Table 1) for all traits: ci/ca (0.71 to 0.85), V_{cmax25}

(21.58 to 46.48 umol CO_2 m2 s-1), J_{max25} (38.48 to 91.44 umol CO_2 m2 s-1), Rd (-1.66 to -2.41 umol CO_2 m2 s-1), Rs (3.76 to 11.70 umol CO_2 m2 s-1), Asat (4.56 to 7.72 umol CO_2 m2 s-1) and Amax (15.88 to 22.86 umol CO_2 m2 s-1). However, we saw less consistency between theory and field measurements regarding leaf economic traits (Appendix 3). Nmass was expected to increase from wet to dry but this is not backed by our field measurements. LMA was slightly higher in the dry sites than in the wet sites as theoretically expected, but not a gradual increase. Pmass increased gradually from wet to dry plots, (from 0.94 to 1.67 g kg-1) along the gradient in accord with global observation. Although the link among soil nitrogen, leaf nitrogen and photosynthesis was frequently made (Walker *et al.*, 2014; Gvozdevaite *et al.*, 2018), we found that such a link is rather ambiguous along the aridity gradient on site scale.

From a water transpiration perspective, the hypotheses were consistent with field measurements for leaf traits. AS/AL was higher in drier sites (359.62 to 901.66 cm2 m-2) and TLP was more negative in drier sites (-1.33 to -1.63 Mpa). However, no consistency was found between theoretical expectations and field measurements for any xylem-related traits. Along the aridity gradient, there was an increasing trend of field Kp toward drier sites (from 28.62 to 59.29 kg m-1 Mpa-1 s-1), against the xylem safety-efficiency trade-off. Behind the above trend, vessel diameter and vessel density also contradicted the hypotheses. Vessel diameter did not change along the aridity gradient, while vessel density increased toward drier sites (from 49.14 to 82.07 micron). The drier sites (KOG) had higher Kp, higher twig density and higher wood density than the wetter sites on site scales, but we also found Kp negatively correlated with twig density on species scales (see Appendix 4). ANK-01 had very high wood density and twig density which breaks the increasing trend formed by other plots. To conclude, the trends of all photosynthetic traits were successfully predicted by theories based on VPD alone. As leaf economy traits, soil nutrients and soil moisture (Θ or α) overall did not have a clear trend along the gradient, considering nutrient and water deliveries to leaves does not seem to aid the prediction of variation of photosynthetic traits along the aridity gradient.

With variance partitioning, we found that the plot-to-plot trends of all traits were dominated by inter-specific rather than intra-specific variation (i.e., components [a] are smaller than [b] in Appendix 5). Such a finding was expected as there are few common species between plots. The

analogous patterns between twig and wood density along the aridity gradient also supported species turnover since twig density was field measured and wood density was parsed from a global database by species (Zanne *et al.*, 2009). To double-check the conclusion of predominant interspecific variation, we recalculated community weighted means by assuming that the same species share the same value of trait (i.e. remove intraspecific variation) and extrapolated trait values to forest plots without trait measurements. We found that the conclusions in Table 1 still hold after extrapolation (Appendix 5). The trend of trait variation from plot to plot could be well re-constructed on a species basis, which hints at the possibility of extrapolation to other sites with species composition information or upscaling to larger scales. Nonetheless, for within plot variance, intraspecific variation or measurement errors (component [d]) were large for most traits: accounting for 95% of turgor loss point variance, followed by V_{cmax25} (74%) and J_{max25} (66%).

The coordination between photosynthesis and water transportation

Data from our West African aridity gradient reveal a weak positive correlation between Kp and AS/AL, contradictory toHypothesis 15, and inconsistent with the negative correlation that emerged on global scales (Appendix 4). AS/AL for the Ghanaian aridity gradient was higher than the pantropical average (Appendix 4). For hypothesis 16, we further explore the link between AS/AL, Kp and photosynthetic trait using PCA. Species with both high AS/AL and Kp tend to have higher V_{cmax25} and lower ci/ca. Such species tend to be deciduous and appear more in drier plots (Figure 2). There was a larger variance of hydraulic traits compared to photosynthetic traits (Figure 2). The pattern is consistent if we redo the above PCA with Asat instead of V_{cmax25} (Appendix 4). This finding supports hypothesis 16 (Table 1) as well as equation 3.

Discussion

The trend of traits along the aridity gradient

Although most hypotheses (Table 1) have been tested with spatially varying aridity at multiple scales (Harrison *et al.*, 2021), testing them along the Ghana aridity gradient helps to scrutinize the

pattern in the absence of temperature variation. The patterns of all photosynthetic traits measured along the aridity gradient (ci/ca, J_{max25}, V_{cmax25}, Dresp, Rs, Asat, Amax, namely hypotheses 1-7) are consistent with the theoretical expectations, which underscores that aridity is a direct and critical driver of photosynthetic traits, in absence of confounding effect with temperature. The increase of photosynthetic capacity towards drier sites is useful in explaining multiple previous observations, including that (1) savanna has higher photosynthesis rates than wet evergreen forest (Gvozdevaite, 2018; Oliveras *et al.*, 2020) (2) woody savanna has sparse canopy but similar net primary productivity to wet evergreen forest (Moore *et al.*, 2018) (3) for wet Amazonia forests, leaves flushed in dry season have higher photosynthetic capacities which increase forest productivity (Wu *et al.*, 2020; Green *et al.*, 2020).

From a water transportation perspective, forests in drier sites have higher TLP, lower H_{max} and higher AS/AL (agreed with hypotheses 8-10), in support of a greater mid-day transpiration stream. However, hypotheses derived from the safety-efficiency trade-off (hypotheses for Kp and vessel diameter) were not in agreement with measurements along the aridity gradient. It is possible that the trade-off may work well for single-species studies (Pritzkow *et al.*, 2020) and become weak on large scales and across species (Gleason *et al.*, 2016; Grossiord *et al.*, 2020b). Much higher deciduousness in KOG (dry site) than in the wet sites may play a role as higher hydraulic efficiency was reported from deciduous species or more deciduous forests (Choat *et al.*, 2005; Chen *et al.*, 2008; Liu *et al.*, 2021). We reported a negative correlation between AS/AL and Kp at global scales but a positive correlation along the aridity gradient (Appendix 4). One of the reasons for these contrasting opposite correlations may lie in a geographical sampling bias – the global dataset with scarce data points from West Africa compared with the Ghanaian dataset. The other possibility could be a confounding effect by temperature or vegetation type at the global scale (a Simpson's paradox); for example, a negative correlation between AS/AL and Ks was reported globally (Mencuccini *et al.*, 2019b) and on continental (Australia) scales (Gleason *et al.*, 2012), but an insignificant correlation was also reported for tropical forest stands on local scales without varying temperature (Poorter *et al.*, 2010; Schuldt *et al.*, 2013; Hoeber *et al.*, 2014).

By assuming that traits with a clear and strong trend along the aridity gradient are more tightly bound with aridity (Figure 1), ci/ca, TLP and AS/AL was found to be the most aridity-driven traits.

The runners-up are Rd, Rs, J_{max25}, and V_{cmax25}, which was thought acclimated to ci/ca and light intensity (Wang *et al.*, 2017b). Although ci/ca, Vcmax25, Kp and AS/AL all vary from wet to dry sites, the PCA (Figure 2) further illustrates that, surprisingly, it is photosynthetic traits instead of hydraulic traits that contrast species from wet to dry sites (also from evergreen to deciduous). Given that large photosynthetic traits variation from wet to dry plot was induced by species turnover (Appendix 5), our studies hint that facing a drier climate, if allowed time, West African forests photosynthesis could adapt to a drier climate by changing species abundance with possibly more deciduousness and higher photosynthesis capacity albeit less stomatal openness (Aguirre-Gutiérrez *et al.*, 2019). Without consideration of the positive effect of aridity on photosynthetic capacity, models could possibly underestimate forest productivity under future drier climates.

Combining photosynthesis and hydraulic hypotheses

Our analysis unifies photosynthesis and hydraulic hypotheses to explain plant strategies along the aridity gradient. Namely, species in drier sites (with more deciduousness) tend to develop a photosynthesis strategy with less stomata openness (ci/ca), stronger photosynthetic capacities (J_{max25} and V_{cmax25}) with more maintenance cost (higher Rd and Rs), quicker photosynthesis rate (Asat) and larger maximum transpiration, supported by large Kp and large AS/AL. The product of AS/AL and Kp is a proxy of water delivery per leaf area, which was previously found well correlated with proxies of photosynthesis rate: Asat (Santiago *et al.*, 2004), quantum yield of electron transport (Brodribb & Feild, 2000) and electron transfer rate (Brodribb *et al.*, 2002). The large variance of wood traits (way larger than leaf traits) (Mencuccini *et al.*, 2019b), hints that plants might have a wide range of choices of traits combinations to provide adequate water transportation (Sperry *et al.*, 2002; Prentice *et al.*, 2014) in drier sites to support faster photosynthesis. Further investigations into xylem functioning are required to understand how larger water transportation was achieved in drier sites. Notably, we successfully predicted plants photosynthesis strategies along the aridity gradient (hypothesis 1-7) based solely on VPD without incorporating leaf economic traits nor soil moisture. Nonetheless, our theoretical deduction implicitly assumes that plants in the drier site could arrange water transportation (e.g., high AS/AL and high Kp in Figure 2) and have adequate access to belowground water. Regarding the ongoing discussion on the impact of VPD versus soil moisture, soil moisture may be playing a role at other

temporal scales (e.g., daily) (Liu *et al.*, 2020; Fu *et al.*, 2022) or under extreme soil drought (Sperry *et al.*, 2002).

Conclusion

Along the aridity gradient, we found that species with both higher AS/AL and Kp (greater potential mid-day transpiration steam) tend to have higher Vcmax25 and lower ci/ca, which appears more in drier sites with more deciduous species. With such a working example in West Africa, the study not only underscores the importance of incorporating the positive effect of aridity on photosynthesis capacity in carbon modelling but also simplifies the coupling between carbon and water cycle: future modelling studies, following our theoretical framework, could estimate site-time-averaged leaf-level photosynthesis simply from VPD only and consider soil moisture (or water availability) in simulating forest stands dynamic such as drought-induced mortality or seasonality (Hubau *et al.*, 2020; Bauman *et al.*, 2022).

Data availability

Figures could be downloaded from

https://github.com/Hzhang-ouce/Ghana_rainfall_trait_variation_optimality_github. To reproduce figures, data and R codes mentioned in the main text could also be found in the above repository.

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Conflict of interest

The authors have no conflicts of interest to declare that are relevant to the content of this article.

Author contributions

IO, YM, ICP, and HZ designed the research and interpreted the results. DS did the hydraulic modelling. YM, AG, TP, MB, KZ, SAB, JAG, IO, HZ contributed to data collection. HZ carried out the analyses and wrote the paper with inputs and revisions from all co-authors.

Table 1 Traits name, unit, hypotheses and findings from field measurements along the rainfall gradient, Green color denotes consistency between theory and our field data. Orange color denote inconsistency.

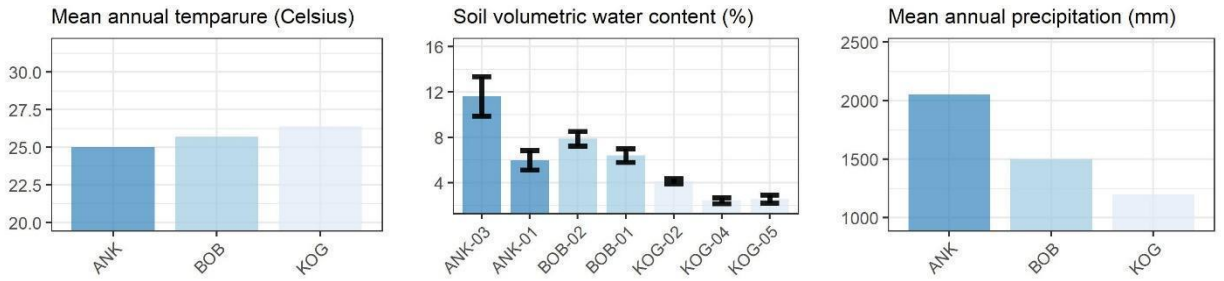
#	Hypotheses	Data	Consistent
	Variables associated with photosynthesis and respiration (Optimality theory)		
1	Toward drier sites, the ratio between leaf-internal and ambient CO2 (ci/ca, %) (from 13C) **decreases**.	Decrease	✓
2	Toward drier sites, Rubisco carboxylation capacity at 25 C° (Vc_{max25}, umol CO2 m2 s-1) **increases**.	Slight increase	✓
3	Toward drier sites, electron transport capacity at 25 C° (J_{max25}, umol CO2 m2 s-1) **increases**.	Slight increase	✓
4	Toward drier sites, light saturated assimilation rate at 400 ppm (Asat, umol CO2 m2 s-1) **increases**.	Increases	✓
5	Toward drier sites, light saturated assimilation rate at 2000 ppm (Amax, umol CO2 m2 s-1) **increases.**	Increase	✓

6	Toward drier sites, leaf dark respiration (Rd, umol CO2 m2 s-1) **increases**.	Increase	✓
7	Toward drier sites, specific stem respiration (Rs, umol CO2 m2 s-1) **increases.**	Increase	✓
	Variables associated with water transportation		
8	Toward drier sites, Sapwood to leaf area ratio (Huber value) (AS/AL, cm2 m-2) **increases.**	Increase	✓
9	Toward drier sites, turgor loss point (TLP, MPa) becomes more negative.	More negative	✓
10	Toward drier sites, plant stature, calculated as maximum tree height of a species (H_{max}, m) **decreases**.	Slight decrease	✓
11	Toward drier sites, wood density (g cm-3) and twig density (g cm-3) **increase** (if following the safety-efficiency trade-off).	Slight increase	✓
12	Toward drier sites, potential specific hydraulic conductivity (Kp, kg m-1 Mpa-1 s-1) **decreases** (if following the safety-efficiency trade-off).	Slight increase	
13	Toward drier sites, vessel diameter (micron) **decreases.** (if following the safety-efficiency trade-off).	No trend	
14	Toward drier sites, vessel density (mm-2) **decreases.** (if following the safety-efficiency trade-off).	Increase	
15	AS/AL and Kp are negatively correlated. (if following safety-efficiency trade-off, and global scale analysis – see introduction)	Positive correlation	
16	For species with high A_S/A_L and Kp, there is high Vcmax (or high Asat)	See Figure 3	✓

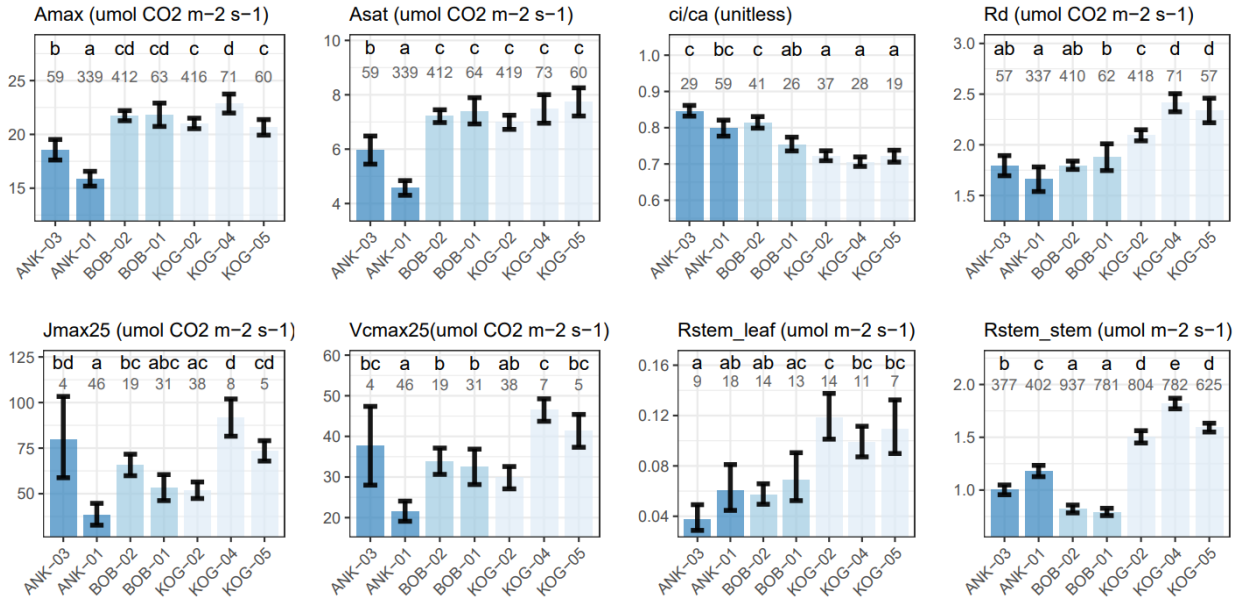
'Data' column summarize patterns in Figure 1. A trend of trait is qualitatively recognized if KOG (dry region) is significantly different to ANK (wet region) while BOB ranks between. 'Slight increase' suggest that the pattern fits the above criteria broadly albeit one plot behave inconsistently. Colours indicate results that are consistent (green), weakly consistent (light green) and inconsistent (orange) with theoretical expections. Ticks in the column 'consistent' indicate consistency between hypothesies and data

484

MAT, MAP and soil moisture



Variables associated with photosynthesis and respiration



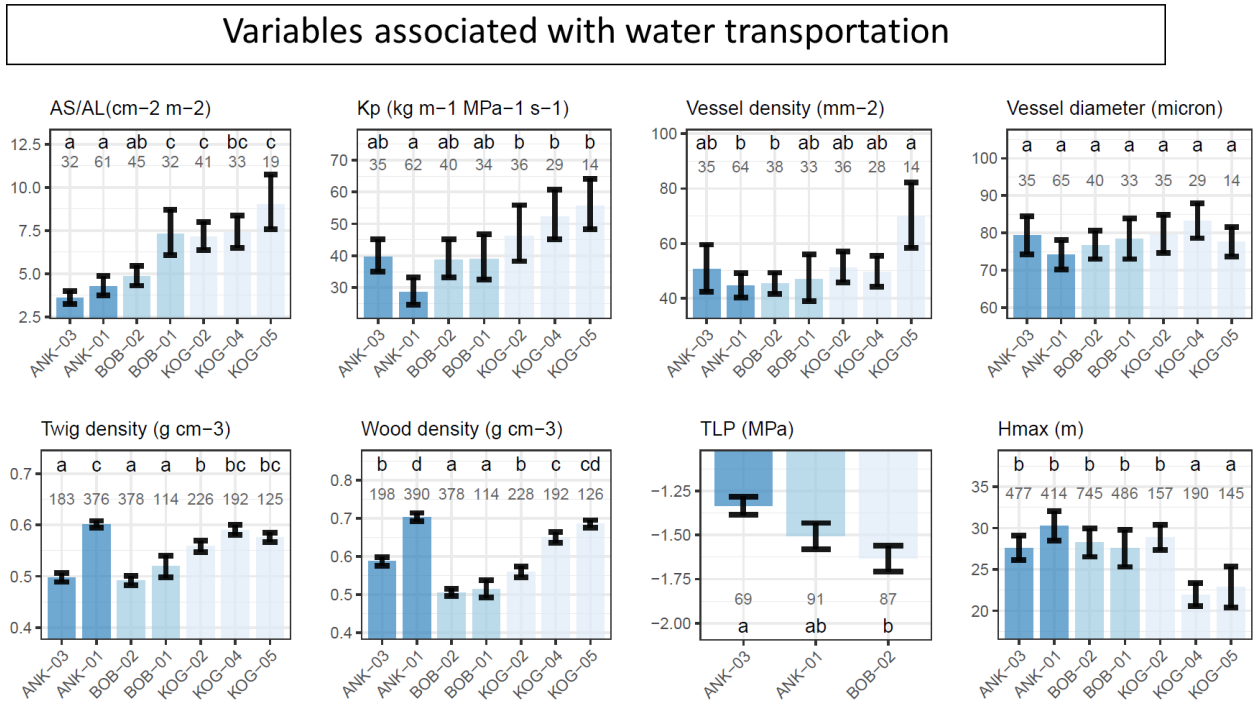
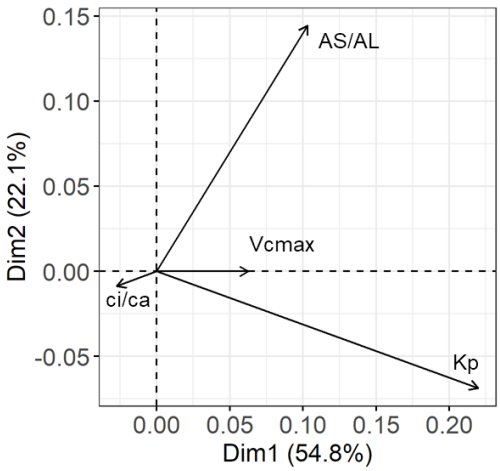
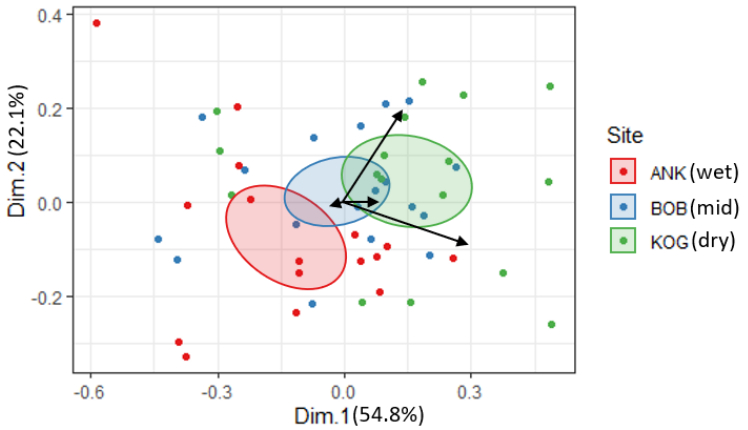


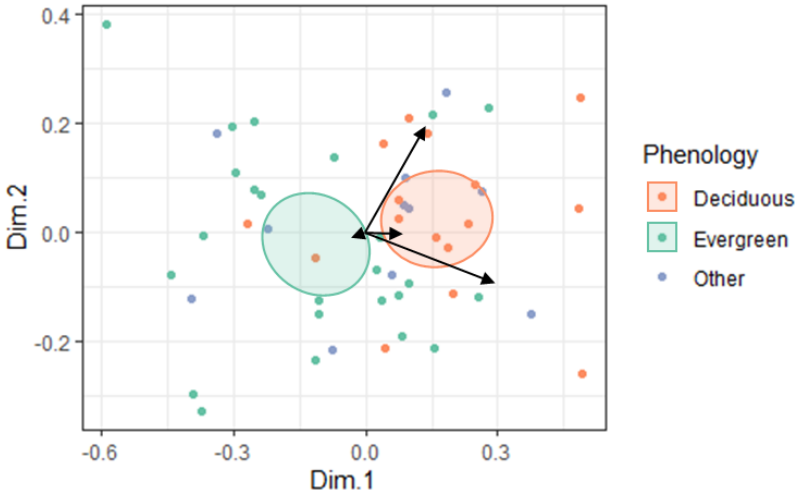
Figure 1 Plot scale community weighted mean (with standard error) from the wettest (left) to the driest (right) plot. Mean annual air temperature, precipitation and soil volumetric water content at 12 cm depth were also shown. Forest plots are arrayed from left to right in order of increasing aridity according to the aridity gradient description described in the text. The number denotes the number of samples, which could be a leaf, a branch, a tree or a species depending on the variable. The letters denote significance (P<0.05) in plot-to-plot difference.


AS/AL
Vcmax
ci/ca
Kp
Dim2 (22.1%)
Dim1 (54.8%)
0.15
0.10
0.05
0.00
-0.05
0.00
0.05
0.10
0.15
0.20

500


Site
ANK (wet)
BOB (mid)
KOG (dry)
Dim.2 (22.1%)
Dim.1 (54.8%)
0.4
0.2
0.0
-0.2
-0.6
-0.3
0.0
0.3

501


Phenology
Deciduous
Evergreen
Other
Dim.2
Dim.1
0.4
0.2
0.0
-0.2
-0.6
-0.3
0.0
0.3

502

Figure 2 Principal components analysis for Huber value (AS/AL), the ratio between leaf internal and ambient CO_2 (ci/ca), Rubisco carboxylation capacity at 25 degree (Vcmax25) and potential specific conductivity (Kp) on species scale. Values are transformed to achieve normal distribution but not standardized to equal variance; therefore the length of arrows denotes the variance of the specific trait. The ellipses for each site are confidence ellipses around group mean points. The PCA axes in all figures are identical. Note that the three figures display the same PCA, but with a different classification of scatter points.

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