**Research paper**

**Running head:** Soil and climate effects on photosynthetic traits

**Title:** Global soil and climate effects on leaf photosynthetic traits and rates

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**Abstract**

**Aim** The influence of soil properties on photosynthetic traits in higher plants is poorly quantified in comparison to that of climate. We addressed this situation by quantifying the unique and joint contributions to global leaf-trait variation from soils and climate.

**Location** Terrestrial ecosystems worldwide.

**Methods** Using a trait dataset comprising 1509 species from 288 sites, with climate and soil data derived from global datasets, we quantified the effects of 20 soil and 26 climate variables on light-saturated photosynthetic rate (Aarea), stomatal conductance (gs), leaf nitrogen and phosphorus (Narea and Parea) and specific leaf area (SLA) using mixed regression models and multivariate analyses.

**Results** Soil variables were stronger predictors of leaf traits than climatic variables, except for SLA. On average, Narea, Parea and Aarea increased and SLA decreased with increasing soil pH and with increasing site aridity. gs declined and Parea increased with soil available P (Pavail). Narea was unrelated to total soil N. Joint effects of soil and climate dominated over their unique effects on Narea and Parea, while unique effects of soils dominated for Aarea and gs. Path analysis indicated that variation in Aarea reflected the combined independent influences of Narea and gs, the former promoted by high pH and aridity, the latter by low Pavail.

**Main conclusions** Three environmental variables were key for explaining variation in leaf traits: soil pH and Pavail, and the climatic moisture index (ratio of precipitation to potential evapotranspiration). Although the reliability of global soils datasets lags behind that of climate datasets, our results nonetheless provide compelling evidence that both can be jointly used in broad-scale analyses, and that effects uniquely attributable to soil properties are important determinants of leaf photosynthetic traits and rates. Still, a significant future challenge is to better disentangle the covarying physiological, ecological, and evolutionary mechanisms that underpin trait-environment relationships.

**Introduction**

Natural selection promotes coordination in plants between the acquisition of soil-derived resources (water and nutrients), capture of solar radiation, and the uptake and fixation of CO2 from the atmosphere. The relative availability of key resources to plants varies by orders of magnitude over biogeographical gradients (e.g. Vitousek et al., 2004; Huston et al., 2012). Identifying how this variation shapes plant ecological strategies and key strategy traits is one of the central questions for ecology and biogeography (Westoby & Wright, 2006).

Photosynthesis can be construed as an economic process (Givnish et al., 1986). A trade-off between the substitutable costs of maintaining the capacities for carboxylation (Vcmax) and transpiration was theoretically predicted and then confirmed by experimental observation along an Australian aridity gradient with annual precipitation ranging from *ca*. 400 to 1100 mm (Prentice et al., 2014). From dry to wet habitats, plants maintain comparable photosynthetic rates by increasing their water use with high stomatal conductance (gs) while reducing investment in photosynthetic proteins resulting in low leaf N and Vcmax (Wright et al., 2003). Analogously, along a gradient from nutrient-poor to nutrient-rich habitats, plants were shown to rely increasingly on high leaf N while reducing water use by operating at lower gs (Wright et al., 2001). However, along the gradient studied by Wright et al. (2001), covariation of soil texture, cation exchange capacity, organic matter content and total N and P concentrations precluded a more differentiated analysis of soil effects.

Moreover, the impact of soil on photosynthetic traits has rarely been studied at a global scale (Ordoñez et al., 2009; Ordonez & Olff, 2013). Investigation of this relationship is challenging because climate is both a major control of photosynthetic traits (e.g. Reich & Oleksyn 2004) and an important driver of soil development. According to Albrecht’s conceptual model (Huston, 2012), soil total exchangeable bases, soil pH, soil total P and N content, and plant productivity should all decline along a gradient from intermediate to high rainfall, and from young high-latitude soils to older, low-latitude well-weathered soils (Walker & Syers, 1976). Soil fertility, sometimes defined by exchangeable base cations or soil pH (Quesada et al., 2010), might thus be expected to be inversely related to water availability and this trade-off might be reflected both in increasing stomatal conductance and decreasing carboxylation capacity towards warm and wet climates.

However, this one-dimensional view of covariation between soils and climate is likely an oversimplification. Soil fertility can also be defined in several other ways. Conceptual models of long-term ecosystem development have tended to focus on the negative covariation between time-trajectories of P and N availability in soils, with highest productivity at intermediate N:P ratios (Vitousek, 2004). In such schemes N is assumed to be more limiting in young soils, often at higher latitudes, since it accumulates mainly via atmospheric fixation of N2 and becomes available to plants mainly via decomposition of organic matter; whereas in old and deep soils, mostly at lower latitudes, P provided mainly by the parent rock chemistry and its weathering rates becomes a limiting factor for plant growth (Reich & Oleksyn 2004; Peltzer et al., 2010). In this scheme the relative cost associated with the maintenance of carboxylation should increase at the extremities of soil development time-trajectories, either limited by soil and leaf N or by soil and leaf P (Niinemets et al., 1999; Reich et al., 2009; Maire et al., 2012). Finally, biogeochemical models of ecosystems have tended to adopt a narrow definition of fertility, focused on the ability of soils to release plant-available forms of nutrients from litter and soil organic matter (SOM), the decomposition of which is supposed to be mainly a function of the initial SOM and temperature (Hakkenberg et al., 2008), as well as which micro-organisms are present (Fontaine et al., 2011). The implications of this scheme for photosynthetic costs are less clear. Globally, these differing concepts of soil fertility continue to exist side-by-side in the literature but, to date, none of the broad concepts has been embedded in a global, predictive framework for plant traits. Indeed, shifting and ambiguous definitions of ‘fertility’ may have hindered the development of such a framework. With sufficient data, however, it should be possible to tease apart the effects of the various edaphic drivers on photosynthetic traits, and to separate influences of edaphic and climatic determinants of photosynthesis.

Recently, a global soil dataset with consistency, reliability and resolution approaching those available for climate has become available with SoilGrids (ISRIC, 2013), which is complementary to the ongoing update of the conventional Harmonised World Soil Database (FAO et al., 2012). These soils data can be linked with global datasets containing climate variables and plant traits, making it possible for the first time to quantify the unique contribution of soil variables to leaf traits across the range of global ecosystem types. We performed such an analysis, with the following questions: (1) How do leaf photosynthetic traits vary with different facets of soil fertility? (2) What are the most individually-important soil and climate variables in terms of explaining variation in these leaf traits? (3) What proportions of leaf trait variation can be accounted for by joint effects of soils and climate, as opposed to by unique effects of soils and of climate? As climate and soil co-vary, the joint effect of soil-climate may dominate the unique effects of climate and soil (Reich & Oleksyn 2004). As different soils are encountered in a given climatic envelope, a significant unique effect of soils may be expected. (4) Variation among species in photosynthetic rates depends both on variation in leaf N and in gs. Are these two independent trait dimensions promoted by independent climate and soil dimensions? (5) Finally, what is the minimum set of environmental and trait variables to represent interrelationships between photosynthetic rates and associated traits? To answer each question, a step-by-step statistical approach was followed (described below), with the ultimate aim to disentangle soil and climate effects on leaf traits and photosynthetic rates.

**Material and Methods**

**Trait data**

The ‘Glopnet’ dataset (Wright et al., 2004) provided the starting point for present analyses. Data of field-measured photosynthetic capacity (Aarea, µmol m-2 s-1), stomatal conductance to water vapour (gs, mmol m-2 s-1), N and P per unit leaf area (Narea and Parea, g m-2, respectively) and specific leaf area (SLA, cm2 g-1) were supplemented by other sets of geo-referenced observations of these traits (Appendix S1 in Supporting Information). The final database (Appendices S2-3) consisted of 2400 Species×Site combinations including 288 sampled sites and 1509 species from 165 families. 325 species occurred at more than one site. The dataset contained a variety of growth forms (661 trees, 399 shrubs, 313 herbs, 88 grasses, 32 ferns and 16 vine species), phenologies (316 deciduous, 14 semi-deciduous and 735 evergreen species), and physiologies (i.e., C3 and C4 species, N2-fixing and non-fixing species). Aarea varied 190-fold across the dataset (*n* = 2337, from 0.34 to 65.05 µmol m-2 s-1), gs varied ca. 110-fold (*n* = 1035, from 21 to 2272 mmol m-2 s-1), Narea and Parea varied ca. 40 (*n* = 1643 from 0.26 to 9.47 g N m-2) and 50-fold (*n* = 512 from 0.017 to 0.923 g P m-2), respectively, and SLA varied ca. 50-fold (*n* = 1965, from 12.8 to 608 cm-2 g-1). By comparison, the 2004 Glopnet dataset had Aarea data for 825 Species×Site combinations, and gs data for 500.

**Environmental data**

*Climatic drivers*

Photosynthetically-active quantum flux density, temperature, rainfall and aridity are key climatic determinants of plant processes. Twenty-six climate variables representing these aspects of climate were considered (Table S3-1). When available, mean annual temperature and precipitation data were taken from the source publications for the leaf data. Otherwise, climate data were extracted from a global, three-dimensionally interpolated 10’×10’ data set for 1961-1990 (Climatic Research Unit, CRU CL2.0, New et al., 2002). We obtained monthly and annual means of temperature, rainfall, fractional sunshine duration and relative humidity. We also considered maximum and minimum values, seasonal variability, and growing-season mean values (defined alternatively based on a 0˚C and a 5˚C basis) of temperature, precipitation and sunshine duration. Next, several bioclimatic variables were calculated following Wang et al. (2014): annual global radiation, total annual incident radiation during the growing season, and annual equilibrium evapotranspiration (a function of net radiation and temperature). Aridity was (inversely) described by the moisture index (MI; ratio between precipitation and potential evapotranspiration, PET), with PET calculated in two ways: PETF (using the Penman-Monteith formulation; FAO, 2004), and PETQ (using equilibrium evapotranspiration to represent potential evapotranspiration; Wang et al., 2014), yielding MIF and MIQ, respectively (see Table S3-1 for full list of descriptions).

*Edaphic drivers*

Soil variables that express long-term pedogenetic characteristics, to which plants adapt over generations, can be contrasted with those reflecting more rapid within-season changes (Peltzer et al., 2010). We considered only the former type, choosing to avoid fast-changing variables like N mineralisation rate. Key edaphic determinants of plant processes include the texture and structure of soils, ion exchange capacity, and macronutrient contents of the top soil layer (see Table S3-1 for full list). Soil data were extracted using the ‘*raster*’ package in R 3.0.1 (R Core Team, 2013) from three, spatially interpolated, global datasets. SoilGrids (0-22.5cm layer, ISRIC, 2013) – an automated system that produces soil datasets derived from digital soil mapping (Hengl et al., 2014) – and the Harmonised World Soil Database (0-30cm layer, FAO et al., 2012) are interpolated at 30” × 30” resolution and provide the majority of soil variables (organic matter content, pH, cation exchange capacity, texture and structure of soils). Soil N content and C:N ratio, aluminium saturation and available water holding capacity of the 0-20 cm layer were extracted from the 5’×5’ ISRIC-WISE dataset (Batjes, 2012). If several soil types occurred within a grid cell, soil property estimates correspond to the area-weighted profile mean.

We also constructed a dataset for soil available P concentration (Pavail) based on information from several sources (see Appendix S4 for details). In brief, we first assembled geo-located soil profiles from several soil phosphorus datasets (e.g. Batjes, 2011a; Shangguan et al., 2013; Tóth et al., 2013). When the distance from the nearest profile was less than 100 km we recorded the nearest soil profiles for each site in the plant trait dataset. Otherwise, we did a literature survey to search for data from closer locations. Pavail values were harmonized to a single chemical extraction method (Bray & Kurtz, 1945), based on published conversion factors. The broad-scale reliability of the harmonised Pavail data was confirmed using categorical information: the global distribution of soil P retention potential (Batjes, 2011b) and the weathering stage associated with the soil orders of plant trait sites (Appendix S4).

Climate conditions varied widely among the 288 study sites: mean annual temperature ranged from -21.4°C to 27.3°C, annual precipitation from 23 to 5406 mm, mean annual moisture index from 0.09 to 6.54, covering most of the temperature-rainfall space in which higher plants are found. Soil conditions also varied widely: total exchangeable bases (TBA) ranged from 75 to 1801 cmol kg-1, soil pH from 3.5 to 8.4, total soil N (NTOT) from 0.3 to 16.7 g kg-1, Pavail from 0.2 to 960 mg P2O5 kg-1, and clay fraction from 2 to 42 % (Figs. S3).

**Data analysis**

*Data selection and transformation* - Being right-skewed, all plant traits were log-transformed. Environmental variables were subjected to the Yeo-Johnson transformation (‘*car*’ package; R core team, 2013); this provides a powerful way of reducing skewness and can be applied to variables that include negative values (see details in Table S6-1).

Five methodological steps were defined, each one dedicated to one of the five questions presented in the introduction. Details, benefits and limitations of each step are described in Table S6-2.

*Step 1: Defining key dimensions of soil fertility and quantifying their relationships with leaf traits*

A general theoretical approach based on existing conceptual models of soil and ecosystem development over geological time scales (Vitousek, 2004; Peltzer et al., 2010; Huston, 2012) was used to predict relationships between soil pH and each of several main facets of soil fertility, i.e. TBA, organic C content (Corg), Ntot, Pavail, and available water holding capacity (AWHC). We compared the observed relationships to those predicted, first fitting quadratic regressions (to accommodate non-linearity) and then linear models whenever the square term of the quadratic model was non-significant (see Appendix S8 for more details). A systematic analysis of the impact of each soil and climate variable on each trait was realized (Figs. 2, S8). In mixed models, the fixed-effect term was the soil or climate variable allocated to each site; site and species were considered as random intercepts (making standard assumptions of normality, independence and homoscedasticity). The site and species effects were included to reflect the hierarchical structure (multiple species at multiple sites) and the unbalanced and nested structure (different number of samples/species between sites) in the sampling design. Models were fitted using the R package ‘*lme4*’ and adjusted *r*2 values () were calculated following Moles et al. (2009).

*Step 2: Selecting the most important climatic and soil variables for explaining leaf trait variation*

Next, for each trait we used a stepwise multiple mixed regression model to select up to four explanatory variables from among the various available climate and soil variables (Table S3-1), by minimizing the Akaike information criterion (Legendre & Legendre, 2012). Site and species effects were treated as random factors. R packages ‘*lme4*’ and ‘*MuMIn*’ were used.

*Step 3: Quantifying unique and joint effects of soils and climate for explaining variation in each leaf trait*

In this step we used variation partitioning and Venn diagram illustration (Legendre & Legendre, 2012) to partition the total variation explained in each leaf trait into components explained uniquely by the matrix of soil variables, uniquely by the matrix of climate variables, or (jointly) explained by the combined soil and climate matrices. For these analyses we used the soil and climate variables identified as part of Step 2 (see Table 1 for the selected soil and climate variables) and multiple mixed regression models. The unique effect of soil (or climate) was calculated as the difference between the full model and the climate (or soil) model. The joint effect of soil and climate was calculated as the difference between the summed of soil and climate models and the of the full model.

*Step 4: Quantifying the explanatory power of soils and climate for the matrix of leaf traits*

Photosynthetic rates can be understood as the outcome of coordinated investments in water transport capacity, needed to support a high rate of gs, *versus* Rubisco carboxylation capacity, indexed by Rubisco activity (Vcmax) – potentially related to both Narea (e.g. Wright et al., 2003) and Parea (e.g. Niinemets et al., 1999). To test whether and how soil and climate variables can distinctively promote these different drivers of leaf photosynthesis it is important to consider the relationships among leaf traits in the same analysis (Steps 4 and 5). First, we used redundancy analysis (‘*vegan*’ package, R core team, 2013) to quantify how much of the variation in the matrix of leaf traits could be explained by the matrices of the most important soil and climate variables selected at Steps 2 and 3. For leaf traits we used Aarea, gs, Narea and SLA (giving a dataset of 647 species from 99 sites). Parea, with its considerably smaller sample size, was left out of this analysis.

*Step 5 – Disentangling direct and indirect effects of leaf traits, soil and climate on photosynthetic capacity*

We used path analysis (‘*lavaan*’ package, R core team, 2013) to explore how variation among species in Aarea can best be understood as driven by both direct and indirect effects of gs, Narea, SLA and the key environmental drivers identified in previous steps, selecting the model that was the least different from the observations (*p*-value > 0). Note that Steps 4 and 5 are complementary (Table S6-1), with Step 4 testing the relationships between matrices without *a-priori* constraints, while Step 5 allowed us to evaluate possible *causal* effects of soil independent of climate on leaf traits (Legendre & Legendre, 2012).

**Results**

**Step 1a: Two dimensions of soil ‘fertility’**

Figure 1 (panels a-e) summarises expected relationships between soil pH and each of several dimensions of soil fertility. From high to low soil pH (right to left) – that is conceivably, from young soils where the parent rock supplies cations and phosphorus, to older and more highly weathered soils, remote from the parent material but enriched in SOM – Figure 1 indicates:

* A decrease of total exchangeable bases, but an increase in Al and Fe content (Fig. 1a).
* An increase in total C and N and AWHC, due to the accumulation of SOM (Fig. 1b-d). In addition, Navail is expected to follow Ntot up to a maximal value at intermediate pH, where optimal conditions for microbial nitrogenase activity are reached. Thereafter, Navail decreases steeply with increasing pH (Walker & Syers, 1976).
* A decrease in Ptot (Lambers et al., 2008; Fig. 1e) with increasing distance (and time) to the parent rock, where P is sourced. However, Pavail may show a humped distribution as P can co-precipitate with Ca at high pH and with Fe and Al at low pH.

Our data substantially matched these predictions (Figs. 1f-i). As soil pH increased, so did TBA, soil base saturation and to a lesser extent soil carbonate content, while Al saturation decreased (correlations given in Table S7-3). Quadratic relationships accounted for the relationships between pH and Corg and between pH and Ntot (Figs. 1g,h). AWHC and the climatic moisture index (MI) decreased linearly with pH (Fig. 1i). Contrary to expectation, however, no relationship was found between pH and Pavail (Fig. 1j). High Pavail was encountered at high-pH sites that were characterised by low carbonate content, but also at low pH sites characterised by low Al saturation.

These relationships suggested the existence of two principal dimensions of soil fertility. Soil pH indexes a first dimension along which exchangeable bases, Navail, Corg, Norg and AWHC covary, and the availability of micronutrients and N trade off with the availability of water. A second, largely independent dimension is indexed by Pavail, which covaries negatively with Al saturation, soil depth and clay content, and positively with gravel content (Table S7-3).

**Step 1b: Relationships between individual leaf traits and soil variables**

We quantified bivariate relationships between the five photosynthetic traits and five soil variables (Pavail and 4 variables from fertility dimension 1: soil pH, Corg, Ntot, and AWHC). Aarea, Narea and Parea all increased linearly with soil pH (*r*2 = 0.12 to 0.17; Fig. 2), while SLA decreased (*r*2 = 0.06). Note that the corresponding mass-basis traits also increased with soil pH, but with notably lower *r*2 than on an area basis (all *r*2 < 0.03, *p* < 0.002; not shown).

As expected from their negative co-variation with soil pH along fertility dimension 1 (Fig. 1), Corg, Ntot and AWHC affected SLA, Narea, Parea and Aarea in the directions opposite to the pH-related effects (Fig. 2). The pH-leaf trait relationships all remained significant after accounting for co-variation with mean annual temperature and precipitation (dashed lines in Fig. 2). However, this was not the case for relationships involving Corg, Ntot and AWHC.

Stomatal conductance, gs, showed little patterning along fertility dimension 1, the strongest relationship being a very weak dependence on soil N (*r*2 = 0.02; Fig. 2l). By contrast, both gs (negative) and Parea (positive) showed strong patterning along fertility dimension 2 (i.e. varying with Pavail). These relationships were little changed by concurrently accounting for climate (dashed fitted lines, Figs 2v,x). Unexpectedly, Pavail was the strongest single environmental predictor of gs (the strongest climate predictor being precipitation seasonality, *r*2 = 0.06; Fig. S8-1). Indeed, the single strongest predictor for each leaf trait was a soil variable (pH for Aarea, Narea and SLA; Pavail for gs and Parea; full details in Fig. S8-1).

**Step 2: Selection of the most important soil and climate variables**

As in bivariate relationships (Figs S81-2) but using stepwise multiple regressions, for explaining variation in each trait soils did a better job than climate, and in the case of Aarea and gs soils explained more than twice as much variation as climate (*r*2 = 0.195 and 0.241 versus 0.098 and 0.102, respectively; Table 1). As judged by *F*-values, soil pH and Pavail were the two soil variables that had the greatest effect on leaf traits, while MIQ was the most important climate variable (Table 1).

**Step 3: Quantification of unique and joint effects of soil and climate on leaf traits**

Using variation partitioning, 21-31% of variation was explained for each trait except Parea, with 54% (Fig. 3). Overall, soils explained more variation in leaf traits than did climate, with this effect strongest for Aarea and gs. For the other traits (Narea, Parea and SLA), about half the total variation explained was accounted for by the common patterns of variation in climate and soils (the “joint” effects).

**Step 4: Multidimensional co-variation between soils, climate and leaf traits**

We used redundancy analysis to better understand how the structure in the matrix of leaf traits could be explained with the structure in the matrix of the most important soil and climate variables (selected at Step 2). Note, first, that Aarea covaried significantly with gs, Narea, Parea and SLA (*r*2 = 0.76, 0.14, 0.07, 0.01, respectively). Thirty percent of variation in the four-trait matrix was explained by soils and climate (Fig. 4). Vectors representing variation in Narea and gs were orthogonal and clearly associated with a number of environmental variables, while the vectors for Aarea and SLA were also orthogonal to each other, and less clearly associated with environmental variables. In this analysis Narea was mainly explained by soil pH and by MIQ, with high values of Narea found in arid sites on soils with high pH. gs was mainly explained by Pavail, bulk density, sand content and growing season temperature, with high values of gs found in warm sites on compact soils with low Pavail values.

**Step 5: Interdependencies between key site variables and photosynthetic traits**

Three environmental variables were repeatedly shown to be key for explaining variation in leaf traits: soil pH, soil available P, and moisture index. We used path analyses to explore the interdependencies between these variables and the key photosynthetic traits, Aarea, Narea and gs. The most parsimonious path analysis model explained 64% of the variation in Aarea (Fig. 5). This diagram shows that high MI promotes acid soils. High MI and acid soils both, independently, promote low Narea. High Pavail and arid climate both, independently, promote low gs. Both gs and Narea independently determine Aarea, in accord with theory (Wright et al., 2003). There are also significant direct effects of MI and pH on Aarea that are in the same direction as, but not accounted for, by the effects of Narea and gs. Note that when SLA was added (considering its impact on Narea, gs and Aarea, and depending on MIQ and pH), the models were consistently far weaker; hence they are not presented.

**Discussion**

Climate plays a key role in soil development (Jenny, 1941); this leads to correlations among present-day soil and climate variables, and interactive effects of soils and climate on plant traits. We identified two main dimensions of environmental variation, key to understanding variation in leaf photosynthetic traits, which we discuss in relation to concepts of soil and ecosystem development.

**A soil pH – aridity dimension**

The first dimension was most strongly associated with soil pH (and exchangeable cations) decreasing with increasing precipitation and MIQ. Higher values of Narea, Parea and Aarea were found in more arid sites and on higher pH soils, but gs was unrelated to this dimension.

The tendency for species to have higher Narea (and, less so, Parea) at drier sites is well known (Field et al., 1983; Schulze et al., 1998), and accords with theory which predicts the predominance of high Narea strategies as a means to economise on water use during photosynthesis (Farquhar et al., 2002; Wright et al., 2003, discussed further below). By contrast, broad-scale patterning of leaf traits with soil pH has rarely been reported (but see Han et al., 2011) and is correspondingly less well understood. These pH-related relationships were not simply secondary correlations flowing from the well-documented regional negative relationships between soil pH and precipitation, but likely relate to non-climatic determinants of soil pH, like parent rock and topography (Jenny, 1941). Soil pH is implicated in many soil chemical, enzymological and microbial processes that affect micronutrient and nutrient availability (see Sinsabaugh & Follstad Shah, 2012 as a review) and, therefore, Narea and Parea. Considered across a broad gradient of soil types, higher pH should generally equate to faster and/or higher availability of nutrients held in SOM and overall reduce the acquisition costs of N and thus the costs of achieving a given biochemical capacity for photosynthesis.

Conversely, higher SOM concentration (indexed by Corg or Ntot) does not necessarily denote higher N availability. In acid conditions SOM becomes recalcitrant, and N availability is correspondingly low (Jenny, 1941). Hence, here and elsewhere (Santiago et al., 2005; Ordoñez et al., 2009), we found the counter-intuitive result that leaf N decreased with increasing soil total N.

Interestingly, the first dimension of soil fertility associated partially with the variation of Aarea seems to be unrelated to gs. Thus, the tendency of plants sampled locally to be strongly co-varying in Aarea and gs and hydraulic properties (Reich, 2014) does not hold in the same fashion across very broad climate and soil gradients, supporting the hypothesis that trade-offs between water vs. nutrient use predominate at larger scales.

**The soil available P dimension**

The second key environmental dimension was represented by Pavail in the topsoil horizon, co-varying with the sand content and bulk density of soil, and site temperature (Fig. 4; Table S7-3,4). Both leaf Parea and gs showed strong patterning with this dimension, with higher Parea but lower gs (but not Aarea) on soils with higher Pavail.

Our study sites represented a broad range of soil types and Pavail, from highly weathered soils where P limitation is widespread (representing 33% of our sites, e.g. Oxisols; Table S4-4), to less (low) weathered soils with typically higher Pavail (21% of our sites, e.g. Inceptisols). While the Pavail part of our soil dataset was unavoidably underpinned by fewer soil profile data than for variables such as pH and Corg, our confidence in these data was boosted by observing positive relationships of Pavail with Parea, altitude and latitude, and its negative relationships with clay content, soil depth, and Al saturation (Table S7-4) – echoing relationships known from regional field studies (Vitousek, 2004; Walker & Syers, 1976).

We have various prospective explanations for the observation that species on higher P soils tend to team their maximum photosynthetic rates with lower stomatal conductance, but no clear way yet to identify the most likely explanation, nor to place them into an optimality framework as has been done for climate-related effects on gs (e.g. Medlyn et al., 2011).

Experimentally lowering soil nutrient availability is known to stimulate higher root:shoot ratios (e.g. see Poorter et al., 2012 for a comprehensive analysis), which may in turn improve plant water balance, and hence allow for a higher gs. Conversely, at a given root:shoot ratio, an increase in gs in response to nutrient deficiency has been proposed as an evolutionary mechanism to improve plant nutrition, through an increase in the transpiration rate and the mass-flow of water from the surrounding soil (Edwards et al., 1998; Cramer et al., 2009). This “mass-flow” hypothesis is generally thought to apply more so to soil inorganic N than to less mobile P (Cramer et al., 2009), but higher gs has also been observed under P deficiency for some species (Raven et al., 2004).

Alternatively, in ‘least-cost’ photosynthetic optimality theory (Wright et al., 2003), water and nitrogen supplies are considered as substitutable resources to secure carbon, and the optimisation of Aarea involves minimising the sum of costs for acquiring and using N and water in photosynthesis. At higher soil N availability, where N acquisition costs are lower and therefore water acquisition costs are relatively higher, plants are expected to operate at a given Aarea with a higher Narea and lower gs. It is conceivable that soil P and leaf P also fit into this framework, e.g., that higher leaf P enables a higher carboxylation capacity for a given leaf N (Niinemets et al., 1999; Reich et al., 2009). The same prediction (a higher Narea and/or a lower gs for a given Aarea) would be made for a scenario where N acquisition costs were lower because of higher N availability due to more alkaline soil. Perhaps all of these effects could come into play in understanding the general trade-off between Vcmax and water use (Farquhar et al., 2002; Wright et al., 2003; Prentice et al., 2014).

**Limitations of our analyses**

Underpinning the use of gridded soils data, we made the assumption of a high signal-to-noise ratio, and overall good match between ‘actual’ and spatial dataset values. Our observations of geography-soil, climate-soil and trait-soil relationships, which were in agreement with many ones observed in literature with *in situ* soil variables measured at various scales (see details in Appendices S5 and Table S7-4), supported this. Nonetheless, we stress that local-scale variation in soil properties can certainly be large (Yemefack et al., 2005) and that for more detailed assessments, values measured *in situ* at the respective plant trait sites would be ideal.

While one’s ability to reliably tease apart the independent roles of soil and climate is limited in various ways in any statistical analysis (and especially since climate and soils co-vary) we chose path analysis as the method that most closely approached the issue of identifying causal structures (Legendre & Legendre, 2012). In combination with and complementary to the other used approaches (see Table S6-2 for benefits and limitations of each statistical method), we provided evidence that soils modify Aarea, gs and Narea independently from climate. That said, we must not forget the possibility that these patterns may just be (or also be) markers of longer-term and more important factors associated with soil development, like parent rock, topography, soil age and vegetation (Jenny, 1941).

**Conclusion**

A key result of our study is that, in a multivariate trait-environment space (Figure 4), there are two distinguishable dimensions of soil-climate variables influencing the two leaf traits (Narea and gs) that, together, largely constrain photosynthetic activity. Soil pH and available P emerged as the best soil predictors of variation along these gradients and, indeed, overall we found stronger patterning of photosynthetic traits according to unique effects of soils than to those of climate. Plant geographers have long-recognised that plant traits vary in concert with soil properties (e.g. Schimper, 1903), but only rarely have such patterns been quantified at a broad spatial scale. This work represents an important step towards a better understanding of geographic variation in leaf photosynthetic strategies, and to progress towards more reliable modelling of global vegetation function.

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Additional references to the data sources used in this study are found in appendices S1 and S2 at the DRYAD Digital Repository (http://datadryad.org/).

**Biosketch**

This research team aims to develop better understanding of trait-environment interactions, particularly for use in “next-generation” vegetation models based on plant functional traits.

Expertise within the team extends from plant ecology to physiology to soil science and ecological theory.

Author contributions: VM, IJW, ICP conceived the ideas and drafted the article; IJW assembled the dataset with help from AO and VM. VM performed the analyses. All authors contributed to the writing.

**Table Legends**

**Table 1**. Multiple mixed regression relationships between area-based leaf functional traits (Aarea, leaf photosynthetic rate; gs, stomatal conductance; Narea, leaf nitrogen content; Parea, leaf phosphorus content; and SLA, specific leaf area) and soil and climate subsets of environmental variables. Following a stepwise procedure criterion selecting the most important variables among 26 climate or 20 soil variables (see methods and Table S3-1 for details) based on an AIC criterion, linear mixed regression models were used to measure the impact of environmental variables on each trait. Site and species were treated as random factors (intercepts). The adjusted r2 and Aikaike information criterion (AIC) are provided for each regression model (see methods for details on *r*2 calculation). *F*- and *p*-values for type III-error models are specified for each fixed soil factor. Factors 1 to 4 correspond to the rank of each fixed factor that was selected in the regression model. Leaf trait variables were log-transformed and environmental variables were power-transformed as described in Methods. Arrows indicate the sign of the coefficient estimate. See Tables S8-4,5 for equation details. °, *p* < 0. 1; \*, *p* < 0.05; \*\*, *p* < 0.01; \*\*\*, *p* < 0.001. Abbreviations: MIQ, Moisture index representing the ratio between annual precipitation and equilibrium evapotranspiration; TMPrange, mean diurnal temperature range; SUNmax, maximum monthly fractional sunshine duration; TMPmax, maximal monthly temperature; TMP0nb,number of days with daily temperature above 0˚C; PPTseason, seasonality of precipitation; RH, relative humidity; pH, soil pH; Ntot, soil total nitrogen content; CECS, cation exchange capacity, Pavail, available soil phosphate content; SALT, soil salinity; SAND, soil sand content; SILT, soil silt content; BULK, soil bulk density.

**Figure Legends**

**Figure 1:** Theoretical (a-d) and observed (e-h) relationships between soil variables describing the availability of main resources (cations, nitrogen, phosphorus and water) that plants use in photosynthesis. Soil pHwater is considered here as a proxy of the stage of soil evolution, and thus as a key variable expressing the dynamics of soil resources between the different sites used in this study. The various panels show dynamics of: (a,f) total soil exchangeable bases; (b,g) soil organic C content; (c,h) soil available nitrogen and total N content; (d,i) soil available water holding capacity, considering also precipitation (PPT) and moisture index (MI); and (e,j) soil available phosphorus and total P content (prediction for Ptot based on Lambers, 2008). Regression models (*n* = 288 sites): (f) log(TBA) = -0.40 + 0.22·pH, *r*2 = 0.50; (g) log (Corg) = 1.09 - 0.04·pH2 + 0.31·pH, *r*2 = 0.33; (h) log (Ntot) = -0.91 - 0.05·pH2 + 0.47·pH, *r*2 = 0.12; (i) log(AWHC) = 1.40- 0.38·pH, *r*2 = 0.10; pH = 5.9- 2.1·log(MIQ), *r*2 = 0.54. All relationships were significant at *p*-value = 0.001 level.

**Figure 2:** Relationships between area-based leaf photosynthetic traits and soil variables considered in the theoretical soil development model (Fig. 1). Leaf photosynthetic rate (*n* = 2400; a, f, k, p, u), stomatal conductance (*n* = 1070; b, g, l, q, v), leaf nitrogen content (*n* = 1704; c, h, m, r, w), leaf phosphorus content (*n* = 532; d, i, n, s, x) and specific leaf area (*n* = 1964; e, j, o, t, y) regressed on soil pH (a-e), soil organic C content (f-j), soil total nitrogen content (k-o), soil available water holding capacity (p-t) and soil available phosphate content (u-y) according to linear relationships using mixed regression models with site and species as random factors. Solid lines correspond to the significant regressions for which statistical information from mixed regression models (*r*bi2 and *p*-value) are reported on each caption. Equations are reported below. Dashed lines correspond to the impact of the soil variable in multiple mixed regression models, including two important climatic variables that can impact leaf traits (PPTmean and TMPmean, Wright et al., 2004). These conditional slopes (‘*visreg*’ package, R core team, 2013) indicated the bivariate soil-trait relationship calculated while holding constant (at their median) the two climate variables. Significance of the soil variable and its relative importance, *ri*, (‘*relaimpo*’ package, R core team, 2013) in the multiple mixed regression model is reported on each caption. Statistical significance is indicated using asterisks, \*, *p* < 0.05; \*\*, *p* < 0.01; \*\*\*, *p* < 0.001. Equations of bivariate relationships: (a) log(Aarea) = 0.49 + 8.09·10-2·pH; (c) log(Narea) = -0.18 + 7.47·10-2·pH; (d) log(Parea) = -1.45 + 9.02·10-2·pH; (e) log(SLA) = 2.26 - 4.26·10-2·pH; (f) log(Aarea) = 1.15 – 0.13·log(Corg);(h)log(Narea) = 0.48 – 0.16· log(Corg); (j) log(SLA) = 1.84 + 0.12· log(Corg); (l) log(gs) = 2.29 + 0.18· log(Ntot); (m) log(Narea) = 0.28 – 0.15· log(Ntot); (o) log(SLA) = 1.99 + 0.11· log(Ntot); (q) log(gs) = 2.57 – 0.24· log(Pavail); (s) log(Pa) = -1.16 + 0.19· log(Pavail); (w) log(Narea) = 0.66 – 0.34· log(AWHC); (x) log(Pa) = -0.37 – 0.47· log(AWHC).

**Figure 3:** Partitioning of the respective variation in leaf photosynthetic rate (Aarea), stomatal conductance (gs), leaf nitrogen content (Narea), leaf phosphorus content (Parea) and specific leaf area (SLA) between the unique effect of soil, the unique effect of climate and the joint effect of soil and climate variables. Multiple mixed regressions were used to compute the adjusted R-squared of the fixed effects (climate and soil variables)**.** Site and species were considered as random factors.Soil and climate variables used in these analyses were the ones revealed to be most relevant by a stepwise model-selection procedure: MIQ, SUNmax, TMPmax, TMP5nb, PPTseason, RH, TMPrange, pH, Ntot, Pavail, SILT, SAND, BULK, CECS and SALT, that respectively are moisture index, maximum monthly fractional sunshine duration, maximal monthly temperature, number of days with daily temperature above 5˚C, seasonality of precipitation, relative humidity, mean diurnal temperature range, soil pH, soil total nitrogen content, available soil phosphate content, soil silt and sand contents, soil bulk density, cation exchange capacity and soil salinity. Statistical significance is indicated using asterisks, two asterisks denoting *p* < 0.01.

**Figure 4**: Redundancy analysis predicting the composition and structure of leaf photosynthetic traits (Aarea, Narea , gs and SLA) from the composition and structure of the most important soil and climate variables (selected by a stepwise procedure, see Fig. 3 caption). See abbreviations in Figure 3 caption.

**Figure 5.** Path analysis depicting the direct and indirect effects of the main environmental predictors of leaf photosynthetic rates Aarea through its covariation with stomatal conductance (gs) and leaf nitrogen content (Narea). Environmental variables were selected based on the results of Figure 4 and were soil pH (pH), moisture index (MIQ) and soil available phosphorus content (Pavail). The path coefficients are the simple standardised regression coefficient. The goodness-of-fit and the unexplained variance of Aarea, Narea and gs are given. A Pearson correlation between Narea and gs was tested and was not significant.

**Supporting Information**

**Supplement 1**: Extension of the Global Plant Trait Network (GLOPNET) database

**Supplement 2**: Dataset

**Supplement 3**: Details on soil and climate variables and their biogeographic representation

**Supplement 4**: Details on soil available phosphorus data

**Supplement 5**: Discussion on the quality of soil and climate data

**Supplement 6:** Details on data analysis

**Supplement 7**: Details on soil-soil, climate-climate and soil-climate analyses

**Supplement 8**: Details on plant traits – environment analyses

**Table 1**

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Trait** | **Factors** | ***n*** | ***r*2** | ***AIC*** | ***F-***  **Factor 1** | ***F-***  **Factor 2** | ***F-***  **Factor 3** | ***F-***  **Factor 4** |
| **Climate model** | |  |  |  |  |  |  |  |
| Aarea | MIQ + TMPrange + SUNmax | 2337 | 0.098\*\*\* | -886 | ↓20.8\*\*\* | ↓5.6\* | ↑3.5˚ | - |
| gs | TMPmax + TMP0nb + PPTseason | 1035 | 0.102\*\*\* | -38 | ↑8.7\*\* | ↓5.4\* | ↑7.9\*\* | - |
| Narea | MIQ + TMPrange | 1643 | 0.178\*\*\* | -1726 | ↓53.9\*\*\* | ↓5.5\* | - | - |
| Parea | MIQ + RH | 512 | 0.312\*\*\* | -353 | ↓27.9\*\*\* | ↑16.3\*\*\* | - | - |
| SLA | SUNmax + TMPmax + TMP0nb | 1965 | 0.146\*\*\* | -1474 | ↓41.1\*\*\* | ↑13.6\*\*\* | ↓30.8\*\*\* | - |
|  |  |  |  |  |  |  |  |  |
| **Soil model** | |  |  |  |  |  |  |  |
| Aarea | pH + Ntot + CECS | 2337 | 0.195\*\*\* | -928 | ↑90.0\*\*\* | ↑19.1\*\*\* | ↓25.6\*\*\* | - |
| gs | pH + Ntot + CECS + Pavail | 1035 | 0.241\*\*\* | -128 | ↑28.0\*\*\* | ↑24.8\*\*\* | ↓19.3\*\*\* | ↓67.0\*\*\* |
| Narea | pH + Ntot + SALT | 1643 | 0.193\*\*\* | -1736 | ↑38.0\*\*\* | ↓5.5\* | ↑9.2\*\* | - |
| Parea | pH + Pavail + SALT + SAND | 512 | 0.440\*\*\* | -361 | ↑8.8\*\* | ↑19.5\*\*\* | ↑6.7\* | ↓7.2\*\* |
| SLA | pH + Ntot + SILT + BULK | 1965 | 0.159\*\*\* | -1461 | ↓15.4\*\*\* | ↑3.2˚ | ↑14.4\*\*\* | ↓5.0\* |