PREDICTING LEAF PHYSIOLOGY FROM SIMPLE PLANT AND CLIMATE ATTRIBUTES: A GLOBAL GLOPNET ANALYSIS

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Abstract. Knowledge of leaf chemistry, physiology, and life span is essential for global vegetation modeling, but such data are scarce or lacking for some regions, especially in developing countries. Here we use data from 2021 species at 175 sites around the world from the GLOPNET compilation to show that key physiological traits that are difficult to measure (such as photosynthetic capacity) can be predicted from simple qualitative plant characteristics, climate information, easily measured ("soft") leaf traits, or all of these in combination. The qualitative plant functional type (PFT) attributes examined are phylogeny (angiosperm or gymnosperm), growth form (grass, herb, shrub, or tree), and leaf phenology (deciduous vs. evergreen). These three PFT attributes explain between one-third and two-thirds of the variation in each of five quantitative leaf ecophysiological traits: specific leaf area (SLA), leaf life span, mass-based net photosynthetic capacity (A_{mass}), nitrogen content (N_{mass}), and phosphorus content (P_{mass}). Alternatively, the combination of four simple, widely available climate metrics (mean annual temperature, mean annual precipitation, mean vapor pressure deficit, and solar irradiance) explain only 5–20% of the variation in those same five leaf traits. Adding the climate metrics to the qualitative PFTs as independent factors in the model increases explanatory power by 3–11% for the five traits. If a single easily measured leaf trait (SLA) is also included in the model along with qualitative plant traits and climate metrics, an additional 5–25% of the variation in the other four other leaf traits is explained, with the models accounting for 62%, 65%, 66%, and 73% of global variation in N_{mass}, P_{mass}, A_{mass}, and leaf life span, respectively. Given the wide availability of the summary climate data and qualitative PFT data used in these analyses, they could be used to explain roughly half of global variation in the less accessible leaf traits (A_{mass}, leaf life span, N_{mass}, P_{mass}); this can be augmented to two-thirds of all variation if climatic and PFT data are used in combination with the readily measured trait SLA. This shows encouraging possibilities of progress in developing general predictive equations for macro-ecology, global scaling, and global modeling.

Key words: leaf life span; nitrogen; phosphorus; photosynthesis; plant functional type; specific leaf area.

INTRODUCTION

Foliage attributes such as leaf structure, nutrient content, and net photosynthetic capacity are key determinants of carbon dioxide and water vapor fluxes between vegetation and the atmosphere at every temporal and spatial scale and of biogeochemical cycles that link soil, climate, and atmosphere at the same scales. Thus, the ability to characterize key leaf functional traits such as photosynthetic capacity for species and communities at regional, continental, and global scales is important for a variety of scientific disciplines, including global biogeography and macro-ecology (Diaz et al. 2004), as well as for vegetation, carbon balance, and land surface models (e.g., Haxeltine and Prentice 1996, Bonan et al. 2003, Sitch et al. 2003) such as those used to predict responses to changes in land use, atmospheric chemistry, and climate.

Many ecosystem process models simplify real vegetation by dividing species into categories called "plant functional types" (PFTs). Leading models include the Sheffield, LPJ, and NCAR dynamic global vegetation models (Woodward et al. 1995, Bonan et al. 2003, Sitch et al. 2003, Woodward and Lomas 2004) and biogeographic and biogeochemical models such as BIOME4 (Kaplan et al. 2003) and BIOME-BGC (White et al. 2000). In these models, each PFT has a particular set of traits and makes up a particular proportion of the vegetation at a site. But recent progress in understanding ecological strategy variation across plant species (Reich et al. 1997, 2003, Wright et al. 2004) suggests possibilities for building new vegetation schemes that are conceptually cleaner, computationally easier, and underpinned by richer data and that express trait variation more satisfactorily.

Variation across species in most ecologically important traits is naturally continuous rather than divided into classes. Further, although traits such as leaf life span or mass-based leaf nitrogen content differ on average between herbs, grasses, and woody plants, there is wide

spread within categories and broad overlap between them (Reich et al. 1997, Wright et al. 2004). Similarly, comparisons between habitats often show overlapping ranges of trait values, despite different averages. Thus, an alternative to using PFTs in vegetation models would be to describe trait variation among sets of coexisting species with a mean and an index of spread for each trait.

Although a wealth of gas exchange data has been published, there is an inevitable bias towards economically important species in developed regions of the world, with few data available from some less developed regions (Wright et al. 2004, but see Han et al. 2005, He et al. 2006). This imbalance is a potential limitation to the generality of global models of land surface processes. Our objective in this paper is to advance our capacity to predict patterns of variation in leaf traits, with a view to improving coverage for regions where ecophysiological data are scarce. We ask whether well-known qualitative characteristics of species, which are often used to define plant functional groups, provide a useful foundation for making such predictions, particularly when combined with other widely available data, such as climate data. Second, we ask whether these qualitative plant characteristics are more poorly, similarly, or better related to plant ecophysiological traits than are climate variables, which are also generally more widely available than ecophysiological data. Third, we ask whether the addition of information about an easily obtained leaf trait, specific leaf area (SLA), to the PFT and climate data allows substantial improvements in ability to predict the less accessible traits such as gas fluxes, chemistry, and leaf life span. If so, this would suggest that coordinated programs to measure SLA could be used to improve global data bases about leaf physiology in general. We focus on SLA because this trait, besides being easy to measure, is a strong (positive) correlate of the photosynthetic capacity and potential relative growth rate of plants and inversely related to the degree of physical defense of a leaf (Reich et al. 1991, 1997, Wright and Westoby 2002, Cornelissen et al. 2003).

We used the Global Plant Trait Network (GLOP-NET) database (Wright et al. 2004, 2005) to assess several alternative approaches to estimating photosynthetic capacity, leaf life span, leaf nitrogen content, and leaf phosphorus content from more easily obtained and more widely available data. This database covers 2222 species from 175 sites on six continents. The present paper builds on previous work that has used these data to assess the generality of scaling relationships among quantitative leaf ecophysiological traits that define trade-off surfaces (e.g., Wright et al. 2004) or the relationship of such surfaces to large-scale climate variability (Wright et al. 2005).

METHODS

Leaf and climate data

Data were compiled from both published and unpublished sources, although all quantitative data were published in Wright et al. (2004). Only site-based data sets were used, i.e., those to which we could reasonably attach climate data. The total database consists of 2548 species–site combinations from 175 sites: 2021 different species in total, with 342 species occurring at more than one site (data sources and the data set itself are available in appendices associated with Wright et al. [2004]). Site mean annual temperature (MAT) ranged from −16°C to 27.5°C, and mean annual rainfall ranged from 133 to 5300 mm/yr. This covers most of the range of MAT/rainfall space in which higher plants are found. We focus on the following leaf traits, all defined as in Wright et al. (2004): photosynthetic capacity per unit leaf mass (A_{mass}); leaf nitrogen and phosphorus concentration per unit mass (N_{mass} and P_{mass}); leaf life span; and SLA, defined here as the one-sided projected area of foliage per unit dry mass (Cornelissen et al. 2003).

Species were grouped in PFTs by the simplest possible groupings: phylogeny (contrasting gymnosperms and angiosperms), growth form (grasses, forbs, shrubs, and trees), and leaf habit (deciduous vs. evergreen). The original GLOPNET data set included data for vines and a number of other types. There was insufficient replication of these, so only the four main types were included herein.

Site climate was considered in terms of temperature, rainfall, vapor pressure deficit (VPD), and solar radiation annual, summed or averaged over annual periods as well as for the growth season period only. Details on sources and calculations of climate data were provided in Wright et al. (2004). Results using yearly and growth season climate indices or indices of seasonality were similar; hence for brevity we only report results relating to yearly climate averages. Climate variables were cross-correlated to an extent. Across the 175 sites, VPD and solar irradiance were more closely associated with MAT than with mean annual rainfall although, clearly, both MAT and rainfall affect a property such as VPD.

Where traits were reported separately for sun leaves and shade leaves in the source publications, only the former were used. If data were presented separately for recently matured and old leaves, recently matured leaves were used. That is, where there was a choice, we used data from leaves closer to their "peak" physiological stage, prior to significant age- or light-related decline in nutrient contents and photosynthetic capacity (Reich et al. 1991).

Data analysis

All leaf traits were approximately log-normally distributed across the data set, as were site rainfall and VPD. Accordingly, these variables were $\log_{10}$-transformed prior to analyses. Mean annual temperature and solar radiation were left untransformed since their distribution was approximately normal. Simple correlation and multiple regression analyses were used for

TABLE 1. Multiple regression analyses of five ecophysiological traits (mass-based net photosynthetic capacity [A_{mass}], phosphorus content [P_{mass}], nitrogen content [N_{mass}], leaf life span, and specific leaf area [SLA]) in relation to three plant functional types (PFT) attributes.

Trait	Mean ± SE	R^2	n	Phylogeny F	Growth form F	Leaf habit F
A_{mass}	1.973 ± 0.019	0.51	747	94.9***	32.5***	199.5***
P_{mass}	−1.102 ± 0.046	0.37	736	4.3*	29.5***	153.7***
N_{mass}	0.217 ± 0.010	0.33	1931	28.0***	76.6***	290.2***
Leaf life span	0.965 ± 0.021	0.67	723	77.9***	48.9***	637.9***
SLA	1.991 ± 0.012	0.40	2164	52.3***	92.9***	511.0***

Notes: We report the mean of the logarithm of each parameter and the standard error (SE) of the predicted values; n is sample size. The F values and their significance are shown for each of the dependent variables. All whole models were significant at $P < 0.001$.

* $P < 0.05$; *** $P < 0.001$.

quantifying relationships between single leaf traits and PFT attributes, climate variables, SLA, and their combination. Inclusion of interaction terms did little to improve the variance explained (typically by 1–4%) compared to models without interaction terms (those shown in Tables 1–4). Moreover, models with interactions (including those with all interaction terms or the best models following backwards stepwise regression) had Akaike's Information Criterion values that were similar to or usually greater than the simpler models (no interactions) with fewer terms, and thus the latter models were considered the best. Thus, interactions were uniformly omitted from all presented models (Tables 1–4, Appendices A–C). All statistical procedures were carried out with JMP Statistical Software 5.0.1.a (SAS Institute, Cary, North Carolina, USA).

RESULTS AND DISCUSSION

Easily available qualitative PFT information explained a substantial portion of the total variation in all five leaf functional traits (Table 1, Appendix A). The PFT data by itself explained 33%, 37%, 40%, 51%, and 67% of the variation in N_{mass}, P_{mass}, SLA, A_{mass}, and leaf life span, respectively (these represent whole-model r^2 values with phylogeny, growth form, and leaf habit included). In contrast, climate data (MAT, annual precipitation, mean VPD, and solar irradiance) collectively explained between 5% and 20% of variation in the same five leaf traits (Table 2, Appendix B). Thus, variation among species within sites is sufficiently large that climate alone predicts only a small fraction of leaf functional trait variation (Wright et al. 2005). In

contrast, individual species can be classified according to combinations of major groupings (such as herb vs. trees and deciduous vs. evergreen) that differ in predictable ways in their average leaf traits. Therefore, despite appreciable variation in individual leaf traits within any individual PFT grouping, these differ sufficiently on average among PFTs (Fig. 1) that their (three-way) combination explains one-third to two-thirds of global variation among species in the five leaf traits.

All three PFT groupings (angiosperm/gymnosperm, functional type, or leaf habit) were significant predictors of all five ecophysiological traits in the "PFT alone" models (Table 1, Appendix A). As generally observed previously, species that are gymnosperms, evergreen, or woody on average occupy positions closer to the "slow metabolism" end of the leaf trait gradient than species that are angiosperms, deciduous, or herbaceous (Fig. 1). The "slow metabolism" end of the leaf economics spectrum is associated with low A_{mass}, N_{mass}, P_{mass}, and SLA and persistent leaves (Reich et al. 1997, 1999, Wright et al. 2004). In the "climate-alone" models, from one to four of the climate metrics were significant predictors of each of the five ecophysiological traits, and each climate metric was significant in models for 2, 3, or 4 of the ecophysiological traits (Table 2).

Although most evergreen species have longer-lived leaves than most deciduous species, there is a class of species that are both evergreen and characterized by short-lived foliage (Reich et al. 1997, 1999, Wright et al. 2004). This group of species is numerically small globally (e.g., ~4% of the woody plants for which we know

TABLE 2. Summary of multiple regression analyses of five ecophysiological traits (as in Table 1) in relation to climate metrics: mean annual temperature (MAT), annual precipitation (PPT), mean annual vapor pressure deficit (VPD), and yearly mean daily-summed solar radiation (RAD).

Trait	R^2	n	MAT F	PPT F	VPD F	RAD F
A_{mass}	0.05	764	0.07	6.8***	1.8	2.8
P_{mass}	0.19	737	19.0***	0.4	8.5***	83.6***
N_{mass}	0.12	2026	5.6*	5.1*	0.07	91.9***
Leaf life span	0.10	744	0.08	0.29	0.57	14.3***
SLA	0.20	2331	19.3***	61.3*	4.9*	99.4***

Note: All whole models were significant at $P < 0.001$.

* $P < 0.05$; *** $P < 0.001$.

TABLE 3. Whole-model R^2 values for multiple regression analyses of five ecophysiological traits (as in Table 1) in a series of models with increasing numbers of independent variables.

Model	A_{mass}	P_{mass}	N_{mass}	Leaf life span	SLA
VEGETATION	0.51	0.37	0.33	0.67	0.40
CLIMATE	0.05	0.19	0.12	0.10	0.20
VEG + CLIMATE	0.54	0.43	0.37	0.68	0.51
VEG + CLIMATE + SLA	0.66	0.65	0.62	0.73	
VEG + CLIMATE + SLA + N	0.73	0.76		0.75	
VEG + CLIMATE + SLA + N + leaf life span	0.80	0.76			

Notes: The models labeled "VEGETATION" included phylogeny, growth form, and leaf habit; "CLIMATE" included mean annual temperature, rainfall, mean vapor pressure deficit, and mean solar irradiance; "VEG + CLIMATE" included the first two sets combined; "VEG + CLIMATE + SLA" included the prior set plus SLA; "VEG + CLIMATE + SLA + N" included the prior set plus percentage of nitrogen. See Tables 1, 2, and 4 for more details regarding the models in the first, second, and fourth rows, respectively.

evergreen/deciduous status in the GLOPNET survey), but includes a species type, woody evergreen pioneers, that is important in tropical forests and that has traits similar to woody deciduous pioneers, including short leaf life span, high nutrient concentrations, and high metabolic rates (Reich et al. 1991, 1997, 1999). In the current analyses, our simple division of all taxa into deciduous vs. evergreen classes thus includes species with leaves with deciduous-like characteristics in the evergreen class. Does this weaken our models? We assessed this in two ways. First we created a classification that lumped species into one of two groups: (1) evergreen species with leaf life span ≥8 months and (2) deciduous species plus evergreen species with leaf life span <8 months (similar to dividing all species into those with leaf life span ≥8 months vs. <8 months). Secondly, we simply divided species into those considered "pioneer" species and those that are not. The first classification improved most model fits by 2–5% (compared to Table 1) but requires data quite difficult to obtain. The second classification improved model fits marginally, if at all. Thus, the existence of species with the relatively unusual trait combination of evergreen but short-lived leaves only modestly lessens the predictive power of the simple models based on simple and widely available classifications.

Can we increase explanatory power by combining qualitative plant attributes and climatic data? Adding the climate metrics to the PFT data increased explan-atory power by 3–11% for the five quantitative leaf traits (Table 3), thus accounting for between 37% (N_{mass}) and 68% (leaf life span) of global variation in these five traits. If the most easily measured of the quantitative traits (SLA) is also included in the model, an additional 5–25% of the variation is explained for each of the four other leaf traits, with the result that between 62% and 73% of global variation in N_{mass}, P_{mass}, leaf life span, and A_{mass} can be explained (Tables 3 and 4, Appendix C). The PFT and climate metrics generally remain significant in these models: for instance, A_{mass} was positively related to MAT and solar radiation and was negatively related to rainfall and VPD (Table 4, Appendix C).

Adding N_{mass} to predictive models may also be a viable option. Although not as easy to determine as SLA, the total cost of analyzing, say, 1000 samples for N content would still be 10-fold lower than the cost of purchasing an infrared gas analysis system and associated chambers for making gas exchange measurements. Measuring canopy N_{mass} from remote sensing may also become operationally feasible in the future (Smith et al. 2003). When N_{mass} was added to regression models already containing VEG, CLIMATE, and SLA, an additional 7% and a total of 73% of total variation in A_{mass} was explained (Table 3), or 75–76% of total variation in leaf life span and P_{mass}.

To test whether these multiple regression relationships based on the entire data set would yield reliable

TABLE 4. Multiple regression analyses of four ecophysiological traits (mass-based net photosynthetic capacity [A_{mass}], phosphorus content [P_{mass}], nitrogen content [N_{mass}], and leaf life span) in relation to plant functional type (PFT) information, climate metrics (mean annual temperature [MAT], annual precipitation [PPT], mean annual vapor pressure deficit [VPD], yearly mean daily-summed solar radiation [RAD]), and specific leaf area (SLA).

Trait	R^2	n	Phylogeny F	Growth form F	Leaf habit F	MAT F	PPT F	VPD F	RAD F	SLA F
A_{mass}	0.66	741	35.4***	22.8***	48.4***	8.8**	39.6***	5.9*	8.8**	274.4***
P_{mass}	0.65	724	24.58***	12.7***	7.6**	0.6	31.2***	16.1***	23.8***	423.9***
N_{mass}	0.62	1852	0.03	26.9***	4.5*	0.2	49.9***	4.4*	7.5**	1151.2***
Leaf life span	0.73	671	49.4***	27.4***	259.2***	0.5	0.6	13.2***	9.9**	114.3***

Notes: The F values and their significance are shown for each of the dependent variables. This provides details of the fourth model in Table 3. All whole models were significant at $P < 0.001$.
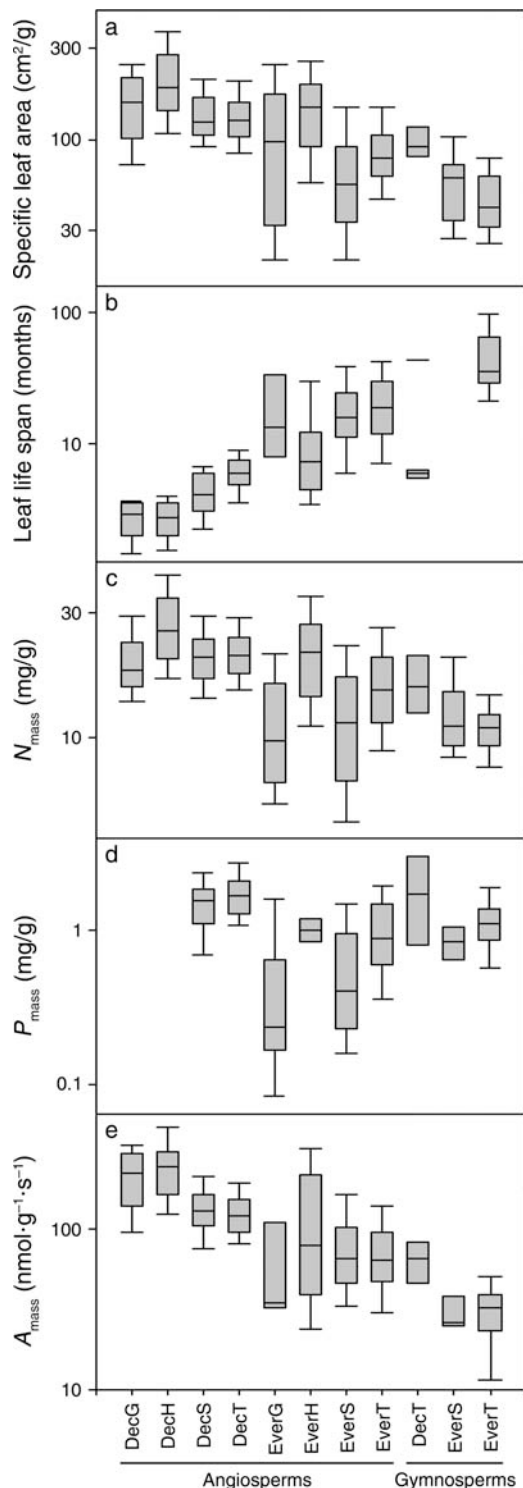
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

FIG. 1. Box plots of five leaf traits: (a) specific leaf area (SLA), (b) leaf life span, (c) mass-based N concentration (N_{mass}), (d) mass-based P concentration (P_{mass}), and (e) mass-based net photosynthetic capacity (A_{mass}), by qualitative plant functional type (PFT) classifications that separate species by phylogeny (angiosperm vs. gymnosperm), leaf habit (Ever, evergreen; Dec, deciduous), and growth form (G, grass; H, herb; S, shrub; T, tree). The box plots summarize the

predictions, we derived the same relationships as shown for the entire data set (Tables 1–4) using one-half of the data (randomly chosen) and then predicted the quantitative leaf traits for the other half of the data set. The fits (Fig. 2) were generally very close to those generated for the entire data set.

There is close coordination, physiologically and evolutionarily, between the five quantitative leaf traits measured in this study (Reich et al. 1997, 1999, Wright et al. 2004), and thus a sizeable fraction of total variation in one trait can be explained by other traits. However, all of these traits require time, effort, and funds to obtain, and all but SLA also require substantial equipment, analytical, or time costs. Thus, other than SLA the other traits do not offer an easy, simple, cheap surrogate index for functional leaf traits, and obtaining SLA data itself is not without time, effort, and cost (Cornelissen et al. 2003). In contrast, the combination of PFT information and simple climate metrics, both generally and freely available, explain a similar fraction, or roughly half (mean of 51% for the five leaf traits; Table 3), of all variation in the selected leaf traits, as do individual leaf traits in relation to one another (mean of 48% for the 10 bivariate relations of the five quantitative leaf traits presented in this paper; Wright et al. 2004). Given the much greater availability of simple PFT information and databases on vegetation distribution than of physiological data, these offer promise for incorporation into predictive models as well as models driven by remotely sensed information. Moreover, the combination of PFT, climate, and SLA explain approximately two-thirds of global variation in the other leaf traits. Given that we do not have enough data to fully explore interactions between PFTs and climate variables and that we use only linear effects, there is ample opportunity for further refinements of such analyses and for development of predictive models that are statistically more sophisticated than used here. We view this as a promising beginning, given that a greater quantity of and better metrics for each of these variables can be obtained, and as well, other metrics may become available (e.g., soils data) that additionally can be used with these in future models.

Improved ability to predict leaf attributes at a species level will be particularly advantageous in multispecies canopies. Given the heterogeneity among species within sites (Reich et al. 1999, Wright et al. 2004), the importance of species and functional-group heterogeneity and diversity to ecosystem processes, including responses to global environmental change (e.g., Reich et al. 2004), and the likelihood that the physiological

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distribution of points for each variable and group. The ends of the box are the 25th and 75th percentiles or quartiles. The gray-shaded area between the quartiles is the interquartile range. The line across the middle of the box is the median value. The lines extending from the ends of the box denote the maximum and minimum values.
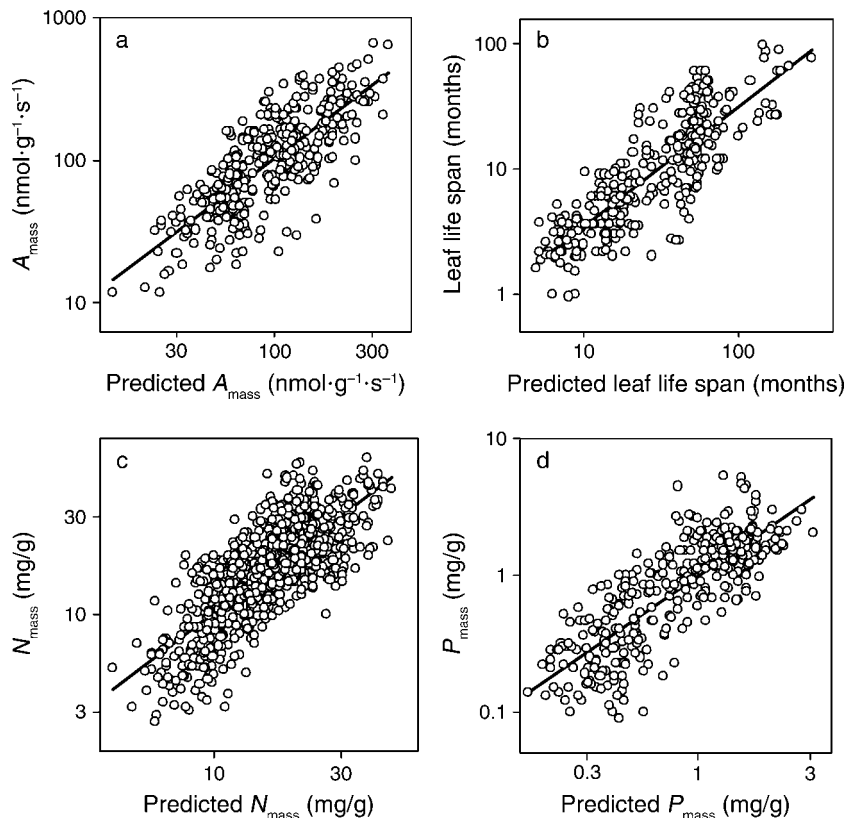
Fig. 2. Relationships between observed and predicted (a) mass-based net photosynthetic capacity (A_{mass}), (b) leaf life span, (c) mass-based N concentration (N_{mass}), and (d) mass-based P concentration (P_{mass}). Predictive equations were generated from a randomly selected half of the data set, using plant functional type (PFT) information, climate data, and specific leaf area, and were applied to the remaining data. Fits (R^2) of the relationships were 0.61, 0.71, 0.59, and 0.66, respectively, for panels (a)–(d) (all $P < 0.0001$), and slopes were near 1:1.

response of a community canopy based on mean values is not necessarily the same as the responses of a real canopy made up of species differing widely in intrinsic leaf traits, it may prove necessary at some point to consider this functional diversity in models (Garnier et al. 2004). In many, but certainly not all, areas of the globe there is some information about the compositional make-up of vegetation communities, even when there is little or no information about ecophysiology. In such cases, predicting the traits of the species in those communities and then aggregating those traits to the community as a whole weighted by their relative abundances will provide not only a mean but a notion of the functional diversity of the community. In contrast, predictions based solely on climate or a dominant functional type would only provide a mean value. As models improve, one would expect that land surface and vegetation dynamics models would incorporate heterogeneity of vegetative properties as well as the average of those properties.

LITERATURE CITED

Bonan, G. B., S. Levis, S. Sitch, M. Vertenstein, and K. W. Oleson. 2003. A dynamic global vegetation model for use with climate models: concepts and description of simulated vegetation dynamics. Global Change Biology 9:1543–1566.

Cornelissen, J. H. C., et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51:335–380.

Díaz, S., et al. 2004. The plant traits that drive ecosystems: evidence from three continents. Journal of Vegetation Science 15:295–304.

Garnier, E., J. Cortez, G. Billès, M.-L. Navas, C. Roumet, M. Debussche, G. Laurent, A. Blanchard, D. Aubry, A. Bellmann, C. Neill, and J.-P. Toussaint. 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85:2630–2637.

Han, W., J. Fang, and D. Guo. 2005. Leaf N and P stoichiometry across 753 terrestrial plant species in China. New Phytology 168:377–385.

Haxeltine, A., and I. C. Prentice. 1996. BIOME3: an equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability and competition among plant functional types. Global Biogeochemical Cycles 10:693–709.

He, J.-S., Z. Wang, X. Wang, B. Schmid, W. Zuo, M. Zhou, C. Zheng, M. Wang, and J. Fang. 2006. A test of the generality of leaf trait relationships on the Tibetan Plateau. New Phytology 170:835–848.

Kaplan, J. O., et al. 2003. Climate change and arctic ecosystems II: modeling, paleodata-model comparisons, and future projections. Journal of Geophysical Research–Atmospheres 108(D19):8171.

Reich, P. B., D. S. Ellsworth, M. B. Walters, J. Vose, C. Gresham, J. Volin, and W. Bowman. 1999. Generality of leaf traits relationships: a test across six biomes. Ecology 80: 1955–1969.

Reich, P. B., D. Tilman, S. Naeem, D. Ellsworth, J. Knops, J. Craine, D. Wedin, and J. Trost. 2004. Species and functional diversity independently influence biomass accumulation and its response to CO_2 and N. Proceedings of the National Academy of Sciences (USA) 101:10101–10106.

Reich, P. B., C. Uhl, M. B. Walters, and D. S. Ellsworth. 1991. Leaf lifespan as a determinant of leaf structure and function among 23 amazonian tree species. Oecologia 86:16–24.

Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1997. From tropics to tundra: global convergence in plant functioning. Proceedings of the National Academy of Sciences (USA) 94: 13730–13734.

Reich, P. B., I. Wright, J. Cavender-Bares, J. Craine, J. Oleksyn, M. Westoby, and M. B. Walters. 2003. The evolution of plant functional variation: traits, spectra, and strategies. International Journal of Plant Sciences 164:s143–s164.

Sitch, S., B. Smith, I. C. Prentice, A. Arneth, A. Bondeau, W. Cramer, J. O. Kaplan, S. Levis, W. Lucht, M. T. Sykes, K. Thonicke, and S. Venevsky. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Global Change Biology 9:161–185.

Smith, M. L., M. E. Martin, L. Plourde, and S. V. Ollinger. 2003. Analysis of hyperspectral data for estimation of temperate forest canopy nitrogen concentration: comparison between an airborne (AVIRIS) and a spaceborne (Hyperion) sensor. IEEE Transactions on Geoscience and Remote Sensing 41:1332–1337.

White, M. A., P. E. Thornton, S. W. Running, and R. R. Nemani. 2000. Parameterization and sensitivity analysis of the BIOME–BGC terrestrial ecosystem model: net primary production controls. Earth Interactions 4:1–85.

Woodward, F. I., and M. R. Lomas. 2004. Vegetation dynamics—simulating responses to climatic change. Biological Reviews 79:643–670.

Woodward, F. I., T. M. Smith, and W. R. Emanuel. 1995. A global land primary productivity and phytogeography model. Global Biogeochemical Cycles 9:471–490.

Wright, I., P. B. Reich, and M. Westoby, and GLOPNET researchers. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Wright, I. J., and M. Westoby. 2002. Leaves at low versus high rainfall: coordination of structure, lifespan and physiology. New Phytologist 155:403–416.

Wright, I. J., et al. 2005. Modulation of leaf economic traits and trait relationships by climate. Global Ecology and Biogeography 14:411–421.

APPENDIX A

Model parameters for the models shown in Table 1 (*Ecological Archives* A017-078-A1).

APPENDIX B

Model parameters for the models shown in Table 2 (*Ecological Archives* A017-078-A2).

APPENDIX C

Model parameters for the models shown in Table 4 (*Ecological Archives* A017-078-A3).