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Responses of leaf traits to climatic gradients: adaptive variation vs. compositional shifts

T.-T. Meng^{1,2,3}, H. Wang⁴, S. P. Harrison^{4,5}, I. C. Prentice^{4,6}, J. Ni^{3,7,8}, and G. Wang³

¹Beijing Enterprises Water Group Limited, Beijing, China

²Beijing Beihuaqingchuang Environmental Science and Technology Co., Ltd., China

³State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Science, Beijing, China

⁴Department of Biological Sciences, Macquarie University, Sydney, Australia

⁵Centre for Past Climate Change and School of Archaeology, Geography and Environmental Science (SAGES), University of Reading, Whiteknights, Reading, UK

⁶AXA Chair in Biosphere and Climate Impacts, Grand Challenges in Ecosystems and the Environment and Grantham Institute – Climate Change and the Environment, Department of Life Sciences, Imperial College London, Silwood Park Campus, Ascot, UK

⁷Alfred Wegener Institute for Polar and Marine Research, Potsdam, Germany

⁸State Key Laboratory of Environmental Geochemistry, Institute of Geochemistry, Chinese Academy of Science, Guiyang, China

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Correspondence to: H. Wang (angwanh@gmail.com)

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BGD

12, 7093–7124, 2015

**Responses of leaf
traits to climatic
gradients**

T.-T. Meng et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Abstract

Dynamic global vegetation models (DGVMs) typically rely on plant functional types (PFTs), which are assigned distinct environmental tolerances and replace one another progressively along environmental gradients. Fixed values of traits are assigned to each PFT; modelled trait variation along gradients is thus driven by PFT replacement. But empirical studies have revealed “universal” scaling relationships (quantitative trait variations with climate that are similar within and between species, PFTs and communities); and continuous, adaptive trait variation has been proposed to replace PFTs as the basis for next-generation DGVMs.

Here we analyse quantitative leaf-trait variation on long temperature and moisture gradients in China with a view to understanding the relative importance of PFT replacement vs. continuous adaptive variation within PFTs. Leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC) and nitrogen content of dry matter were measured on all species at 80 sites ranging from temperate to tropical climates and from dense forests to deserts. Chlorophyll fluorescence traits and carbon, phosphorus and potassium contents were measured at 47 sites. Generalized linear models were used to relate log-transformed trait values to growing-season temperature and moisture indices, with or without PFT identity as a predictor, and to test for differences in trait responses among PFTs.

Continuous trait variation was found to be ubiquitous. Responses to moisture availability were generally similar within and between PFTs, but biophysical traits (LA, SLA and LDMC) of forbs and grasses responded differently from woody plants. SLA and LDMC responses to temperature were dominated by the prevalence of evergreen PFTs with thick, dense leaves at the warm end of the gradient. Nutrient (N, P and K) responses to climate gradients were generally similar within all PFTs. Area-based nutrients generally declined with moisture; N_{area} and K_{area} declined with temperature, but P_{area} increased with temperature.

BGD

12, 7093–7124, 2015

Responses of leaf traits to climatic gradients

T.-T. Meng et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Although the adaptive nature of many of these trait–climate relationships is understood qualitatively, a key challenge for modelling is to predict them quantitatively. Models must also take into account that community-level responses to climatic gradients can be influenced by shifts in PFT composition, such as the replacement of deciduous by evergreen trees, which may run either parallel or counter to trait variation within PFTs. The importance of PFT shifts varies among traits, being important for biophysical traits but less so for physiological and chemical traits.

1 Introduction

The plant functional type (PFT) concept has been important in the development of dynamic global vegetation models (DGVMs), which combine vegetation dynamics (changes in vegetation composition, expressed as abundances of PFTs) at the grid cell scale with hydrological and biogeochemical processes driven by the physical environment and modulated by PFT characteristics (Prentice et al., 2007; Prentice and Cowing, 2013). PFT classifications vary among models but nearly all include distinctions of life form (at least, woody vs. herbaceous plants), leaf habit (evergreen or deciduous) and leaf form (broad or needle-leaves). Some models also distinguish climatic tolerance classes, related primarily to different overwintering mechanisms for woody plants (Harrison et al., 2010), and most distinguish C_4 plants. Usually a fixed set of properties (parameter values) is assigned to each PFT. This expedient simplifies modelling, but it is a potential weakness because it disregards continuous adaptive variation within PFTs and the possibility that such variation is “universal” – that is, manifested similarly within and between species, PFTs and communities. Neglect of continuous adaptive variation in models could lead to incorrect assessments of the response of vegetation to climate (Kleidon et al., 2007; Scheiter and Higgins, 2009) and vegetation feedbacks to climate (Alton et al., 2011).

Numerous observational studies have indeed documented continuous relationships between quantitative plant traits and climate (e.g. Werger and Ellenbroek, 1978; Díaz

BGD

12, 7093–7124, 2015

Responses of leaf traits to climatic gradients

T.-T. Meng et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



et al., 1998; Fonseca et al., 2000; Niinemets, 2001; Wright and Westoby, 2002; Wright et al., 2004, 2005a, b; Swenson and Enquist, 2007; Reich et al., 2007; Cornwell and Ackerly, 2009; Meng et al., 2009; Ordoñez et al., 2009, 2010; Albert et al., 2010; Prentice et al., 2011). Analyses of trait–environment relationships have been motivated partly by the objective of improving the representation of plant structural and functional diversity in DGVMs (Woodward and Cramer, 1996; Díaz and Cabido, 1997; Lavorel et al., 2007; Kattge et al., 2011). In a new strand of DGVM development, modelling quantitative trait values rather than PFT abundances is the central objective (Kleidon et al., 2009; van Bodegom et al., 2012, 2014; Scheiter et al., 2013; Fyllas et al., 2014). An advantage of trait-based modelling is that it can take better advantage of the wealth of georeferenced data now available on plant functional traits (Kattge et al., 2011). On the other hand, some leaf traits can have different relationships to climate depending on the PFT (e.g. Barboni et al., 2004; He et al., 2006; Meng et al., 2009). Moreover there are systematic leaf-trait differences between PFTs and these account for a substantial fraction of the total climatically related variation in leaf traits (e.g. Reich et al., 2007; Ordoñez et al., 2009, 2010; He et al., 2010). Thus it is not entirely clear from observational studies to what extent trait–environment relationships are universal; or conversely, to what extent differences in either trait values or trait-environment responses among PFTs are necessary to include in models to describe the totality of vegetation responses to environmental gradients – and, by extension, to directional environmental change.

We address this question here with an analysis of variations in leaf traits in plant communities sampled on long gradients of temperature and moisture availability in China (Fig. 1). The data set consists of > 11 000 quantitative leaf trait determinations on all of the species present at 80 sites, with a wide geographic spread. We consider biophysical traits (leaf area: LA, specific leaf area: SLA and leaf dry matter content: LDMC), field-measured chlorophyll fluorescence traits (the ratio of variable fluorescence to maximal fluorescence: F_v/F_m and the quantum yield of PhotoSystem II: QY), and chemical traits: carbon content by mass (C_{mass}), and nitrogen (N), phosphorus (P)

BGD

12, 7093–7124, 2015

Responses of leaf traits to climatic gradients

T.-T. Meng et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

and potassium (K) contents, expressed on both an area and a mass basis. Thus we consider 12 traits in all. Area-based nutrient contents provide no independent information, as they are simply derived from mass-based nutrient contents and SLA, but they provide an alternative perspective on the regulation of leaf nutrient contents. LA, SLA, LDMC and N were measured at all sites; the other traits were measured at the 47 sites in eastern China, which cover most of the climatic range of the full data set except for the driest climates in the west. Adopting a conventional PFT classification, we analyse variations of each trait with bioclimatic temperature and moisture indices (Harrison et al., 2010) within and across PFTs.

2 Materials and methods

2.1 Sampling sites

The sites (Table 1) represent variation along the major gradients in temperature and moisture and include the major vegetation types in China apart from those unique to high elevations. Thirty-three sites in Xinjiang Autonomous Region in western China sample the extreme dry end of the moisture gradient, with annual rainfall between 12 and 468 mm (160 mm on average). Thirty-three sites on the Northeast China Transect (NECT: Ni and Wang, 2004) lie on an aridity gradient from closed forests with annual rainfall > 700 mm in the east, through grasslands to desert with annual rainfall of < 150 mm in the west. Fourteen sites located in forest reserves on the North–South Transect of Eastern China (NSTEC: Gao et al., 2003) have greater annual rainfall and sample a range from temperate climates in the north to warm-temperate/subtropical climates in the south. The NSTEC sites are also differentiated in terms of rainfall, the sites in the east at any given latitude being wetter than those in the west.

Sampling took place during three summer field campaigns, in 2005 (Xinjiang), 2006 (NECT) and 2007 (NSTEC). All sites were occupied by visually homogeneous uncultivated vegetation with minimal signs of disturbance. Species composition and vegeta-

BGD

12, 7093–7124, 2015

Responses of leaf traits to climatic gradients

T.-T. Meng et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Responses of leaf traits to climatic gradients

T.-T. Meng et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)



[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



Hancock, 2006) with the help of a digital elevation model (Farr et al., 2007). Mean annual temperature (MAT) and precipitation (MAP), mean winter (P_{DJF}) and summer (P_{JJA}) precipitation and of precipitation seasonality and timing (defined as in Prentice et al., 2011) were calculated for each site. Bioclimatic variables were derived as in Gallego-Sala et al. (2010): mean temperature of the coldest month (MTCO) and warmest month (MTWA), growing degree days above 0°C (GDD_0), photosynthetically active radiation during the growing season (PAR_0), annual equilibrium evapotranspiration (EET), Moisture Index ($MI = MAP/EET$), annual actual evapotranspiration (AET) and the Cramer-Prentice α index of plant-available soil moisture ($\alpha = AET/EET$) (Cramer and Prentice, 1988). Available water holding capacity (AWHC) values for the calculation of α were assigned following Prentice et al. (2011), using sand, silt and clay fractions digitized from Shi et al. (2004).

Principal components analysis was performed on standardized climate variables in SPSS. We analysed climate gradients for China as a whole, based on data from 89 623 10 km grid cells, and separately using just the 80 grid cells that included the sampling sites.

2.5 Plant functional types (PFTs)

Plant species were classified as follows: trees (single-stemmed, maximum height > 2 m, subdivided as evergreen broad-leaved, evergreen needle-leaved and deciduous broad-leaved), shrubs (multi-stemmed with maximum height between 50 cm and 2 m, subdivided as evergreen and deciduous), erect dwarf shrubs (multi-stemmed with maximum height < 50 cm), lianas (woody climbing plants with perennial above-ground biomass), climbers (non-woody climbing plants with annual above-ground biomass), forbs, grasses, geophytes and ferns. Climbers and ferns were not included in the statistical analyses, however, as there were too few species of each. The optimum and tolerance of each PFT in terms of α and GDD_0 , recommended by Harrison et al. (2010) as useful and globally applicable indices of effective moisture availability and warmth for plants, were calculated non-parametrically as follows (Fig. 2): the range of each

lar trait variations *within* each PFT, vs. shifts in the occurrence and abundance of PFTs with innately different trait values? (3) Do trait values of some PFTs respond to climate differently from others?

A significance criterion of $P < 0.01$ was adopted for all regression coefficients in all three analyses. This is stringent enough to minimize the chance of “false positives” in analyses (2) and (3). Results are presented as partial residual plots, using the *visreg* package in R. Partial residual plots are the multiple-regression analogue of simple x - y plots in ordinary regression. In plots showing the relationship of each trait to α , the y axis values of the data points are adjusted so as to remove the fitted effect of GDD_0 . Similarly, in plots showing the relationship of each trait to GDD_0 , the y axis values of the data points are adjusted so as to remove the fitted effect of α .

3 Results

3.1 Climate gradients

More than 80 % of the geographic variation in the climate of China can be summarized by variation on two principal axes (Table 2). Each principal axis is defined as a linear combination of variables, and each variable is assigned a “loading” which represents the contribution of that variable to the combination. The first principal axis explains about 60 % of total variation and is related to temperature. MTCO, MAT, MAP, GDD_0 , and P_{DJF} have large positive loadings. The positive loading for MAP reflects the general tendency for absolute amounts of precipitation to increase with temperature. The second axis explains a further 22 % of total variation and is related to moisture vs. aridity. MI, α , P_{JJA} have positive loadings while PAR_0 and MTWA have negative loadings. The similar behaviour of PAR_0 and MTWA reflects an increasing period without clouds, and thus also higher temperatures in summer, as moisture availability decreases. A third axis relating to the timing and seasonality of precipitation accounts for only 9 % of total variation.

BGD

12, 7093–7124, 2015

Responses of leaf traits to climatic gradients

T.-T. Meng et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Responses of leaf traits to climatic gradients

T.-T. Meng et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)



[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



A closely similar pattern emerged from analysis of climate data for the sampling sites (Table 2). This similarity confirms that the pattern of variation in climate across the sites reflects the general pattern of climate gradients across China, and that these gradients can be summarized using two variables, representing growing-season temperature and moisture availability respectively. For all further analysis we used the variables GDD_0 and α . The pattern of variation of GDD_0 and α across China is shown, with the site locations, in Fig. 1. Figure 1 also shows the frequency of different GDD_0 - α combinations among grid cells, and the site positions in this climate space.

3.2 Distribution of PFTs in climate space

The PFTs in our data set show distinct patterns of distribution in climate space (Fig. 2), falling broadly into four groups. (1) Evergreen trees, evergreen shrubs and lianas favour the warmest and wettest climates, corresponding to the warm-temperate broad-leaved evergreen forests of southeastern China, with evergreen needle-leaved trees extending into cooler climates in the north. (2) Deciduous trees and deciduous shrubs favour cooler and drier climates, corresponding to the deciduous forests of central eastern China. (3) Dwarf shrubs, grasses, forbs and geophytes favour still cooler and drier climates, corresponding to the grasslands, steppes and desert steppes of northern and northwestern China. (4) Ferns and climbers are prominent only in cooler and wetter regions of climate space; they occur more widely but not in any abundance, and they were not sampled elsewhere.

3.3 Trait–climate relationships: moisture effects

Significant community-level responses to growing-season moisture availability (α) were found for most traits (Fig. 3, Table 3). Dry climates generally favour small, thick, dense leaves (low LA, low SLA, high LDMC). Dry climates are also associated with slightly, or sometimes greatly, reduced potential and actual quantum yield. The steepest overall relationships to α are for LA (5.8), SLA (1.6), and N_{area} and K_{area} (−1.1) and P_{mass} (0.7)

(Table 3: values in parentheses are slopes of \ln trait-values vs. α). The response of N_{mass} to α is slight (0.25) compared to the response in N_{area} .

Inclusion of PFTs as predictors (Fig. S1 in the Supplement) shows that there are some differences among PFTs in the typical trait values found at any given α . This is most obvious for biophysical traits – LA, SLA and LDMC – and area-based nutrients. Needle-leaved evergreen trees stand out, having small, thick leaves, and high area-based nutrient contents, relative to other PFTs. The magnitudes of the regression coefficients against α for the different traits in this analysis are similar to those in Fig. 3, but now P_{area} (in common with the other area-based nutrients) shows a significant negative effect of α . This relationship within PFTs is obscured in Fig. 3 by the abundance of needle-leaved evergreen trees, with their very low SLA and therefore high P_{area} values, towards the wet end of the gradient.

Where significant trait-PFT interactions in the response to α are found (Fig. S2), the responses are qualitatively (and usually, quantitatively) similar from one PFT to another. Regression coefficients for LA vs. α range from 3.8 to 6.1, with deciduous shrubs and forbs showing significantly steeper responses than the rest. Regression coefficients for SLA range from 1.3 to 2.5 with forbs showing the steepest increases. Regression coefficients for LDMC range from -0.35 to -1.5 with forbs showing the steepest decreases. Different PFTs have different responses of QY to moisture, with geophytes responding most and forbs least. Neither area- nor mass-based nutrients show any significant differences among PFTs.

3.4 Trait–climate relationships: temperature effects

Significant overall responses to growing-season warmth (GDD_0) were also found for most traits (Fig. 4, Table 3). Warm climates favour thick and dense leaves (low SLA and high LDMC). Warmer climates also show somewhat reduced potential and actual quantum yield. The steepest overall relationship of any trait to GDD_0 is for SLA (-1.5) (Table 3: numbers in parentheses are slopes of \ln trait values against $\text{GDD}/10^4$). Relatively steep slopes are also shown for N_{mass} (-1.1), P_{area} (1.4) and K_{mass} (-1.1).

Responses of leaf traits to climatic gradients

T.-T. Meng et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Including PFTs as predictors shows some differences among PFTs at any GDD_0 value, similar to those shown for α (Fig. S3). But the effects on the regression coefficients for GDD_0 are more profound. Most importantly, the within-PFT responses of the three biophysical traits – LA, SLA and LDMC – to temperature are non-significant.

Thus, the overall responses of SLA and LDMC to GDD_0 shown in Fig. 4 *are brought about by PFT replacement*, including the dominance of broad-leaved evergreen trees with low SLA and high LDMC at the warm end of the gradient. Within PFTs, N_{area} and K_{area} both decline with temperature, while P_{area} increases. The lack of a significant relationship at the community level between N_{area} and K_{area} and temperature is due to PFT replacement along the gradient – again, most obviously, the prevalence of broad-leaved evergreen trees with high N_{area} and K_{area} at the warm end of the gradient. Similarly, the steep overall declines in N_{mass} and K_{mass} with GDD_0 are mainly due to PFT replacement.

Relationships to GDD_0 fitted separately within PFTs (Fig. S4) showed fewer significant slopes, and less consistency among PFTs, than the corresponding relationships to α . Individually significant PFT responses of SLA to GDD_0 could be increasing or decreasing (-0.57 to $+1.3$). Slopes of LDMC are negative (-1.6 to -3.0), with forbs and grasses showing the steepest declines. Area- and mass-based nutrients show few significant differences among PFTs in their responses to either GDD_0 ; however forbs show an increase in N_{mass} and more steeply increasing P_{mass} with GDD_0 compared to other PFTs, and evergreen needleleaf trees show a steeper increase in P_{area} .

4 Discussion

4.1 Adaptive significance of trait responses to moisture availability

The observed continuous biophysical trait variations with moisture availability are consistent with previous studies and, qualitatively, reasonably well understood. The decrease in LA towards arid climates allows leaves to avoid overheating in environments

BGD

12, 7093–7124, 2015

Responses of leaf traits to climatic gradients

T.-T. Meng et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Responses of leaf traits to climatic gradients

T.-T. Meng et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



where soil moisture supplies are inadequate for transpirational cooling to be effective. High photosynthetic capacity coupled with high CO₂ drawdown, resulting in a low ratio of internal to ambient CO₂ concentration ($c_i : c_a$), is also adaptive in dry environments (Wright et al., 2003; Prentice et al., 2014a) because of the high transpirational cost of keeping stomata open under conditions of high atmospheric aridity (vapour pressure deficit). Increased photosynthetic capacity requires an increase in N_{area} and a reduction in SLA. Low SLA of plants in arid environments may also allow leaves to avoid transient overheating when wind speeds fall (Leigh et al., 2012). The increase in LDMC with aridity is a key adaptation that allows leaves to maintain hydration even at low water potentials that may arise under drought conditions (Bartlett et al., 2012).

The reduction in QY with aridity points to drought-induced photoinhibition at the arid end of the gradient. Dry climates are characterized by high N_{area} , consistent with a high photosynthetic capacity (compensating for low $c_i : c_a$) as mentioned above. High K_{area} in dry climates is consistent with the role of K in maintaining leaf function under water-limited conditions (Sardans and Peñuelas, 2015). The regulation of leaf P is less well understood, but the trend towards higher P_{area} in dry climates is consistent with a relatively conservative N : P ratio within PFTs. Reduced mass-based N and P in arid climates are consistent with the increased allocation of carbon to leaf structural components in leaves with low SLA.

4.2 Adaptive significance of trait responses to growing-season warmth

The observed tendency towards lower community-level SLA with increasing temperature may be linked to the well-known relationship between SLA and leaf longevity (Wright et al., 2004; Poorter et al., 2009). However, temperature-related trends in SLA within PFTs are mostly non-significant. The overall trend to lower SLA with increasing temperature is mainly driven by the shift from deciduous to evergreen PFTs, which is to be expected given the clear advantage for evergreens in a subtropical climate that favours year-round photosynthesis and growth. Leaves also become more dense (higher LDMC) towards the warm end of the gradient, but within PFTs, the only signifi-

cant responses are for leaves to become less dense with increasing temperature. The community-level response of LDMC is thus driven by PFT replacement, with evergreen broad leaves characterized by high LDMC.

Both potential and actual rates of electron transport in woody plants are reduced at the warm end of the temperature gradient. The effect is seen in both deciduous and evergreen woody plants and is likely caused by heat stress resulting in a reduced efficiency of Photosystem II. The decrease in the potential rate implies that electrons are being diverted to protective mechanisms. The decrease in F_v/F_m is steeper than the decrease in QY.

The decline of both N_{area} and N_{mass} with temperature (after PFT differences have been considered) is consistent with the declining N requirement to achieve a given catalytic activity of photosynthetic proteins as temperature increases (Reich and Oleksyn, 2004). The reasons for declining K_{area} and K_{mass} with temperature are unclear; possibly low temperatures in winter, towards the cold end of the gradient, create a K requirement similar to that caused by drought. The observed increases in both P_{area} and P_{mass} with temperature are opposite to the general tendency of leaf N to increase allometrically with leaf P (e.g. Reich et al., 2010). These trends might reflect an increase in non-photosynthetic electron transport processes that require a large supply of inorganic phosphate.

4.3 Comparison with previous studies of trait variation within and between PFTs

Kattge et al. (2011) also examined trait variability within and between PFTs, in an analysis based on the TRY global plant trait data base. They showed differences in the fraction of total trait variance that could be attributed to PFTs vs. continuous variation within PFTs, with some traits predicted well by PFT identity. But for several traits, including N_{area} and SLA, they found that the largest fraction of the variance (as much as 75%) was found within, not between PFTs. Our analysis extends that of Kattge et al. (2011) in attributing climatically related variation to different sources. We have

Responses of leaf traits to climatic gradients

T.-T. Meng et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Responses of leaf traits to climatic gradients

T.-T. Meng et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)



[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



shown contrasts in the responses of different traits to climate, and also contrasts in their responses to different aspects of climate. In most cases, nutrient traits show similar responses to climate within PFTs to those shown at the community level; and no significant differences were found between the responses within different PFTs. This is in agreement with the finding of Zhang et al. (2012) that climate is a more important predictor of leaf element concentrations (except for S and SiO₂) than species identity. Variations of biophysical traits with respect to moisture availability are also similar within PFTs and at the community level. However, these same traits show patterns of response to temperature that are dominated by differences among PFTs. The differential responses of leaf N and P contents to moisture availability and temperature require further investigation.

4.4 Implications for modelling

It is reasonable to expect that the performance of vegetation models would be improved by representing the values of phenotypically or genotypically plastic traits as state variables, rather than parameters (Prentice et al., 2007). This “adaptive” approach has been adopted explicitly in some recently developed models, e.g. Schymanski et al. (2009) and Scheiter et al. (2013). In the LPJ family of models descended from Sitch et al. (2003), leaf-level photosynthetic capacity (V_{cmax}) is allowed to vary adaptively within PFTs, based on an optimality hypothesis that predicts realistic responses of N_{area} to light, temperature and CO₂ (Dewar, 1996; Haxeltine and Prentice, 1996). On the other hand, the LPJ-family models treat SLA as a PFT-specific parameter and thus do not allow for covariation of SLA with N_{area} , as has been demonstrated to occur, here and in other contexts (e.g. Lloyd et al., 2010; Prentice et al., 2011).

Our findings suggest that vegetation models should retain the PFT concept and a minimal set of PFTs, because the distinctions between woody and herbaceous, deciduous and evergreen, and angiosperm and gymnosperm plant types systematically influence the values of key biophysical traits in ways that would not be predictable from assumed universal relationships. Moreover certain observed overall responses of trait

values to climate, including the decline in SLA and increase of LDMC with increasing temperature in our study, appear to be driven principally by PFT replacement rather than by adaptive variation within PFTs. Nonetheless, the prevalence of continuous, consistent trait variation within and between PFTs for many traits and trait–environment relationships supports the conclusion that models should avoid prescribing fixed, PFT-specific values for most quantitative traits (e.g. Wright et al., 2005). Fixed, PFT-specific values could be replaced by universal adaptive functions of environmental variables: thus reducing the multiplicity of uncertain parameters, while simultaneously increasing the realism of next-generation DGVMs (Prentice et al., 2014b). To do so, however, requires that these functions be well specified and robust. Although some progress has been made in developing trait-based models based on statistical trait–environment relationships, process-based model development requires these responses to be quantitatively predictable, based on explicit hypotheses about the adaptive significance of traits.

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BGD

12, 7093–7124, 2015

Responses of leaf traits to climatic gradients

T.-T. Meng et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



References

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T.-T. Meng et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Responses of leaf traits to climatic gradients

T.-T. Meng et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)



[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



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T.-T. Meng et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Responses of leaf traits to climatic gradients

T.-T. Meng et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Responses of leaf traits to climatic gradients

T.-T. Meng et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Table 1. Characteristics of sampling sites.

Site code	Latitude (° N)	Longitude (° E)	Elevation (m)	Vegetation type	Number of species	GDD ₀ (day °C)	α
NECT01	42.88	118.48	1024	steppe	19	2433.20	0.67
NECT02	43.64	119.02	781	steppe	43	3047.57	0.55
NECT03	43.02	129.78	136	deciduous broad- leaved forest	24	2727.77	0.90
NECT04	42.98	130.08	114	evergreen conifer/ deciduous broad- leaved forest	26	2870.71	0.88
NECT05	43.30	131.15	289	deciduous conifer/ deciduous broad- leaved forest	42	2391.45	0.92
NECT06	43.12	131.00	244	evergreen conifer/ deciduous broad- leaved forest	49	2097.04	0.98
NECT07	43.39	129.67	224	deciduous conifer/ deciduous broad- leaved forest	40	2760.26	0.87
NECT08	43.25	128.64	601	evergreen conifer/ deciduous broad- leaved forest	39	2702.15	0.93
NECT09	43.73	127.03	390	evergreen conifer/ deciduous broad- leaved forest	55	2935.09	0.98
NECT10	43.81	125.68	252	evergreen conifer/ deciduous broad- leaved forest	40	3278.10	0.81
NECT11	44.59	123.51	146	meadow steppe	19	3412.10	0.58
NECT12	44.43	123.27	150	meadow steppe	18	3407.62	0.57
NECT13	43.60	121.84	203	meadow steppe	20	3515.92	0.49
NECT14	44.12	121.77	202	meadow steppe	7	3490.75	0.50
NECT15	44.39	120.55	448	steppe	21	3047.41	0.59
NECT16	44.22	120.37	372	steppe	18	3248.01	0.55
NECT17	43.88	119.38	601	steppe	15	2683.63	0.62
NECT18	43.76	119.12	729	steppe	23	2816.77	0.59
NECT19	43.34	118.49	707	steppe	12	2646.25	0.61

Table 1. Continued.

Site code	Latitude (° N)	Longitude (° E)	Elevation (m)	Vegetation type	Number of species	GDD ₀ (day °C)	α
NECT20	43.19	117.76	889	steppe	23	2583.25	0.62
NECT21	43.22	117.24	1259	steppe	23	2248.48	0.61
NECT22	43.39	116.89	1267	steppe	13	2274.88	0.58
NECT23	43.55	116.68	1261	steppe	22	2410.95	0.56
NECT24	43.69	116.64	1211	steppe	20	2374.09	0.52
NECT25	43.91	116.31	1199	steppe	24	2666.32	0.48
NECT26	43.90	115.32	1196	steppe	27	2509.65	0.44
NECT27	43.94	114.61	1123	desert steppe	19	2716.00	0.37
NECT28	43.83	113.83	1166	desert steppe	14	2895.45	0.28
NECT29	43.80	113.36	1017	desert steppe	11	3104.24	0.25
NECT30	43.72	112.59	974	desert steppe	21	3103.83	0.27
NECT31	43.63	112.17	999	desert steppe	16	3164.51	0.26
NECT32	43.66	111.92	1005	desert steppe	15	3127.61	0.26
NECT33	43.65	111.89	1017	desert steppe	16	3129.06	0.27
NSTEC01	36.24	117.02	368	conifer/deciduous broad-leaved forest	9	4787.79	0.73
NSTEC02	34.64	119.24	59	conifer/deciduous broad-leaved forest	13	5063.76	0.85
NSTEC03	32.05	118.86	76	conifer/deciduous broad-leaved forest	35	5598.22	0.98
NSTEC04	30.29	119.44	299	evergreen broad- leaved forest	21	5294.63	0.98
NSTEC05	29.80	121.79	231	evergreen broad- leaved forest	41	6022.80	0.98
NSTEC06	27.98	119.14	294	evergreen broad- leaved forest	57	5992.46	0.98
NSTEC07	26.59	118.05	239	evergreen broad- leaved forest	59	6345.35	0.98
NSTEC08	24.41	116.34	195	evergreen broad- leaved forest	35	7143.63	0.99
NSTEC09	23.17	112.54	240	evergreen broad- leaved forest	45	7532.60	0.99
NSTEC10	25.32	110.25	199	conifer/deciduous broad-leaved forest	29	6635.23	0.99
NSTEC11	26.84	109.60	390	conifer/deciduous broad-leaved forest	53	5697.20	0.99

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Table 1. Continued.

Site code	Latitude (° N)	Longitude (° E)	Elevation (m)	Vegetation type	Number of species	GDD ₀ (day °C)	α
NSTEC12	28.34	109.73	220	conifer/deciduous broad-leaved forest	39	5457.14	0.99
NSTEC13	33.50	111.49	449	deciduous broad-leaved forest	27	4098.36	0.97
NSTEC14	39.95	115.42	1253	deciduous broad-leaved forest	14	2357.31	0.81
X01	48.19	87.02	272	desert	8	2252.67	0.33
X02	46.40	85.95	701	desert	18	3575.09	0.23
X03	47.04	87.09	620	desert steppe	10	2930.53	0.31
X04	47.83	86.85	499	desert steppe	20	3118.13	0.29
X05	47.94	86.83	481	desert	11	3105.78	0.29
X06	48.17	87.08	709	desert steppe	15	2252.67	0.33
X07	48.11	87.01	1100	shrubland	6	2252.67	0.33
X08	48.33	87.12	1595	meadow	13	1304.34	0.57
X09	47.72	87.02	498	desert steppe	23	3165.82	0.28
X10	47.74	87.54	521	desert steppe	13	3146.09	0.27
X11	47.16	88.70	750	desert	8	3159.38	0.3
X12	46.30	89.55	885	desert	10	3021.81	0.32
X13	45.36	89.40	1068	desert	7	2929.95	0.33
X14	44.12	87.81	513	desert	11	3901.31	0.29
X15	44.08	87.79	583	desert steppe	18	3934.76	0.29
X16	44.07	88.08	852	desert steppe	11	3367.67	0.35
X17	44.00	88.06	1060	meadow	12	3369.92	0.31
X18	43.93	88.11	1430	shrubland	9	3153.82	0.37
X19	42.84	89.44	-91	shrubland	2	5745.44	0.09
X20	42.73	89.44	-136	desert	2	5869.71	0.14
X21	42.69	89.42	-146	desert	2	5989.24	0.08
X22	42.37	88.57	1721	desert	5	3112.29	0.28
X23	42.22	87.76	1445	desert	9	3093.93	0.23
X24	41.81	86.25	1444	desert	3	3617.6	0.19
X26	40.83	84.29	921	desert	4	4893.58	0.07
X27	41.48	84.21	928	desert	3	4678.9	0.21
X28	41.50	84.51	919	desert	3	4644.14	0.11
X29	41.66	84.89	902	desert	5	4520.84	0.10
X30	40.51	89.11	70	desert	3	4865.42	0.04
X31	48.33	87.12	1595	desert	1	1304.34	0.57
X32	40.83	84.29	26	desert	1	4893.58	0.07
X33	43.93	88.11	1430	shrubland	3	3153.82	0.37
X34	43.90	88.12	1935	evergreen conifer forest	9	2037.89	0.70

Responses of leaf traits to climatic gradients

T.-T. Meng et al.

Table 2. Principal components of climate data based on the country-wide, 10 km grid and on the 80 sampling sites. Each component (axis) represents a linear combination of variables. Loadings for variables represent the contribution of each variable to the axis. Values are shown in bold when their magnitude > 0.5.

	country-wide 10 km grid			80 sampling sites		
	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3
MAT	0.883	-0.422	0.179	0.870	-0.462	0.127
GDD ₀	0.879	-0.411	0.142	0.865	-0.474	0.092
MTCO	0.865	-0.144	0.166	0.946	-0.219	0.030
MTWA	0.669	-0.603	0.120	0.572	-0.727	0.223
PAR ₀	0.672	-0.650	0.234	0.642	-0.701	0.106
MAP	0.903	0.407	0.046	0.899	0.427	-0.014
α	0.578	0.744	0.166	0.603	0.753	0.106
MI	0.768	0.623	0.030	0.824	0.560	0.000
P _{DJF}	0.876	0.166	-0.387	0.917	0.200	-0.263
P _{JJA}	0.759	0.540	0.330	0.747	0.599	0.238
Timing	-0.639	0.100	0.702	-0.833	-0.021	0.143
Seasonality	-0.752	0.094	0.384	-0.314	0.204	0.900
Variance explained	60.5 %	21.7 %	9.0 %	59.8 %	25.1 %	8.8 %

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Responses of leaf traits to climatic gradients

T.-T. Meng et al.

Table 3. Regression coefficients for the GLM with only climate variables as predictors.

	Intercept		Alpha		GDD ₀	
	slope	±SD error	slope	±SD error	slope	±SD error
lnLA	1.8167	0.1433	5.8373	0.2025	−0.3682	0.3413
lnSLA	2.3234	0.0434	1.5550	0.0588	−1.5061	0.0979
lnLDMC	5.7544	0.0347	−0.3542	0.0468	0.6490	0.0779
lnFvFm	−0.2400	0.0136	0.1168	0.0196	−0.4191	0.0250
lnQY	−0.7823	0.0213	0.5820	0.0306	−0.1321	0.0391
lnCmass	6.1961	0.0276	−0.0792	0.0424	−0.0831	0.0547
lnNmass	3.1357	0.0419	0.2511	0.0605	−1.0920	0.1033
lnPmass	0.1243	0.0476	0.6884	0.0733	0.4798	0.0944
lnKmass	3.2124	0.0696	−0.1766	0.1072	−1.0956	0.1381
lnNarea	0.8419	0.0462	−1.1027	0.0670	0.0638	0.1142
lnParea	−2.4890	0.0676	−0.2141	0.1043	1.4426	0.1347
lnKarea	0.5975	0.0767	−1.0796	0.1185	−0.1282	0.1530

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

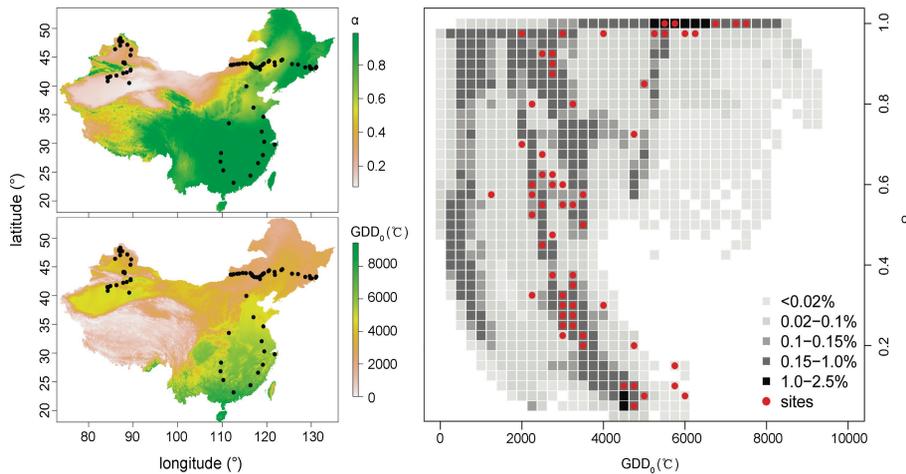



Figure 1. Left: geographic variation in the mean Cramer–Prentice moisture index (α) and annual growing degree days above 0°C (GDD_0) in China. Right: frequency distribution of 10 km grid cells (grey scale) and location of sampling sites (red) in climate space.

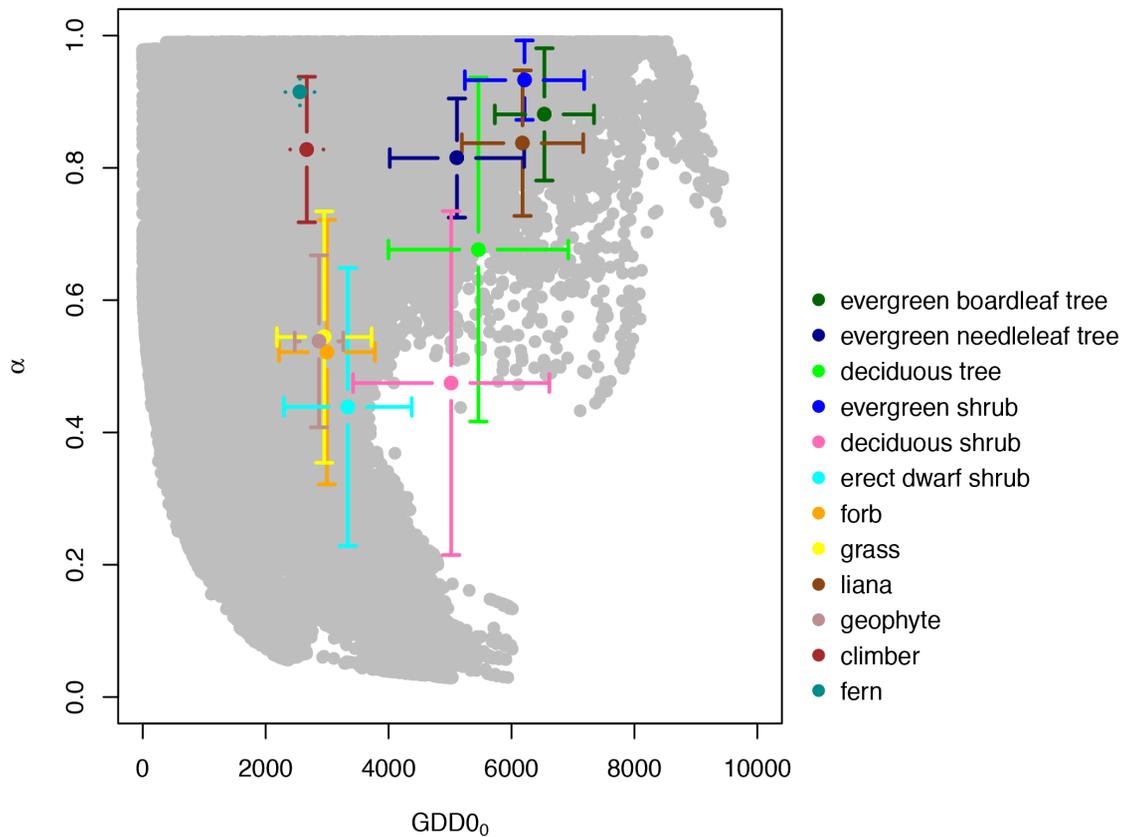


Figure 2. Optima and tolerances of PFTs in climate space, based on data from the sampling sites.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Responses of leaf traits to climatic gradients

T.-T. Meng et al.

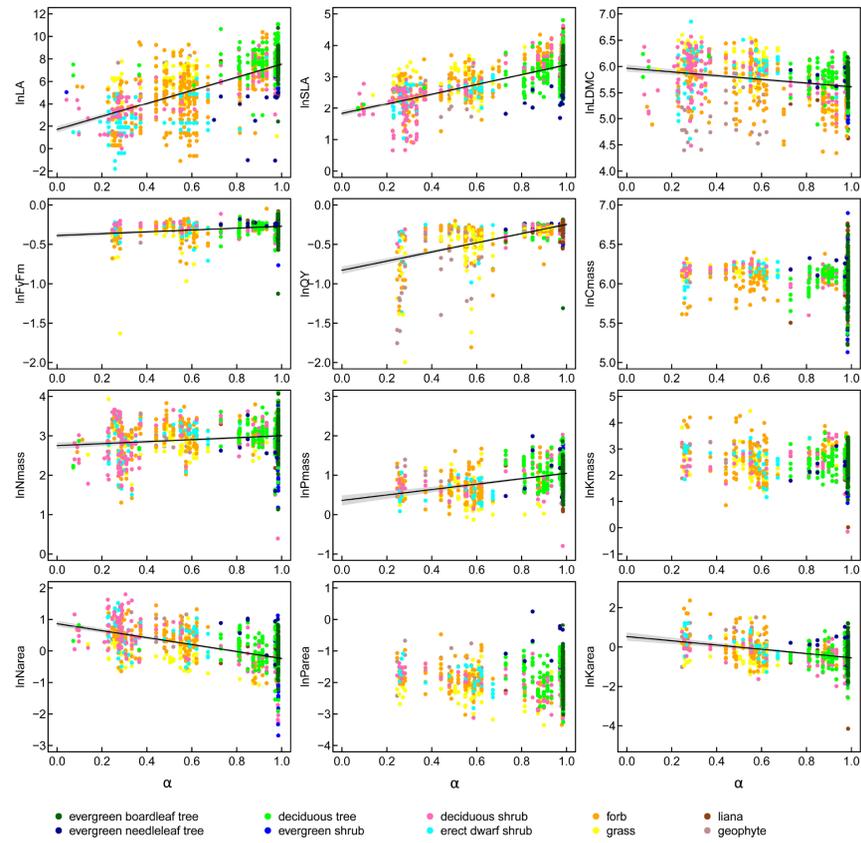


Figure 3. Partial residual plots for the relationships between leaf traits and the Cramer–Prentice moisture index (α), from the GLM analysis summarized in Table 3. Each point denotes a species-site combination; PFTs are indicated by colours. Only significant regression slopes ($P < 0.01$) are shown.

[Title Page](#)

[Abstract](#) [Introduction](#)

[Conclusions](#) [References](#)

[Tables](#) [Figures](#)

[◀](#) [▶](#)

[◀](#) [▶](#)

[Back](#) [Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



Responses of leaf traits to climatic gradients

T.-T. Meng et al.

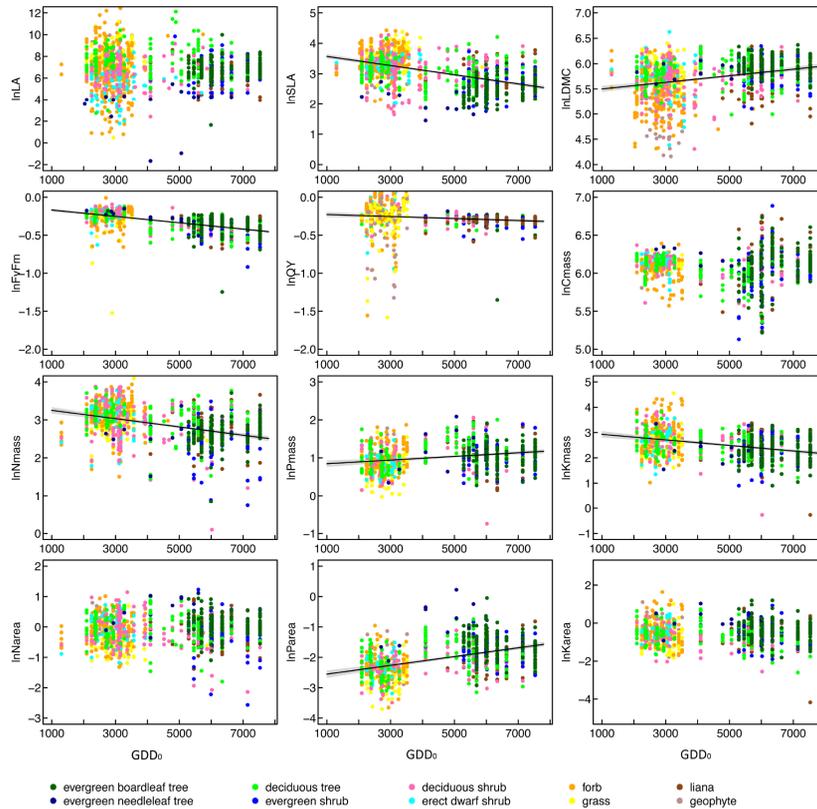


Figure 4. Partial residual plots for the relationships between leaf traits and growing degree days (GDD_0), from the GLM analysis summarized in Table 3. Each point denotes a species-site combination; PFTs are indicated by colours. Only significant regression slopes ($P < 0.01$) are shown.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

