Global patterns in plant height

Angela T. Moles[1]*, David I. Warton[2], Laura Warman[1], Nathan G. Swenson[3], Shawn W. Laffan[4], Amy E. Zanne[5,6], Andy Pitman[7], Frank A. Hemmings[4] and Michelle R. Leishman[8]

[1]Evolution & Ecology Research Centre, School of Biological, Earth and Environmental Sciences, The University of New South Wales, Sydney, NSW 2052, Australia; [2]School of Mathematics and Statistics and Evolution & Ecology Research Centre, The University of New South Wales, Sydney, NSW 2052, Australia; [3]Center for Tropical Forest Science – Asia Program, Arnold Arboretum, Harvard University, Cambridge, MA 02130-3500, USA; [4]School of Biological, Earth and Environmental Sciences, The University of New South Wales, Sydney, NSW 2052, Australia; [5]National Evolutionary Synthesis Center, 2024 W. Main St., Durham, NC 27705, USA; [6]Department of Biology, University of Missouri, St. Louis, MO 63121-4400, USA; [7]Climate Change Research Centre, Faculty of Science, The University of New South Wales, Sydney, NSW 2052, Australia; and [8]Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

Summary

1. Plant height is a central part of plant ecological strategy. It is strongly correlated with life span, seed mass and time to maturity, and is a major determinant of a species' ability to compete for light. Plant height is also related to critical ecosystem variables such as animal diversity and carbon storage capacity. However, remarkably little is known about global patterns in plant height. Here, we use maximum height data for 7084 plant Species × Site combinations to provide the first global, cross-species quantification of the latitudinal gradient in plant height.

2. The mean maximum height of species growing within 15° of the equator (7.8 m) was 29 times greater than the height of species between 60° and 75° N (27 cm), and 31 times greater than the height of species between 45° and 60° S (25 cm). There was no evidence that the latitudinal gradient in plant height was different in the northern hemisphere than in the southern hemisphere ($P = 0.29$). A 2.4-fold drop in plant height at the edge of the tropics ($P = 0.006$) supports the idea that there might be a switch in plant strategy between temperate and tropical zones.

3. We investigated 22 environmental variables to determine which factors underlie the latitudinal gradient in plant height. We found that species with a wide range of height strategies were present in cold, dry, low productivity systems, but there was a noticeable lack of very short species in wetter, warmer, more productive sites. Variables that capture information about growing conditions during the harsh times of the year were relatively poor predictors of height. The best model for global patterns in plant height included only one term: precipitation in the wettest month ($R^2 = 0.256$).

4. *Synthesis.* We found a remarkably steep relationship between latitude and height, indicating a major difference in plant strategy between high and low latitude systems. We also provide new, surprising information about the correlations between plant height and environmental variables.

Key-words: climate, latitude, plant ecological strategy, precipitation, temperature

Introduction

Height is a crucial component of a plant species' ecological strategy. It is central to a species' carbon gain strategy, because height is a major determinant of a plant's ability to compete for light, and because of correlations between plant height and traits such as leaf mass fraction, leaf area ratio, leaf nitrogen per area, leaf mass per area and canopy area (Falster & Westoby 2003). Plant height is also an important part of a

coordinated suite of life-history traits including seed mass, time to reproduction, longevity and the number of seeds a plant can produce per year (Moles & Leishman 2008). These traits are central in determining how a species lives, grows and reproduces. Plant size is also correlated with metabolic rate and with maximum population density (Enquist *et al.* 1998). In addition to having a central role in plant ecological strategy, plant height affects important ecosystem variables such as carbon sequestration capacity (through its relationship with plant biomass) and animal diversity (for example, bird and mammal species diversity are tightly correlated with foliage height

**Correspondence author. E-mail: a.moles@unsw.edu.au

diversity, Macarthur & Macarthur 1961; MacArthur 1964; Recher 1969; August 1983).

Given the obvious importance of plant height and the fact that it is a relatively easily measured plant trait, one might expect global patterns in height to be well known. This is not the case. In this study, we aim to provide the first quantification of global patterns in plant height and the first large-scale, cross-species investigation of relationships between plant height and environmental conditions.

We expected to find that plants were taller in the tropics than at higher latitudes. However, we also expected a large scatter around this relationship, as there is substantial variation in plant height among the coexisting species at most sites. It is clear that tropical rain forest is taller than arctic tundra, and previous work has shown a latitudinal gradient in plant growth form (tropical sites have a higher proportion of trees and a lower proportion of herbs than do temperate sites, Moles *et al.* 2007). Within-species studies of latitudinal gradients in plant height have shown plants to be taller at lower latitudes (e.g. Kollmann & Banuelos 2004; Aguilar-Rodriguez *et al.* 2006; Mendez-Alonzo *et al.* 2008). However, there are ecosystems dominated by tall species at quite high latitudes (e.g. northern boreal forests) and tropical ecosystems that are dominated by relatively short species (e.g. savannas). The tallest plant species (*Sequoia sempervirens* (California) and *Eucalyptus regnans* (Australia)) live at mid-latitudes. Further, the species that coexist in a given ecosystem often have heights that span several orders of magnitude (Foster & Janson 1985; Falster & Westoby 2005).

In addition to asking whether there was a latitudinal gradient in plant height, we also aimed to quantify the shape of the relationship. Ecological patterns are often different in the northern and southern hemispheres (Chown *et al.* 2004). We therefore began by asking whether the relationship between plant height and latitude differed between the two hemispheres. Next, we asked whether there was a step in plant height at the edge of the tropics. A previous study on the latitudinal gradient in seed mass showed a major drop in mean seed mass at the edge of the tropics (Moles *et al.* 2007). This drop in seed mass was most strongly associated with vegetation type and plant growth form (Moles *et al.* 2007). These data led Moles *et al.* to suggest that there might be a switch in life-history strategy around the edge of the tropics, with tall, large-seeded species giving way to shorter, smaller-seeded species. We aimed to test this idea in this study.

It is unlikely that it is latitude *per se* that underlies global patterns in ecological traits and processes – these patterns are much more likely to be driven by correlated factors such as temperature, water availability and net primary productivity (NPP). Thus, our second major aim in this study was to quantify the shape and strength of relationships between plant height and a range of environmental variables.

In summary, our main aims were to:

1 Quantify the shape and strength of the latitudinal gradient in plant height at the cross species level.

2 Determine which environmental variables are most tightly related to plant height.

Materials and methods

DATA COMPILATION AND ERROR CHECKING

Plant height data were compiled opportunistically from previously published studies, from floras and from pre-existing data bases including the LEDA traitbase (Kleyer *et al.* 2008) and Moles *et al.* (2004). Only self-supporting species were included in the data set: all aquatic plants, climbing plants and epiphytes were excluded. To limit biases associated with incomplete sampling of ecosystems (e.g. studies that include only trees), we included data from as many complete floras as possible. We also endeavoured to include information from a wide range of ecosystem types (e.g. forests, shrublands, deserts, tundras, savannas). Growth form data were compiled from pre-existing data bases and from the botanical knowledge of ATM, FAH and LW (see Fig. 1, for a list of categories). The plant height variable we use throughout this study is the maximum height that a species is known to attain at each site. We use maximum height rather than mean height throughout this study, to avoid problems associated with the indeterminate growth of plants, and the fact that the majority of individuals of each species are small seedlings or juvenile plants.

The data we compiled were the maximum achieved height of each species at each sample location. There is clear evidence that disturbances prevent many native plant communities from reaching the maximum height that a site could have supported (Midgley & Niklas 2004). Therefore, this manuscript considers the height plants actually achieve under natural conditions, rather than the theoretical potential height.

We checked the nomenclature to reduce the chances that species were listed in the data base under multiple names (either as synonyms or as spelling errors). Species' binomials were run through the SALVIAS Taxon Scrubber (http://www.salvias.net/pages/taxonscrubber.html). This software does not check for synonyms, rather it standardizes the list of species names in the data base to pre-existing lists of taxa (i.e. it acts primarily as a spell-checker). Genus names were then checked against the Vascular Plant Families and Genera data base from the Royal Botanic Gardens, Kew (http://data.kew.org/vpfg1992/vascplnt.html). Invalid names for angiosperms were updated according to the Angiosperm Phylogeny Website (Stevens 2001 onwards), and names for gymnosperms and ferns were updated according to the Diversity of Life webpage http://www.diversityoflife.org/. Finally, we added unique number identifiers to taxa whose specific epithet was unknown.

We error-checked the height data by checking values for all species whose greatest recorded height in the data set was more than five times the lowest height in the data set, and by ensuring that the extreme values within each growth form were legitimate.

At the end of this process, we had 32 737 height records. However, we were not able to record a physical location for all observations (location data in this study represent the locations at which species were sampled rather than the midpoints of species' ranges). Latitude and longitude were taken from site descriptions in source papers wherever possible. Where necessary, latitudes from nearby features/towns were used in place of exact readings for field sites. If a record came from a state, country or island that spanned < 2.5° of latitude and longitude, the midpoint of the area was entered. If the range was larger than this, then no location data were entered.
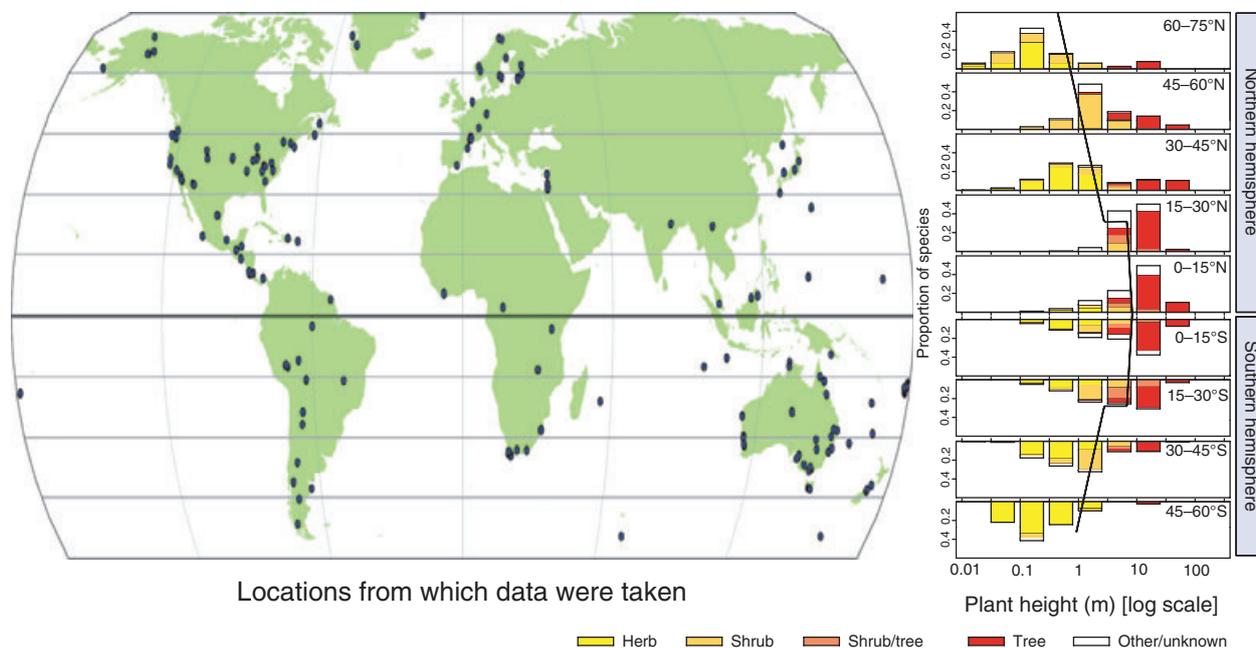
Fig. 1. Global patterns in plant height. The panel at the left shows the locations from which data were taken. The panel at the right shows the latitudinal gradient in plant height. To facilitate interpretation, we have presented the data in frequency histograms for species in each of nine latitudinal bands (these bands correspond to the latitude lines on the map on the left). However, latitude and height are continuous variables, and they were treated as such in all analyses. Data are shaded according to growth form: trees in red, shrub/trees in dark orange, shrubs in light orange, herbs in yellow and species whose growth form was unknown or difficult to classify are shown in white. The black line running across the individual height histograms shows the best-fit relationship between height and latitude.

The final data set comprised 7042 Species × Site combinations, including 5784 different species from 256 families and 1819 different genera (for information on taxonomic composition of the data set see Appendix S6). Data were from 222 locations, ranging from 74°29′ N to 54°30′ S (Fig. 1). While this is the biggest compilation of plant height data made to date, it does have limitations. Some parts of the world (notably Russia, Canada and northern Africa) are under-represented in the data set. Thus, although we endeavoured to include data from all major ecosystem types, some ecosystems are better represented in our data set than others.

ENVIRONMENTAL VARIABLES

Location data were entered into Biome4 (a coupled biogeography and biogeochemistry model, Kaplan *et al.* 2003) to obtain the estimates of NPP and leaf area index (LAI). Biome4 calculates LAI and NPP across the range of plant functional types present in each half-degree grid square, by using climate and soil information linked to an ecophysiologically based photosynthesis and stomatal behaviour model (Kaplan *et al.* 2003). Temperature, precipitation and bioclimatic parameters were derived from the WorldClim data set (Hijmans *et al.* 2005). Altitude data were taken directly from source papers where possible, but if this information was not available, we used altitude data from WorldClim. In total, we had data for 22 environmental variables (Table 1).

STATISTICS

Height was log-transformed before analysis, so that it could be interpreted on a multiplicative scale. Altitude was $\log(y + 1)$-transformed to reduce the influence of a few high-altitude sites, and temperature was $\log(50 - y)$-transformed to reduce the influence of a few sites with exceptionally low temperature.

We constructed linear mixed-effects models (Venables & Ripley 2002) for height, with linear fixed-effects terms for latitude and/or climatic variables measured at each site, and random effects terms for site and species (making standard assumptions of normality, independence and equal variance). The site random-effects term was included to reflect the hierarchical nature of the sampling design, to allow us to measure site-to-site variation not explained by climatic terms, and to account for this when making inferences about climatic correlates of height. The random-effects term for species was included to account for the fact that multiple instances of some species were included in the data set from different locations. Models were fitted using restricted maximum likelihood via the R package LME4 (Bates *et al.* 2008). We used standard diagnostic plots to assess the extent of departures from model assumptions, focusing on linearity, equal variance of residuals and normality of estimated random effects, as well as checking climatic variables for influential values. After data transformation, we found no serious violations.

As a measure of the strength of the association between environmental variables and height, we report the R^2, partitioned into the component explained by climate (using the reduction in residual sum of squares on inclusion of fixed effects terms only), the between-site component that remained unexplained (using the change in residual sums of squares on inclusion of random effects terms) and the within-site component (remaining unexplained variation). Because of the hierarchical nature of our data, with data for multiple species at multiple sites, R^2 was calculated from the residual sum of squares of linear mixed-effects models on centred data rather than using standard formulae.

To study the form of the relationship between height and latitude, we considered the following functions of latitude, all fitted in the linear mixed-effects framework with site and species random effects: a linear function of latitude; a linear function of latitude with different slopes in different hemispheres; and a piecewise linear function of

Table 1. Correlations between $\log_{10}$ plant height and environmental variables. All analyses were performed with linear mixed-effects models including random effects for site and for species. Some of the R^2-values are slightly negative. This is because the model is maximizing likelihood, rather than R^2. A negative R^2 simply indicates that the variable explains almost none of the variation in plant height

Variable	R^2 (cross-site explained)	R^2 (cross-site unexplained)	Slope
Precipitation of wettest month	0.256	0.269	0.003
Precipitation of wettest quarter	0.248	0.277	0.001
Isothermality	0.222	0.302	0.175
Annual precipitation	0.205	0.320	0.0004
Mean temperature of coldest quarter	0.195	0.330	−6.053
Min temperature of coldest month	0.180	0.345	−6.459
Temperature seasonality	0.177	0.348	−0.094
Annual mean temperature	0.170	0.354	−7.239
Mean temperature of driest quarter	0.168	0.357	0.004
Net primary productivity	0.152	0.385	0.001
Temperature annual range	0.141	0.384	−0.027
Precipitation of warmest quarter	0.119	0.406	0.001
Precipitation of coldest quarter	0.085	0.440	0.001
Mean temperature of warmest quarter	0.064	0.461	−8.095
Precipitation seasonality	0.049	0.477	0.004
Mean temperature of wettest quarter	0.040	0.485	−6.194
Precipitation of driest quarter	0.010	0.515	−2.368
Mean diurnal temperature range	0.008	0.517	−0.028
Precipitation of driest month	−0.003	0.528	0.005
Max temperature of warmest month	−0.005	0.530	−5.034
Altitude	−0.016	0.541	−0.246
Leaf area index	−0.020	0.557	0.293

latitude with a drop-off and change in slope at the edge of the tropics. Indicator variables for hemisphere and temperate versus tropics, and their interaction terms, were used to introduce these variables. The significance of each term in the model was measured using likelihood ratio tests.

To find a parsimonious model for predicting height as a function of 22 variables is a non-trivial model selection problem. This problem was complicated by the hierarchical nature of sampling and our desire for the use of a simple and interpretable model selection criterion, which was robust to failure of any of our model assumptions. Hence we used as the criterion for minimization the square root of mean squared error (RMSE), that is, when comparing several models, we compared them on the basis of how small RMSE was. Note that RMSE can be interpreted loosely as an estimate of the magnitude of the typical residual from the fitted model. We used 10-fold cross-validation as a means of estimating the RMSE of species heights at new sites (Hastie *et al.* 2001; Venables & Ripley 2002), hence penalizing models which over-fit the data as well as those which fail to capture important sources of variation in plant height. Thus, we reduced the model selection problem to one of finding the model that would most closely predict the height of plants at new sites (as measured by RMSE). We re-ran our analyses several times using different random assignments of sites to validation groups and considering other cross-validation schemes (from 2- to 20-fold) and found our results robust to this choice.

FINDING THE BEST-FITTING MODEL FOR PREDICTING HEIGHT FROM ENVIRONMENTAL VARIABLES

We started by reducing the initial pool of 22 variables to a smaller number of variables that characterize the key forms of climatic variation. There were seven variables measuring temperature extremes, and we found the combination that best predicts height

out of the following four combinations: (*temperature seasonality*), (*maximum temperature of the warmest month, minimum temperature of the coldest month*), (*mean temperature of the warmest quarter, mean temperature of the coldest quarter*) or (*mean temperature of the wettest quarter, mean temperature of the driest quarter*). The last of these combinations minimized RMSE for predicted plant height and so was used in our all-subset analyses, described below. Similarly, we found the best combination of variables for describing the association between variability in precipitation and height out of: (*precipitation seasonality*), (*precipitation in the coldest quarter, precipitation in the warmest quarter*), (*precipitation in the wettest quarter, precipitation in the driest quarter*) or (*precipitation in the wettest month, precipitation in the driest month*). Of these, the combination (*precipitation in the wettest month, precipitation in the driest month*) was the best predictor of plant height. Finally, we considered measurement of diurnal temperature variation relative to annual temperature range by either using these two variables directly in the model (*mean diurnal temperature range, temperature annual range*) or via (*isothermality*), which is a ratio of the two. The latter was a better predictor. This left us with 10 variables for ensuing analyses (Table 2). Pairwise correlations among these 10 variables are recorded in Appendix S7.

Next, we performed all-subsets regression, using 10-fold cross-validation to find the subset of the 10 variables that minimized RMSE. We considered not just the best-fitting model, but also the most parsimonious model within 1 standard error of the best ('1 standard error rule', Hastie *et al.* 2001) and, as a useful summary of the relative importance of different variables, the proportion of times each variable was selected in the top 10% and top 5% of models, as in Ramp *et al.* (2005).

Models were fitted using the LME4 package (Bates *et al.* 2008) within R version 2.7 (R Development Core Team 2007). Purpose-written code for these analyses is available in Appendix S4.

Table 2. The percentage of times each of the 10 selected variables appeared in the top 5% and 10% of all the possible models fitted via all-subsets regression (1024 models in total). Numbers represent the mean result from two runs of the model set for 10-fold cross validation

	% Times in the top 10% of models	% Times in the top 5% of models
Precipitation of wettest month	96	99
Altitude	57.5	62
Mean temperature of driest quarter	53	53
Annual mean temperature	48	46
Precipitation of driest month	37.5	37
Isothermality	37	39
Annual precipitation	34.5	33
Mean temperature of wettest quarter	34	23
Net primary productivity	10.5	0
Leaf area index	5.5	0

Results

PLANTS REALLY ARE TALLER IN THE TROPICS

We found a strong latitudinal gradient in plant height (Fig. 1). The geometric mean height for plant species growing within 15° of the equator is 7.8 m, compared to only 27 cm for species growing between 60° and 75° N, and 25 cm for species growing between 45° and 60° S. A linear mixed-effects model with random effects for site and species showed a highly significant relationship between plant height and absolute latitude ($R^2 = 0.26$; $P < 0.001$). This change in plant height goes along with a shift from the majority of the plant species at high latitudes being herbs, to the majority of the plant species at low latitudes being trees.

Next, we added a term for hemisphere to the model, to determine whether the relationship differed between hemispheres. If anything, the latitudinal gradient in plant height was marginally steeper in the southern hemisphere than in the northern hemisphere, but the term for hemisphere had a P-value of 0.29. That is, there is no evidence that the latitudinal gradient in plant height is different in the northern hemisphere than in the southern hemisphere.

Next, we added a term for temperate/tropical to the model, to ask whether there was any evidence for a drop in plant height at the edge of the tropics. This term had a P-value of 0.006. Thus, there is some evidence that temperate and tropical regions show different relationships between plant height and latitude, with an estimated 2.4-fold drop in plant height at the edge of the tropics. However, this result should be treated with some caution, as little additional variation in height was explained by the temperate/tropical term (the R^2 remained 0.26, to two decimal places), and a different approach to model selection suggests that the model with latitude only is the best predictor of height. Specifically, while the model with smallest Akaike's Information Criterion includes the temperate/tropical terms, the model with smallest Bayesian Information Criterion score contains latitude only.

Finally, we asked whether the latitudinal gradient in plant height seen across the full data set was also seen within the major taxonomic groups and growth forms represented in the data set. We used linear mixed-effects models identical to that used above, but without a term for hemisphere (because this term did not explain a significant proportion of the variance in the main analysis, and we had fewer degrees of freedom available in the divided data set). The relationships between latitude and height for dicots ($n = 5883$ species) and monocots ($n = 935$ species) were very similar to the relationships seen across the full data set (Appendix S2). The relationships for gymnosperms ($n = 135$) and ferns ($n = 72$) were much weaker, but this is probably due to an inadequate sample size in these smaller groups. On balance, it seems that differences in taxonomy are not artificially obscuring or strengthening the latitudinal gradient in plant height. The relationships between plant height and latitude within herbs ($n = 1869$ species) and shrubs ($n = 2239$ species) were also broadly similar to those seen in the full data set (Appendix S3). However, there was little evidence for a latitudinal gradient in plant height within trees ($n = 2224$ species). Thus, at least part of the latitudinal gradient in plant height is due to a change in the proportion of species of different growth forms.

CORRELATES OF THE LATITUDINAL GRADIENT IN PLANT HEIGHT

The single strongest correlate of plant height was precipitation in the wettest month ($R^2 = 0.26$; Table 1). Variables such as NPP ($R^2 = 0.15$), minimum temperature in the coldest month ($R^2 = 0.18$) and altitude ($R^2 = -0.016$, see Table 1, for explanation of negative R^2-values) explained surprisingly little variation in plant height. However, about half of the variation in plant height in our data set lay among coexisting species within sites (47% of the variation was within sites), so site-to-site variation in climate could only possibly explain half of the variation in global plant height.

We used quantile regressions to describe the shape of the data cloud in the relationships between plant height and each of the environmental variables (Fig. 2, Appendix S1). The results for the 95th quantile were strikingly different to those for the fifth quantile. The slope of the line representing the 95th quantile was not significantly ($\alpha = 0.01$) different from zero in 11 of the 22 relationships between plant height and individual climate variables. Even in those relationships in which the slope of the 95th quantile was significantly different from zero, the slope was relatively modest (the difference between plant height at the lowest value for each climate variable and the plant height at the highest value for each climate variable ranged from 101% to 211%, mean = 140%). The slopes of the lines representing the fifth quantiles were far steeper. All of these lines were significantly different from zero, and there were massive differences between plant height at the lowest and highest value for each climate variable (range from 176% to 3580% difference, mean difference = 1697%). That is, the upper limit of plant height in an ecosystem is only moderately affected by the prevailing environmental conditions,
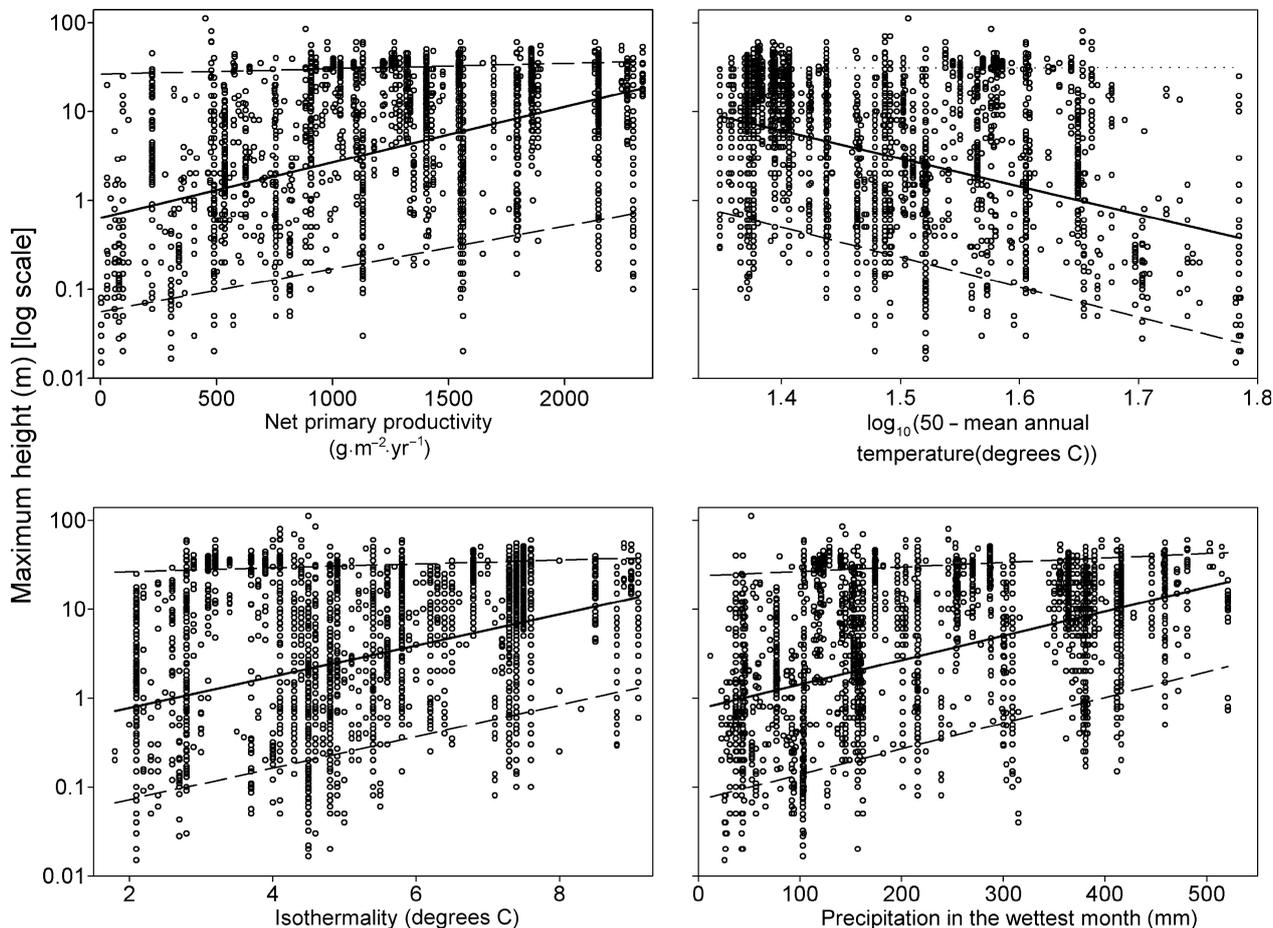
Fig. 2. The relationship between plant height and selected climate variables (relationships for all variables are presented in Appendix S1). Each point represents one Species × Site combination. Solid lines show the results of linear mixed-effects models with random effects for species and site. Dotted and dashed lines show the results of quantile regressions. Dashed lines represent slopes that are significantly different from zero, while dotted lines represent slopes that were not significantly different from zero at an alpha of 0.01. The lines shown are the fifth quantile, and the 95th quantile. Note that the $\log_{10}(50 - y)$ transformation performed on temperature variables converts high raw values to low transformed values.

while the lower limit of plant height responds dramatically to most environmental variables.

Finally, we asked which combination of environmental variables best explained the global patterns in plant height. The terms that were most often included in the top 5% of models were precipitation in the wettest month, altitude, mean temperature of the driest quarter and annual mean temperature (Table 2). The model with the lowest root mean standard error (RMSE; 0.6075 ± 0.0212) contained three terms; precipitation in the wettest month, mean annual temperature and altitude. However, a model including a single term (precipitation in the wettest month) had a statistically indistinguishable RMSE (0.6153 ± 0.0240; Appendix S5). Thus, the most parsimonious model for global patterns in plant height contains just one of our original 22 environmental variables.

Discussion

THE LATITUDINAL GRADIENT IN PLANT HEIGHT

Quantifying global-scale patterns in ecological traits and processes and understanding how environmental variables

shape these patterns is an important goal for ecologists, both for developing our understanding of species' ecological strategies and in terms of the current concern about the potential effects of climate change on the earth's biota (if we do not know how climate affects present-day patterns in ecology, then it will be very difficult indeed to predict the likely impact of climate change). Ecologists have spent a great deal of time studying the latitudinal gradient in diversity (many taxa, including bats, plants, fish, mammals, termites and fossil foraminifera have been shown to be more diverse in the tropics, Rosenzweig 1995). There have also been many investigations of the latitudinal gradient in body size in animal taxa (Bergmann's Rule, which tends to apply to endotherms, but not necessarily to exotherms, Mousseau 1997; Ashton 2002, 2004; Adams & Church 2008). We also have data on large-scale, cross-species patterns in some plant traits, including latitudinal gradients in wood density (higher at low latitudes, Swenson & Enquist 2007), seed mass (higher at low latitudes, Moles *et al.* 2007), extrafloral nectaries (more nearer the equator, Pemberton 1998) and some leaf traits (e.g. leaf N and P are higher at high latitudes, and leaf margins become more dissected and toothed at low temperatures (and thus away from the equator), Reich

& Oleksyn 2004; Royer *et al.* 2005). There is also some evidence that rates of herbivory are higher in the tropics (Coley & Aide 1991; Coley & Barone 1996; Swihart & Bryant 2001). However, latitudinal gradients in many other ecologically important traits and processes remain undescribed. This study provides the first global, cross-species quantification of the latitudinal gradient in plant height.

Finding a latitudinal gradient in plant height is not terribly surprising. However, the slope of the relationship between height and latitude was impressive. The average maximum height of plant species growing within 15° of the equator is 29 times greater than the height of plant species growing between 60° and 75° N, and 31 times greater than the height of plant species growing between 45° and 60° S. As plant height is a central component of a species' ecological strategy, this result suggests that there is a dramatic difference in plant ecological strategy between high and low latitude ecosystems.

The shape of the latitudinal gradient in plant height was somewhat surprising. We initially thought that the different climatic conditions found in the northern and southern hemispheres (especially during the colder northern winters) might lead to a steeper relationship between plant height and latitude in the northern hemisphere. However, we found no evidence for a difference in the latitudinal gradient between the two hemispheres, despite the high statistical power that comes from a large data set. This finding, combined with the relatively low explanatory power (R^2) of the variable 'minimum temperature of the coldest month' suggests that low winter temperatures and the associated risk of freeze-embolisms are less important in determining maximum plant height than is water availability.

This study provided some support for the idea that there is a drop in plant height at the edge of the tropics, and the magnitude of the drop in plant height (2.4-fold) was substantial and comparable to the 7-fold step in seed mass at the edge of the tropics reported by Moles *et al.* (2007). Together, these findings suggest that there might be a sudden switch in ecological strategy at the edge of the tropics. The idea that there is a substantial and sudden shift in plant strategy at the edge of the tropics definitely merits further investigation. Once the existence of such a step has been confirmed, there are many important questions to be addressed. The current global data sets for plant height and seed mass do not have sufficient resolution to determine exactly how plant traits change around the edge of the tropics. Is there a sudden step in strategy, or a zone of rapid transition? Is the switch in plant strategy associated with environmental conditions (for instance, one might ask whether it was associated with the band of deserts around these latitudes)? It would also be interesting to ask whether changes in plant height and seed mass go along with changes in correlated life-history traits such as life span and time to first reproduction, or whether the scaling relationships among these life-history traits depend on environmental conditions.

RELATIONSHIPS WITH ENVIRONMENTAL VARIABLES

The relationships between plant height and environmental variables were all triangular (Fig. 2, Appendix S1). A wide range of plant height strategies was present at sites with low temperature, precipitation and/or productivity. While the driest, coldest, highest and most unproductive sites did lack the very tallest species, species above 10 m were present across most of the range of all of the environmental variables. In contrast, there were relatively few very short species at sites with high temperature, precipitation and/or productivity. The scarcity of very short species in these sites is unlikely to result from a sampling bias (e.g. people focusing on woody species in rain forests), as many entire floras from high-productivity sites were included in this study (including floras of Fiji, Norfolk and Lord Howe Islands, and Barro Colorado Island in Panama). The scarcity of very short species at high-productivity, warm, wet sites seems more likely to result from light attenuation through the canopy reducing light levels nearer the ground to levels below the carbon compensation point for understorey species.

Our finding that there are relatively few small species in highly productive, wet, warm sites is seemingly at odds with Niklas *et al.*'s (2003) findings from an analysis of Gentry's world-wide data base on plant communities (Phillips & Miller 2002). Niklas *et al.* showed that communities in which the majority of the species were found in the smallest size class (but were rarely canopy dominants) were absent at high latitudes, but increased in number towards the equator. There are two possible factors that might explain this discrepancy. First, Gentry's data are from forest plots, and the smallest size-class included was plants with a d.b.h. of 2.5 cm (Phillips & Miller 2002). The omission of herb- and shrub-dominated communities and the exclusion of small plants is an important difference between this study and Niklas *et al.* (2003), as small herbaceous species make up the majority of the diversity at high latitudes (Aarssen *et al.* 2006 and this study), and it is only the very shortest species that are missing from the highly productive sites in this study (Fig. 1). Secondly, Gentry's data come from 0.1-hectare plots (Phillips & Miller 2002). Because of the negative relationship between plant size and the maximum density a species can attain in a community (Enquist *et al.* 1998), relatively few canopy individuals will be sampled in each plot, but a great many small understorey individuals would be sampled. Thus, in a diverse tropical forest, many species that are potential canopy species at a larger scale would appear to be present only in small size classes. This bias would be less pronounced in a temperate forest, where there are fewer canopy dominants in the regional species pool. That is, this size-based sampling bias could lead to an appearance of greater understorey diversity relative to canopy diversity in more species-rich plots.

We initially thought that the coldest temperatures experienced at a site would be an important variable, because extremely low temperatures expose plants to risk of freeze embolism (Sperry & Sullivan 1992). One might expect taller plants to be at greater risk of freeze embolism, because they have fewer, wider conduits in their trunks (Preston *et al.* 2006). However, mean temperature in the coldest quarter of the year and minimum temperature of the coldest month were the fifth and sixth strongest correlates of plant height. There is some

suggestion in our data of an absence of very tall species at sites where the mean temperature of the warmest quarter is below 10 °C (Appendix S1), which would be consistent with the literature on temperature and tree line height (Korner 1998) but we do not have enough data from extremely cold places to be certain about this.

Minimum temperature was not the only poor predictor of plant height: other variables that provide information about climatic conditions during the harshest times of the year for growth were also relatively weakly correlated with height. That is, variables that capture information about the quality of the growing season are much more informative than are variables that capture information about difficult times when growth is low or entirely stopped. This makes sense: many species avoid growing at the harshest times of the year (for instance deciduous species at high latitudes and ephemeral species in deserts).

Altitudinal gradients in plant height are well known within species (e.g. Totland & Birks 1996; Fernandez-Calvo & Obeso 2004; Macek & Leps 2008), and increases in altitude are often associated with decreases in plant height within a region (e.g. Kappelle *et al.* 1995; Wilcke *et al.* 2008). However, altitude was surprisingly weakly related to plant height at a global scale. Despite being the second-worst correlate of plant height in this study (Table 1), a term for altitude was included in the top 5% of models 62% of the time, and altitude was a term in the model with the lowest RMSE. That is, although altitude explains very little of the variation in plant height at the global scale, the variation it does explain is complementary to that explained by the other environmental variables. Altitude has also proved to be a poor predictor in global studies of seed mass (Moles *et al.* 2007) and wood density (Swenson & Enquist 2007). Perhaps one reason for this is that the sudden drop in plant height found at the tree line occurs at different altitudes in different parts of the world.

The relationships between plant height and environmental variables were all relatively weak (Table 1). The weak relationships with environmental variables in this study are consistent with those found for seed mass (temperature, precipitation, NPP and LAI each explained < 16% of the variation in seed mass, Moles *et al.* 2005) and leaf traits (climate explained just 18% of the variation along the principal multivariate trait axis, Wright *et al.* 2005). This simply reflects the fact that a great deal of variation in plant traits is between coexisting species. In this study, about half of the variation in plant height lay within sites, so environmental variables could only possibly explain 50% of the total variation in the data set. Increasing our understanding of the coexistence of such a wide range of height strategies at a single site is an important goal, but this requires a different sort of approach to that used for studies that quantify global patterns in plant traits.

The best model for global patterns in plant height contained just one of our original 22 environmental variables: precipitation in the wettest month. This result surprised us – we had thought that NPP would be the strongest correlate of plant height, because productivity depends on a range of variables, including soil fertility, temperature, available sunlight and precipitation (Krebs 1972). Precipitation at the wettest time of the year is obviously of primary importance in arid and semi-arid regions and in ecosystems with strong seasonality in water availability such as seasonally dry tropical forests. Evidence for a primary influence of water availability has also been found in some mountain systems (Littell *et al.* 2008). However, in very cold places it seems that temperature, rather than water availability, would be of primary importance (Korner 1998).

The importance of water availability in determining the height plant species reach in different parts of the world is in line with the hydraulic limitation hypothesis (Ryan & Yoder 1997; Ryan *et al.* 2006). This hypothesis begins from the observation that with increasing plant height the difficulty in supplying leaves with water also increases. To avoid embolisms caused by extremely negative water pressures, plants are forced to close their stomata, thus decreasing the amount of photosynthesis and diminishing the amount of carbon available for further growth.

This study provides the first cross-species quantification of global patterns in plant height, and our investigations of relationships between plant height and environmental variables turned up a range of interesting and surprising results. These are major advances, but there are still many questions we need to address in this field. Investigating the idea that there is a sudden switch in plant ecological strategy at the edge of the tropics seems particularly important. It would also be interesting to weight the species in studies such as this by abundance, so that extremely common species that dominate vegetation (such as black spruce – *Picea mariana* in boreal forests) receive more weight in analyses than do rare species, and to compare the slope of intraspecific relationships with that of the interspecific relationship. Finally, it will be interesting to go beyond correlations between traits and environment and formally link global patterns in plant strategy with a mechanistic understanding of the processes that affect plant growth and reproduction.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Relationships between plant height and climate variables.

Appendix S2. Relationships between absolute latitude and plant height within the major taxonomic groups.

Appendix S3. Relationships between absolute latitude and plant height within the major growth forms.

Appendix S4. R code used for analyses.

Appendix S5. The relationship between root mean standard error (RMSE) of a model under 10-fold cross-validation and the number of variables in the model.

Appendix S6. Taxonomic composition of data.

Appendix S7. Pairwise correlation coefficients among the 10 selected climatic variables.

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