

RESEARCH
PAPER



Global quantification of contrasting leaf life span strategies for deciduous and evergreen species in response to environmental conditions

A. E. E. van Ommen Kloeke¹, J. C. Douma¹, J. C. Ordoñez¹, P. B. Reich² and P. M. van Bodegom^{1*}

¹VU University Amsterdam, Institute of Ecological Science, Department of Systems Ecology, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands, ²Department of Forest Resources, University of Minnesota, St Paul, MN 55108, USA

ABSTRACT

Aim Species with deciduous and evergreen leaf habits typically differ in leaf life span (LLS). Yet quantification of the response of LLS, within each habit, to key environmental conditions is surprisingly lacking. The aim of this study is to quantify LLS strategies of the two leaf habits under varying temperature, moisture and nutrient conditions, using a global database. We hypothesize that deciduous LLS reflects the length of the growing season, avoiding unfavourable conditions regardless of the cause. Evergreen species adjust to unfavourable periods and amortize lower net carbon gains over several growing seasons, with increasing LLS associated with increasingly short favourable versus unfavourable season lengths.

Location Global.

Methods Data on LLS and environmental variables were compiled from global datasets for 189 deciduous and 506 evergreen species across 83 study locations. Individual and combined effects of measures of seasonality of temperature, water and nutrient availability on length of the growing season and on LLS were quantified using linear mixed models. The best models for predicting LLS were obtained using Akaike's information criterion (AIC) and Δ AIC.

Results The LLS of deciduous and evergreen species showed opposite responses to changes in environmental conditions. Under unfavourable conditions, deciduous LLS decreases while evergreen LLS increases. A measure of temperature alone was the best predictor of the growing season. The LLS of deciduous species was independent of environmental conditions after expressing LLS in relation to the number of growing seasons. Evergreen species, on the other hand, adjusted to unfavourable conditions by increasing LLS up to four growing seasons. Contrary to expectations, variation in LLS was best explained solely by temperature, instead of by combined measures of temperature, moisture and nutrient availability. Shifts in the photosynthesis to respiration balance might provide a physiological explanation.

Main conclusions Temperature, and not drought or nutrient availability, is the primary driver of contrasting responses of LLS for different leaf habit types.

Keywords

Deciduous, evergreen, evaporative demand, favourable period, growing season, leaf habit, leaf life span, mixed model analysis, N-mineralization, temperature.

*Correspondence: P. M. van Bodegom, VU University Amsterdam, Institute of Ecological Science, Department of Systems Ecology, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands.
E-mail: peter.van.bodegom@falw.vu.nl

INTRODUCTION

Global patterns of plant species distribution have intrigued ecologists for centuries, but are still not fully understood (Woodward *et al.*, 2004; Westoby & Wright, 2006). In particular, the distribution of deciduous versus evergreen species has attracted considerable attention since it was first reported by Harper in 1914 (Monk, 1966; Kikuzawa, 1991; Reich *et al.*, 1992; Kikuzawa & Ackerly, 1999; Givnish, 2002; Lavorel & Garnier, 2002). One long-held explanation is that, in seasonal climates, evergreen species persevere and are increasingly common as the length of the annual unfavourable season increases (Kikuzawa, 1991; Reich *et al.*, 1992; Reich, 1995). However, observations (Chabot & Hicks, 1982; Reich *et al.*, 1992; Reich, 1995; Kikuzawa & Ackerly, 1999; Woodward *et al.*, 2004) show a broad range of environments where evergreen and deciduous species co-exist. Thus, both leaf habit types are viable at the same locations, irrespective of the actual environmental conditions.

Evergreen and deciduous species are defined strictly by whole-canopy phenology, and have typically been shown to be morphologically and functionally distinct. The most obvious trait for distinguishing between the functioning of deciduous and evergreen species is 'leaf life span' (LLS) or leaf longevity (Chabot & Hicks, 1982; Reich, 1995; Kikuzawa & Ackerly, 1999). In general, evergreen species have a longer LLS than deciduous species, despite some overlap in LLS among the two leaf habits, especially in (aseasonal) tropical rain forests where fast-growing evergreen pioneer species have a short LLS because they nearly continuously produce new leaves and senesce old ones (Kikuzawa, 1991; Reich *et al.*, 1992, 2004). The two leaf habits have long been considered to represent different strategies for coping with environmental conditions (Monk, 1966; Chabot & Hicks, 1982; Aerts, 1995; Kikuzawa, 1995). The deciduous leaf habit may be considered an 'opportunistic' strategy (with high leaf area per mass, leaf nutrient contents and photosynthetic capacity compared with evergreens), capable of achieving high rates of carbon gain when environmental conditions are favourable (Chabot & Hicks, 1982; Reich *et al.*, 1992, 1999). Deciduous species shed their leaves as seasonal conditions become unfavourable, thereby avoiding maintenance costs (Kikuzawa, 1995; Givnish, 2002) and unknown costs of leaf adaptations to desiccation, freezing and their combination. The evergreen leaf habit, on the other hand, is considered a more 'conservative' leaf strategy (Reich *et al.*, 1999; Wright *et al.*, 2004). One advantage of 'evergreenness' is that these species may continue to photosynthesize during some part of the unfavourable season when deciduous species cannot, i.e. tolerating unfavourable conditions (Mooney & Dunn, 1970; Chabot & Hicks, 1982; Gerdol *et al.*, 2000; Westoby *et al.*, 2002). In this way, evergreen leaves amortize ongoing maintenance costs and low net carbon gains by persisting for several growing seasons (Wright *et al.*, 2004; Ogaya & Peñuelas, 2007; Reich *et al.*, 2007; Harrison *et al.*, 2010).

However, also within a leaf habit, there is considerable variation in LLS, which is crucial to understand given the important role of LLS in ecosystem processes. Different environmental

conditions have been hypothesized to drive this variation. In various studies, LLS has been shown to respond to temperature, water accessibility, nutrient availability and light availability. Wright and co-workers found that LLS had different responses to climate variables for deciduous and evergreen species (Wright *et al.*, 2004, 2005). In particular, the LLS of evergreen and deciduous species showed contrasting patterns in relation to mean annual temperature (MAT; Wright *et al.*, 2005; Reich *et al.*, 2007). Moreover, this pattern was also seen in relation to mean annual precipitation (MAP), although to a lesser degree. On a global scale, the relationship of LLS to water availability also becomes apparent, with a positive correlation between LLS and potential evapotranspiration (Wright *et al.*, 2004). In addition, soil fertility is negatively correlated with LLS (Reich *et al.*, 1992; Wright *et al.*, 2002; Oleksyn *et al.*, 2003; Cavender-Bares *et al.*, 2004). Givnish (2002) hypothesized that soil fertility is the main driver of LLS. Finally, light availability is a strong driver of LLS (Reich *et al.*, 2004, 2007), but as most of this variation is extremely local we will not consider it further here.

Despite various published reviews on how LLS may be affected by different environmental conditions, the need remains for a comprehensive quantitative analysis to address the question raised by Chabot & Hicks (1982) more than 25 years ago: 'How is the length of a leaf's life span related to environmental factors?'. Expanding the work of Wright and co-workers, the aim of this study is to quantify global LLS strategies of the two leaf habits under varying environmental conditions by applying advanced statistics in a multivariate context. We had three aims: (1) to quantify which environmental condition (alone or in interaction) drives deciduous and evergreen LLS; (2) to simplify sources of variation in LLS by expressing LLS in relation to the number of growing seasons; and (3) to quantify the number of growing seasons of an evergreen LLS compared with a deciduous LLS as a function of environmental conditions. The long-held hypothesis is that deciduous species avoid unfavourable periods by only having leaves during one growing season. As a consequence, we expect a constant LLS for deciduous species after expressing LLS in relation to the number of growing seasons. Evergreen species, on the other hand, will increase LLS as conditions become less favourable in order to compensate for both additional (maintenance) costs and reduced carbon gain, associated with tolerating unfavourable conditions.

METHODS

Leaf habit and LLS database

The starting point of our analysis of LLS patterns was the Global Plant Trait Network (GLOPNET) database (Wright *et al.*, 2004) which covers 2548 species from 175 study locations on six continents. To create a more balanced dataset, the database was extended by including more than 200 LLS data points on species from other than warm, dry regions that dominated the dataset (Appendix S1 in Supporting Information). To avoid interference of growth form with our results, only woody species were used

in the analyses. In total, 695 individual entries containing LLS data from 83 study locations on all vegetated continents were included. For some studies, leaf habit (deciduous or evergreen) was inquired, when unknown from the study reference, using studies or websites with information on the species from close to the study location. More detailed classifications of leaf habits (e.g. semi-deciduous) were avoided in order to be able to detect globally applicable patterns.

To investigate the applicability of LLS for distinguishing between deciduous and evergreen leaf habit types, LLS versus other traits was analysed using Gaussian mixture density fitting. A detailed description and analysis can be found in Appendix S2.

Environmental data

Variation of LLS was related to temperature, water and nutrient conditions in a given environment. Despite the wealth of studies on variation of LLS, only a few studies report climate and soil characteristics for the same locations. For consistency, and to allow global analysis, we only used data on climate and soil variables extracted from a single source per variable, using the georeferences of the study locations.

As a measure of temperature, we used MAT (°C). Data were obtained from a global 10-arcmin gridded dataset of mean monthly surface climate data – the Climatic Research Unit (CRU) (New *et al.*, 2002). The CRU creates climate surfaces using weather station data (1961–90) of climatological normals. Some alpine sites had to be corrected using actual temperature data measured at the study site, as the CRU tends to underestimate temperature conditions at high altitudes. Degree days,

another commonly used variable for temperature, was not used as it showed a high correlation with MAT (Appendix S3, Table 1).

For water metrics, MAP (mm year⁻¹), evaporative demand (ETo; mm year⁻¹) and MAP/ETo were used, which are all common measures of water conditions (Givnish, 2002; Schenk & Jackson, 2002; Maherali *et al.*, 2004). MAP was obtained through the CRU (New *et al.*, 2002). Using station data from the CRU, ETo was calculated based on Allen *et al.* (1998), who defined ETo as the Penman–Monteith potential evapotranspiration while assuming constant vegetation and roughness attributes. This calculation makes ETo independent of the actual vegetation. MAP/ETo shows the extent to which water supply restricts plant growth (Harrison *et al.*, 2010).

For nutrient status, the commonly applied soil N/C ratio, indicating the general quality of soil organic matter (Ordoñez *et al.*, 2009), was used. Average data for a soil depth of 0–100 cm were obtained using the Global Gridded Surfaces of Selected Soil Characteristics (IGBP-DIS) dataset (Global Soil Data Task Group, 2000). The soil N/C ratio provides only a very rough approximation of nutrient availability to the vegetation (Aerts & Chapin, 2000). Therefore, and given that nitrogen is globally the most important limiting nutrient, an estimate of the net nitrogen mineralization rate (N-mineralization; mg N/kg soil/year) was used in addition. N-mineralization integrates the potential nitrogen pool available for plants and the controlling factors of nitrogen cycling. N-mineralization was estimated using a simplified mineralization model (Ordoñez *et al.*, 2009) based on CENTURY v.4 (Parton *et al.*, 1987). Temperature and moisture correction factors for N-mineralization were obtained from monthly values of air temperature and moisture supply,

Table 1 Overview of significant bivariate and multivariate models to predict log leaf life span (LLS, months) as driven by temperature, water and nutrient availability and their interactions.

Variables in model	Δ AIC (Δ_i)	Intercept	Main effect 1	Main effect 2	Main effect 3	Interaction	Variance explained (%)
Deciduous							
MAT	0.0	0.588	0.009				29.3
ETo	5.2	0.550	0.0001				18.5
Log MAP/ETo	8.4	0.733	-0.183				11.1
Evergreen							
MAT + MAT × log MAP/ETo	0.0	1.579	-0.019			0.019	59.2
MAT + MAP + soil N/C ratio	0.6	1.705	-0.021	0.0001	-2.211		59.9
MAT + log MAP/ETo + interaction	1.9	1.594	-0.020	-0.040*		0.022	59.1
ETo	8.8	1.761	-0.0004				52.4
MAT	12.2	1.583	-0.019				50.1
Log MAP/ETo	35.5	1.272	0.442				31.2
Soil N/C ratio	45.9	1.809	-4.797				22.2
MAP	59.2	1.477	-0.0001				6.8

*Main effect is not significant ($P > 0.05$), but the interaction is significant.

MAT, mean annual temperature; MAP, mean annual precipitation; ETo, evaporative demand; AIC, Akaike information criterion.

Only multivariate models with a Δ AIC (Δ_i = AIC value – AIC best model) less than 2 are listed here. The best models are shown in bold. Main effects and interactions are given as the unstandardized estimates of the slopes of each leaf habit. As an estimate of the variance explained by the model, the ratio of the variance among sites explained by the model compared with a 'null model' without environmental drivers is included.

obtained from the CRU (New *et al.*, 2002). Information on bulk density and soil texture at the study locations came from IGBP-DIS (Global Soil Data Task Group, 2000) and the Global Soil Texture and Derived Water-Holding Capacities dataset (Webb *et al.*, 2000), respectively. For local conditions these metrics may be less accurate, which must be kept in mind when interpreting the outcomes of analyses below.

Quantification of environmental drivers of LLS

Bivariate and multivariate analyses of LLS versus temperature, water and nutrient variables, or their combinations, were quantified for deciduous and evergreen species separately. For this we used linear mixed models with maximum likelihood (ML) methods, available in SPSS v.15.0 (Bolker *et al.*, 2009). In contrast to the analyses presented in Wright *et al.* (2005), an advantage of our mixed model analysis is that it explicitly takes into account that there is more than one data observation (LLS) at each study location. By taking study location as a random factor, it accounts for the fact that errors within each study location are likely to be correlated, i.e. non-independent. Temperature, water, nutrient variables and their interactions were treated as fixed effects. For all bivariate and multivariate analyses of LLS, we used a dataset of a total of 189 observations and 37 study locations for deciduous species and 506 observations and 80 study locations for evergreen species. Bivariate analyses were carried out using all available observations for each LLS–temperature, LLS–water and LLS–nutrient combination. To avoid problems of collinearity among the variables, only variables with a Pearson correlation between -0.7 and 0.7 were included in the multivariate analyses (see Appendix S3, Table 1). All possible bivariate and multivariate models for deciduous and evergreen LLS are included in Appendix S3 and Table 2.

Competing multivariate models to predict LLS were evaluated with Akaike's information criterion (AIC) as a measure of goodness of fit: the lower the AIC value, the better the model. In addition, the ΔAIC (Δ_i), the difference in AIC between each model and the best model, was used. A $\Delta_i < 2$ indicates substantial

evidence for the competing model, whereas larger differences suggest that the model is unlikely to be the optimal model (Burnham & Anderson, 2002). Furthermore, models were compared through χ^2 -tests which test if there is a significant difference between two models based on their difference in AIC value and their difference in the number of variables in the model (degrees of freedom). A significant χ^2 -test ($P < 0.05$) indicates that a more extended model is significantly better than a simpler model.

Mixed models do not have a direct equivalent to r^2 or any direct measure for estimating total explained variance (as in regression methods). Therefore, the effects of study location were expressed as variances and compared with the error variance (analogous to a variance component analysis). Comparing the unexplained variance of a particular model with the unexplained variance of the null model (with only study location) gives insight into how much of the unexplained variance among study locations is explained by the environmental conditions.

LLS data were approximately log-normally distributed (right-skewed); hence they were \log_{10} -transformed prior to analyses in order to attain approximate normality and homogeneity of residuals. Although normality is not an assumption for mixed models, log transformations created a homogeneous distribution of the data points to approach linear relations. Of all the other variables, only MAP/PET and soil N-mineralization were log-transformed. All other variables showed an approximately normal distribution without transformation.

Expressing LLS in relation to the number of growing seasons

In order to express LLS in relation to the number of growing seasons, we first determined which environmental variable best predicted the length of the growing season. The length of the growing season was defined as the longest period of consecutive days in a calendar year with favourable environmental conditions. For growing seasons defined by temperature, this was the number of days per year without ground frost at the study location. Below this threshold, days were regarded as non-

Table 2 Overview of models to predict log leaf life span (LLS, months) as a function of the length of the growing season based on the longest periods of consecutive days in a year with temperature $> 0^\circ\text{C}$, MAP $>$ ETo (including a buffer for the water holding capacity) and N-mineralization > 0 , alone and in combination.

Predictor of growing season length	AIC	ΔAIC (Δ_i)	Intercept	Main effect	Variance explained (%)
Temperature	−316.1	0.0	0.299	0.0013	34.6
Temperature + N-mineralization	−309.2	6.9	0.599	0.0005	21.3
N-mineralization	−309.1	7.0	0.598	0.0005	21.1
Temperature + moisture + N-mineralization	−305.5	10.6	0.647	0.0005	12.9
Moisture + N-mineralization	−305.4	10.7	0.647	0.0005	12.6
Temperature + moisture	−302.6	13.5			n.s.
Moisture	−300.9	15.3			n.s.

As an estimate of the variance explained by the model, the ratio of the variance among sites explained by the model compared with a 'null model' without environmental drivers is included. The best model is shown in bold.

AIC, Akaike information criterion; MAP, mean annual precipitation; ETo, evaporative demand; n.s., not significant.

Table 3 Overview of significant bivariate models and multivariate models, to predict log leaf life span (LLS), expressed as number of growing seasons, driven by temperature, water and nutrient availability and their interactions.

Variables in model	$\Delta AIC (\Delta_i)$	Intercept	Main effect 1	Main effect 2	Main effect 3	Interaction	Variance explained (%)
Deciduous	No significant models found						
Evergreen							
MAT + MAP + soil N/C ratio + MAP \times SoilN/C	0.0	1.133	-0.023	-0.0004	-7.551	0.006	71.2
ETo	22.6	0.726	-0.0004				57.2
MAT	25.6	0.536	-0.020				55.3
Log MAP/ETo	53.6	0.199	0.482				34.6
Soil N/C ratio	65.5	0.783	-5.219				24.4
MAP	79.4	0.432	-0.0001				8.9

As an estimate of the variance explained by the model, the ratio of the variance among sites explained by the model compared with a 'null model' without environmental drivers is included. The best model is shown in bold.

AIC, Akaike information criterion; MAT, mean annual temperature; MAP, mean annual precipitation; ETo, evaporative demand.

functional (Lambers *et al.*, 1998). For growing season defined by water availability, this was the number of days with a precipitation surplus (MAP > ETo) and the subsequent days during which the profile available water capacity (derived from IGBP-DIS; Global Soil Data Task Group, 2000) was depleted. The threshold for nitrogen availability was defined as the number of days with a positive N-mineralization. Combined measures for the growing season were defined by the combinations of favourable temperature, moisture and nitrogen. All variables were based on linear interpolations of monthly available data.

Based on the proposition that deciduous LLS is related to the length of the growing season, bivariate analyses of deciduous LLS versus these seven measures of the growing season were quantified with mixed model analyses. The best model (i.e. the one with the lowest AIC value) for defining the growing season was thereupon used to express LLS in relation to the number of growing seasons.

Quantifying the number of growing seasons of evergreen LLS versus deciduous LLS

As the length of the growing season is reflected in LLS, a comparison of evergreen and deciduous LLS is affected by the leafless period of deciduous species during unfavourable periods (Westoby *et al.*, 2002; Oliveira & Peñuelas, 2004; Kikuzawa & Lechowicz, 2006). Consequently, expressing LLS of both leaf habits as a function of the number of growing seasons allows us to make direct comparisons of LLS across locations with varying growing season length (Kikuzawa, 1995; Diemer, 1998; Kikuzawa & Lechowicz, 2006). This was calculated as the number of full calendar years plus the fraction of the final growing season. Again mixed model analysis was used to evaluate bivariate and multivariate models of LLS versus temperature, water and nutrient variables, or their combinations. All possible bivariate and multivariate models for deciduous and evergreen LLS (in growing seasons) are included in Appendix S3 and Table 3.

The components of the best model for predicting evergreen LLS (growing seasons) were further analysed through the standardized partial regression coefficients. These indicate the relative contribution of each environmental variable to LLS, while statistically holding all other variables constant (Schielzeth, 2010). The predictors were standardized across sites for each environmental driver ($n = 80$ sites), using mean = 0 and standard deviation = 1.

To quantify the number of growing seasons of evergreen LLS compared with deciduous LLS, we calculated predicted LLS (growing seasons) based on the best model for evergreens and the average significant intercept for deciduous LLS, respectively. Relating these predicted LLS values to the predicted length of the growing season allowed a direct comparison of deciduous and evergreen LLS as the length of the growing season changes.

RESULTS

Variation in LLS

LLS was highly variable, ranging between 1.48 and 258 months. Although by definition deciduous species maintain their leaves for all or part of one growing season and most evergreens have a LLS (especially in the temperate zone) that is longer than one growing season, extensive overlap exists between the two LLS strategies (Fig. 1). Some have argued that the considerable overlap in LLS between deciduous and evergreen species would hamper the applicability of LLS to distinguish deciduous and evergreen strategies or that leaf habit types should be investigated on a whole-plant level (see Givnish, 1988; Aerts, 1995; Schenk & Jackson, 2002). However, in an additional analysis applying Gaussian mixture density fitting (Appendix S2), we showed that LLS as a single functional trait is appropriate for distinguishing deciduous from evergreen species in 91% of cases. Additional inclusion of leaf mass per unit area (LMA) or leaf nitrogen content only slightly improved the distinction, whereas rooting depth and stem specific density did not

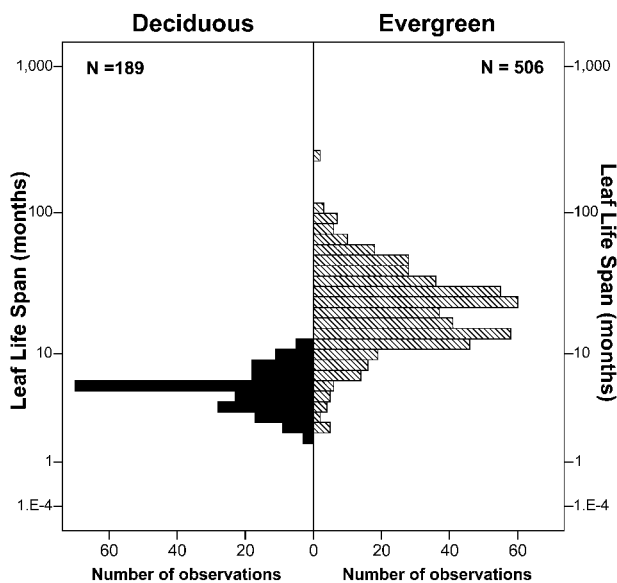


Figure 1 Combined histogram showing variation in leaf life span of deciduous and evergreen species.

improve predictions at all. Exclusion of evergreen species with a short LLS from analyses had minimal impact on the ability of LLS to differentiate between deciduous from evergreen species.

Quantification of environmental drivers of LLS

A total of 58 models for evergreen species and 59 models for deciduous species were analysed for LLS (months) (Appendix S3, Table 2). Half of the common measures of environmental conditions (MAT, ETo, MAP/ETo) showed a significant relation for both deciduous and evergreen LLS (Fig. 2, Table 1). Additionally, evergreen LLS responded to MAP and soil N/C ratio. The expected contrasting patterns for deciduous versus evergreen LLS were observed when both leaf habits showed a relationship to an environmental variable. For instance, LLS of deciduous species decreased when MAT decreased, whereas evergreen LLS increased when MAT decreased. MAT explained the most variance among sites (29.3%) of all models for deciduous species. Interestingly, none of the other bivariate or multivariate models gave a plausible explanation for deciduous LLS (months) ($\Delta_i > 2$).

For the LLS (months) of evergreen species, MAT plus the interaction of MAT \times log MAP/ETo was the best model, explaining 59.2% of the total variance. The significant interaction term was positive, indicating that as MAT increases, the slope of LLS on log MAT/ETo becomes flatter. Only two other multivariate models for evergreen LLS had a $\Delta_i < 2$, both of which included MAT and a measure of water accessibility. In contrast, all bivariate models gave a less plausible explanation for evergreen LLS (months) ($\Delta_i > 2$), even though they had significant intercepts and main effects.

Expressing LLS in relation to the number of growing seasons

Out of the seven measures for estimating the length of the growing season, a single measure of temperature was shown to be the best model (Table 2), explaining 34.6% of total variance. Surprisingly, all other single or combined measures of the length of the growing season were less plausible ($\Delta_i > 2$). This means that the global patterns in growing season was best predicted by temperature alone instead of combinations of environmental conditions. Hence, the consecutive number of days per year without ground frost at the study location was used to define the length of the growing season and to express all LLS accordingly.

Quantifying the number of growing seasons of evergreen LLS versus deciduous LLS

A total of 60 models for evergreen species and 58 models for deciduous species were analysed for LLS per number of growing seasons (Appendix S3, Table 3). Expressing LLS per number of growing seasons completely eradicated all bivariate and multivariate effects on deciduous LLS (Fig. 3), as was the aim. A constant LLS of 0.66 growing seasons remained. In contrast, growing season LLS of evergreen species was still significantly affected by MAT, ETo, MAP, log MAP/ETo and soil N/C ratio (Fig. 3, Table 2) with the same trends as for the original LLS. This suggests that evergreen species respond similarly to environmental gradients in terms of their LLS, regardless of the length of the growing season. The best model for predicting evergreen LLS (growing seasons) was the combined effect of MAT, MAP, soil N/C ratio and the interaction of MAP \times soil N/C ratio, explaining 71.2% of the total variance. This was higher than any model for LLS (months), indicating that expressing LLS per number of growing seasons effectively removes residual variance from LLS. All other models were less plausible, based on Δ_i . This best model reveals that evergreen LLS depends on several environmental conditions at the same time. Even so, on analysing the model more closely, MAT turned out to be by far the largest contributor to the model with a standardized partial regression coefficient of 0.53, while those of MAP, soil N/C ratio and the interaction MAP \times soil N/C ratio were 0.15, 0.11 and 0.22, respectively.

The best evergreen LLS model was used to predict LLS (growing seasons) for each study location. There were no significant models for deciduous LLS (growing seasons). Therefore the average of significant intercepts of models was taken. Plotting the predicted LLS against the predicted length of the growing season enabled us to quantify the number of growing seasons of evergreen LLS compared with a deciduous LLS as environmental conditions change (Fig. 4). This showed that evergreen species need up to four growing seasons (compared with an average LLS of 0.66 growing seasons for deciduous species) to make a living in environments with a short growing season (< 100 days). Moreover, it seems that evergreen LLS rarely equals deciduous LLS. Even at a maximum growing

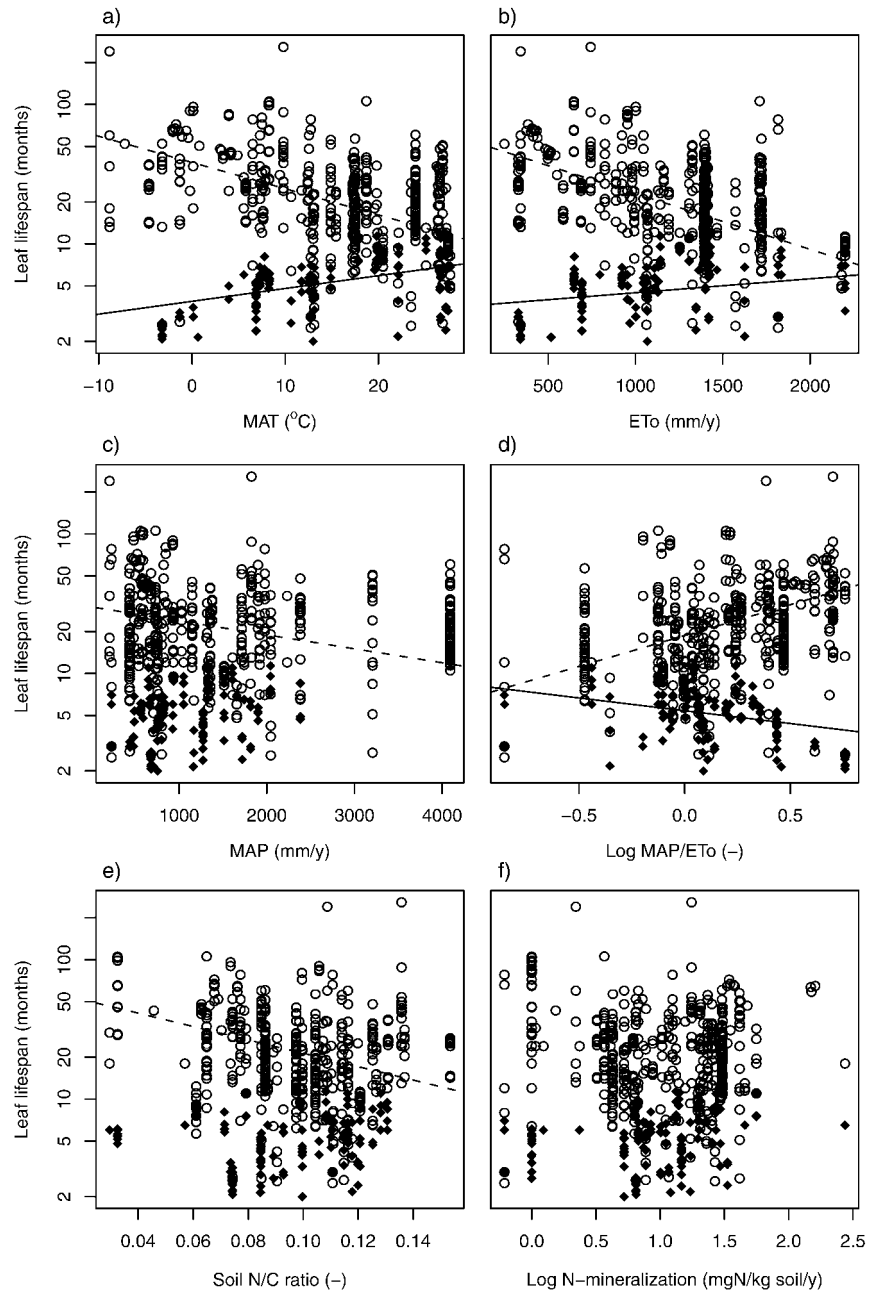


Figure 2 Relationships between leaf life span (log transformed) and measures of temperature, water and nutrient availability: (a) mean annual temperature (MAT, °C), (b) evaporative demand (ET₀, mm year⁻¹), (c) mean annual precipitation (MAP, mm year⁻¹), (d) log MAP/ET₀, (e) soil nitrogen/carbon ratio (g g⁻¹), and (f) log N-mineralization (mg N/kg soil/year). Symbols: ◆, deciduous species; ○, evergreen species. Solid and dashed lines indicate significant ($P < 0.05$) relationships of deciduous and evergreen species, respectively.

season, i.e. in aseasonal environments, evergreens need on average a LLS that is twice that of deciduous species.

DISCUSSION

On a global scale, considerable overlap exists in the distribution of deciduous and evergreen species, despite the generally large differences in leaf traits between them (Reich *et al.*, 1992; Kikuzawa & Ackerly, 1999; Woodward *et al.*, 2004). Indeed, it is unmistakable from global data that both deciduous and evergreen species co-exist across large environmental gradients regardless of the conditions present (Figs 2 & 3). The aim of this

study was to quantify these global LLS strategies of the two leaf habits under varying environmental conditions.

Two spectra of LLS upon changes in environmental conditions

The contrasting responses of LLS to environmental conditions of both leaf habit types represent two different, but viable and successful, strategies for dealing with the same problem: to shed or not to shed (Kikuzawa, 1995). A clue to the ecological mechanisms underlying these strategies was provided when expressing LLS as number of growing seasons (Fig. 3, Table 3). Deciduous

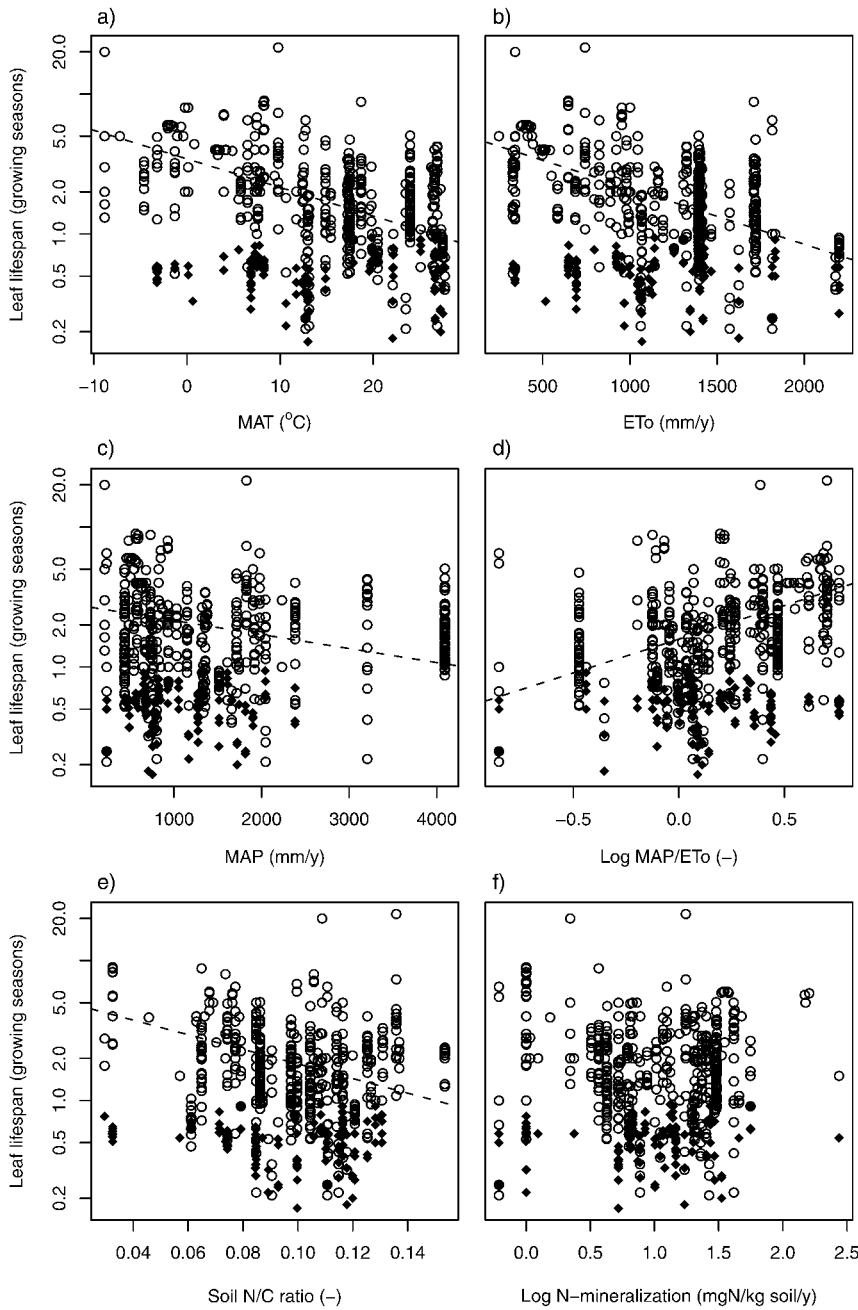


Figure 3 Relationships between leaf life span, log-transformed and expressed as number of growing seasons, and measures of temperature, water and nutrient availability: (a) mean annual temperature (MAT, °C), (b) evaporative demand (ET₀, mm year⁻¹), (c) mean annual precipitation (MAP, mm year⁻¹), (d) log MAP/ET₀, (e) soil nitrogen/carbon ratio (g g⁻¹), and (f) log N-mineralization (mg N/kg soil/year). Symbols: ♦, deciduous species; ○, evergreen species. Solid and dashed lines indicate significant ($P < 0.05$) relationships of deciduous and evergreen species, respectively.

species attain a profitable leaf habit strategy by avoiding unfavourable conditions and achieving high carbon gains within one growing season. Indeed, upon expressing LLS in growing seasons based on temperature, LLS of deciduous species became independent of changes in environmental conditions. On average, our predicted deciduous LLS was 0.66 growing seasons. However, a slightly higher value, but below 1, to account for the fraction of the growing season ‘lost’ by bud burst, leaf elongation and resorption, was expected. Consequently, our adjustment may have been conservative, even though, in general, growing season LLS approximated growing conditions at a particular location well. The use of interpolated monthly data instead of daily observations may account for this difference.

In contrast to deciduous species, general patterns in evergreen LLS response did not change after expressing LLS per number of growing seasons. Evergreen LLS still strongly responded to environmental conditions, demonstrating that evergreen species adjust to unfavourable conditions by truly increasing LLS (and concomitantly affecting other leaf economic traits). The best model for explaining evergreen LLS (growing seasons) was complex, suggesting that a combination of environmental conditions affects the evergreen leaf net carbon gains. Depending on the local conditions, different environmental drivers may contribute to the evergreen LLS strategy, together causing a continuous gradient of LLS values.

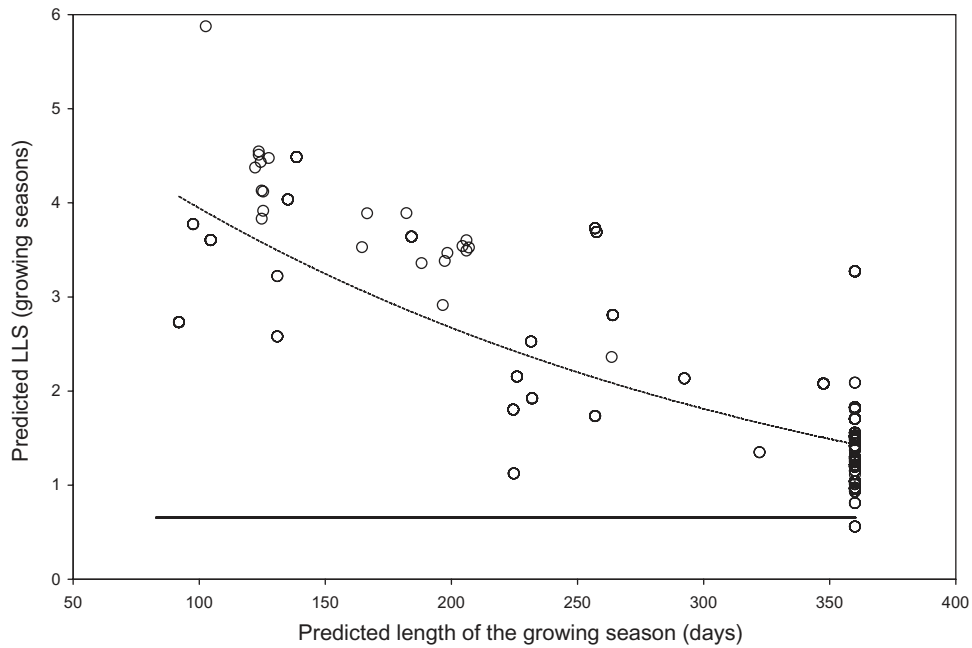


Figure 4 Predicted leaf life span (LLS) of evergreen species (in number of growing seasons) based on the best model (MAT + MAP + soil N/C ratio + MAP \times soil N/C ratio) relative to the predicted length of the growing season based on temperature. The solid line indicates the average of significant ($P < 0.05$) intercepts of deciduous LLS (growing seasons). The dashed line depicts the trend line of change in predicted evergreen LLS (growing seasons) versus the length of the growing season.

The importance of temperature as a driver of LLS

In our analysis, temperature was consistently the most important factor driving LLS and the growing season. For instance, temperature contributed to the best models for explaining LLS (months) for both deciduous and evergreen species (Table 1). Moreover, temperature alone was the best predictor of the length of the growing season, instead of water or nutrient availability or combinations thereof. Finally, temperature made the most substantial contribution (53%) to the best model predicting evergreen LLS expressed in relation to the number of growing seasons.

Physiological changes in leaf traits due to water limitations include decreases in photosynthetic capacity and increases in LMA for a given LLS (Reich *et al.*, 1999; Gerdol *et al.*, 2000). Plants generally respond to a lack of nitrogen with lower leaf nitrogen content and decreasing leaf biomass, and thus decreasing photosynthetic capacity (Aerts & Chapin, 2000). These changes result in a reduction of carbon gain for a plant, compensated by an extended period of time for return on investments and thus increased LLS (Givnish, 2002). It was therefore expected that a high LLS of evergreen species would be associated with nitrogen and water stress (Aerts, 1995; Kikuzawa & Ackerly, 1999; Gerdol *et al.*, 2000; Wright *et al.*, 2002). Our results show, however, that the integrative physiological response to temperature is stronger than that to nutrient and water variables at a global scale. However, locally, water and nutrient availability may be more important. This was reflected in the best model for evergreen LLS, for which water and nutri-

ent conditions together explained the other half of the LLS variance. For deciduous LLS, temperature was the single most important driver.

A shift in the balance between respiration and photosynthesis may explain the observed strong negative relation between temperature and evergreen LLS. At low and decreasing temperatures, respiration costs decrease (Wright *et al.*, 2006; Atkin *et al.*, 2008) yet photosynthetic carbon assimilation decreases even faster (e.g. Sage & Kubien, 2007). As a consequence, net carbon gain is consistently lower at low temperatures, across various functional groups (Campbell *et al.*, 2007). Other functional plant traits linked to leaf habit strategy do not seem to be able to explain this negative relation. For instance, LMA and leaf nitrogen content show much less pronounced trends with temperature (Wright *et al.*, 2005; Ogaya & Peñuelas, 2006, 2007; Campbell *et al.*, 2007).

Implications for unravelling global leaf habit strategies

The two leaf habit types may co-occur, in which deciduous species pursue temperature-driven favourable periods and evergreen species may strongly extend their LLS to compensate for low net carbon gains. Apparently, the evergreen leaf is very expensive in unfavourable environments in terms of ongoing maintenance costs, compared with a deciduous leaf, while construction costs are deemed similar for both types (Hikosaka, 2005). Maintenance costs of an evergreen leaf habit remain

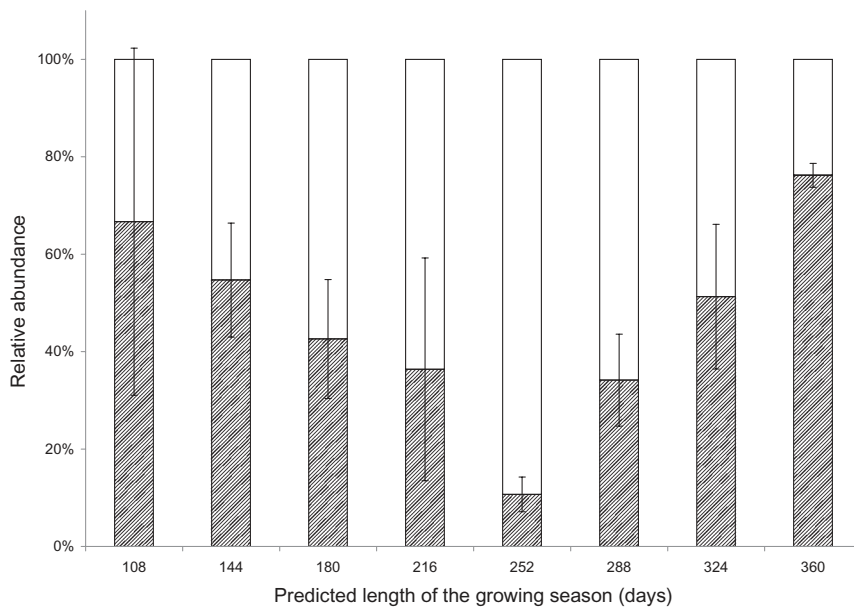


Figure 5 Relative number of observations and the 95% confidence interval (assuming a standard binomial distribution) of deciduous (white bars) and evergreen (hatched bars) species in relation to a binned length of the growing season based on temperature (days). Each bin equals 36 days.

during unfavourable periods, resulting in maintaining leaves for more growing season cycles than deciduous ones in order to make a living under the same conditions. For example, at low temperatures, our evidence suggests that evergreens require leaves to persist for approximately four times as many growing season cycles as deciduous species to be equally viable (Fig. 4).

As the length of the growing season increases, the number of growing season cycles needed for the evergreen leaf habit to be competitive decreases. The LLS of the two leaf habits become almost equal in aseasonal environments (Fig. 4). Such overlap in LLS has also been reported for other aseasonal tropical environments, independent of those in our database (Reich *et al.*, 2004; Poorter & Bongers, 2006; Santiago & Wright, 2007). In our analyses, LLS of evergreen species in aseasonal systems had any value between 0.6 and 3.3 growing seasons (Fig. 4). This variation was independent of moisture conditions (results not shown). In aseasonal tropical environments, the net carbon gain of an evergreen leaf may even be higher per year than that of a deciduous leaf thanks to the spreading of construction costs over several growing seasons. This may also explain why evergreen species tend to be particularly dominant in aseasonal tropical environments where carbon gains are always possible (Chabot & Hicks, 1982).

Indeed, strong differences in abundance of a respective leaf habit become apparent as a function of the length of the growing season (Fig. 5), if we assume that the number of observations at a given location represents abundance (i.e. assuming that all plant species in our database were locally dominant). Interestingly, this pattern quantitatively reproduces more qualitative descriptions (e.g. Kikuzawa, 1991; Harrison *et al.*, 2010) and reveals which LLS strategy is most successful at a particular location. Even though the length of the growing season does not create thresholds determining the occurrence of leaf habits or LLS, it may be applied to predict local abundance of a respective leaf habit.

CONCLUSIONS

This study advances the global quantitative analysis of the influence of different environmental conditions on LLS. Our analysis enabled quantification of deciduous and evergreen LLS by correcting for multiple data points at a given study location and expressing LLS in relation to the number of growing seasons. The two leaf habits co-occur at all locations and our data show a continuum in LLS values as the length of the growing season changes. This is in contrast to previously hypothesized abrupt changes in leaf habit strategy and leaf habit occurrence upon crossing a threshold value. Temperature was the most important driver of the growing season and global LLS patterns, although local conditions of water or nutrient availability may additionally affect evergreen LLS.

ACKNOWLEDGEMENTS

This study was carried out in the framework of project A1 of the Dutch national research program Climate Change and Spatial Planning (<http://www.klimaatonderzoeknederland.nl>). We would like to thank Ian Wright (Macquarie University) for stimulating discussions at the initiation of this research and Colin Prentice and an anonymous referee for their constructive comments.

REFERENCES

- Aerts, R. (1995) The advantages of being evergreen. *Trends in Ecology and Evolution*, **10**, 402–407.
- Aerts, R. & Chapin, F.S. (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research*, **30**, 1–67.
- Allen, R.G., Pereira, L.S., Raes, D. & Smith, M. (1998) *Crop evapotranspiration – guidelines for computing crop water*

- requirements. FAO Irrigation and Drainage Paper 56. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Atkin, O.K., Atkinson, L.J., Fisher, R.A., Campbell, C.D., Zaragoza-Castells, J., Pitchford, J.W., Woodward, F.I. & Hurry, V. (2008) Using temperature-dependent changes in leaf scaling relationships to quantitatively account for thermal acclimation of respiration in a coupled global climate-vegetation model. *Global Change Biology*, **14**, 2709–2726.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, **24**, 127–135.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. Springer-Verlag, New York.
- Campbell, C., Atkinson, L., Zaragoza-Castells, J., Lundmark, M., Atkin, O. & Hurry, V. (2007) Acclimation of photosynthesis and respiration is asynchronous in response to changes in temperature regardless of plant functional group. *New Phytologist*, **176**, 375–389.
- Cavender-Bares, J., Kitajima, K. & Bazzaz, F.A. (2004) Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. *Ecological Monographs*, **74**, 635–662.
- Chabot, B.F. & Hicks, D.J. (1982) The ecology of leaf life spans. *Annual Review of Ecology and Systematics*, **13**, 229–259.
- Diemer, M. (1998) Life span and dynamics of leaves of herbaceous perennials in high-elevation environments: ‘news from the elephant’s leg’. *Functional Ecology*, **12**, 413–425.
- Gerdol, R., Iacumin, P., Marchesini, R. & Bragazza, L. (2000) Water- and nutrient-use efficiency of a deciduous species, *Vaccinium myrtillus*, and an evergreen species, *V. vitis-idaea*, in a subalpine dwarf shrub heath in the southern Alps, Italy. *Oikos*, **88**, 19–32.
- Givnish, T.J. (1988) Adaptation to sun and shade – a whole-plant perspective. *Australian Journal of Plant Physiology*, **15**, 63–92.
- Givnish, T.J. (2002) Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. *Silva Fennica*, **36**, 703–743.
- Global Soil Data Task Group (2000) *Global Gridded Surfaces of Selected Soil Characteristics (IGBP-DIS)*. Available on-line <http://daac.ornl.gov> (accessed June 2008) from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA.
- Harrison, S.P., Prentice, I.C., Barboni, D., Kohfeld, K.E., Ni, J. & Sutra, J.P. (2010) Ecophysiological and bioclimatic foundations for a global plant functional classification. *Journal of Vegetation Science*, **21**, 300–317.
- Hikosaka, K. (2005) Leaf canopy as a dynamic system: ecophysiology and optimality in leaf turnover. *Annals of Botany*, **95**, 521–533.
- Kikuzawa, K. (1991) A cost–benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. *The American Naturalist*, **138**, 1250–1263.
- Kikuzawa, K. (1995) Leaf phenology as an optimal strategy for carbon gain in plants. *Canadian Journal of Botany*, **73**, 158–163.
- Kikuzawa, K. & Ackerly, D.D. (1999) Significance of leaf longevity in plants. *Plant Species Biology*, **14**, 39–45.
- Kikuzawa, K. & Lechowicz, M.J. (2006) Toward synthesis of relationships among leaf longevity, instantaneous photosynthetic rate, lifetime leaf carbon gain, and the gross primary production of forests. *The American Naturalist*, **168**, 373–383.
- Lambers, H., Chapin, F.S. & Pons, T.L. (1998) *Plant physiological ecology*. Springer-Verlag, New York.
- Lavelle, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.
- Maherali, H., Pockman, W.T. & Jackson, R.B. (2004) Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology*, **85**, 2184–2199.
- Monk, C.D. (1966) An ecological significance of evergreenness. *Ecology*, **47**, 504–505.
- Mooney, H.A. & Dunn, E.L. (1970) Photosynthetic systems of Mediterranean-climate shrubs and trees of California and Chile. *The American Naturalist*, **104**, 447–453.
- New, M., Lister, D., Hulme, M. & Makin, I. (2002) A high-resolution data set of surface climate over global land areas. *Climate Research*, **21**, 1–25.
- Ogaya, R. & Peñuelas, J. (2006) Contrasting foliar responses to drought in *Quercus ilex* and *Phillyrea latifolia*. *Biologia Plantarum*, **50**, 373–382.
- Ogaya, R. & Peñuelas, J. (2007) Leaf mass per area ratio in *Quercus ilex* leaves under a wide range of climatic conditions. The importance of low temperatures. *Acta Oecologia*, **31**, 168–173.
- Oleksyn, J., Reich, P.B., Zytowski, R., Karolewski, P. & Tjoelker, M.G. (2003) Nutrient conservation increases with latitude of origin in European *Pinus sylvestris* populations. *Oecologia*, **136**, 220–235.
- Oliveira, G. & Peñuelas, J. (2004) Effects of winter cold stress on photosynthesis and photochemical efficiency of PSII of the Mediterranean *Cistus albidus* L. and *Quercus ilex* L. *Plant Ecology*, **175**, 179–191.
- Ordoñez, J.C., van Bodegom, P.M., Witte, J.P.M., Wright, I.J., Reich, P.B. & Aerts, R. (2009) A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography*, **18**, 137–149.
- Parton, W.J., Schimel, D.S., Cole, C.V. & Ojima, D.S. (1987) Analysis of factors controlling soil organic-matter levels in great-plains grasslands. *Soil Science Society of America Journal*, **51**, 1173–1179.
- Poorter, L. & Bongers, F. (2006) Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology*, **87**, 1733–1743.
- Reich, P.B. (1995) Phenology of tropical forests – patterns, causes, and consequences. *Canadian Journal of Botany–Revue Canadienne de Botanique*, **73**, 164–174.

- Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs*, **62**, 365–392.
- Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C. & Bowman, W.D. (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology*, **80**, 1955–1969.
- Reich, P.B., Uhl, C., Walters, M.B., Prugh, L. & Ellsworth, D.S. (2004) Leaf demography and phenology in Amazonian rain forest: a census of 40 000 leaves of 23 tree species. *Ecological Monographs*, **74**, 3–23.
- Reich, P.B., Wright, I.J. & Lusk, C.H. (2007) Predicting leaf physiology from simple plant and climate attributes: a global GLOPNET analysis. *Ecological Applications*, **17**, 1982–1988.
- Sage, R.F. & Kubien, D.S. (2007) The temperature response of C-3 and C-4 photosynthesis. *Plant Cell and Environment*, **30**, 1086–1106.
- Santiago, L.S. & Wright, S.J. (2007) Leaf functional traits of tropical forest plants in relation to growth form. *Functional Ecology*, **21**, 19–27.
- Schenk, H.J. & Jackson, R.B. (2002) The global biogeography of roots. *Ecological Monographs*, **72**, 311–328.
- Schielzeth, H. (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, **1**, 103–113.
- Webb, R.W., Rosenzweig, C.E. & Levine, E.R. (2000) *Global soil texture and derived water-holding capacities data set*. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, TN.
- Westoby, M. & Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution*, **21**, 261–268.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125–159.
- Woodward, F.I., Lomas, M.R. & Kelly, C.K. (2004) Global climate and the distribution of plant biomes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 1465–1476.
- Wright, I.J., Westoby, M. & Reich, P.B. (2002) Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. *Journal of Ecology*, **90**, 534–543.
- Wright, I.J., Reich, P.B., Westoby, M. *et al.* (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.
- Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K., Lee, W., Lusk, C.H., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Warton, D.I. & Westoby, M. (2005) Modulation of leaf economic traits and trait

relationships by climate. *Global Ecology and Biogeography*, **14**, 411–421.

- Wright, I.J., Reich, P.B., Atkin, O.K., Lusk, C.H., Tjoelker, M.G. & Westoby, M. (2006) Irradiance, temperature and rainfall influence leaf dark respiration in woody plants: evidence from comparisons across 20 sites. *New Phytologist*, **169**, 309–319.

SUPPORTING INFORMATION

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

Appendix S1 Extending the Global Plant Trait Network (GLOPNET) database: included independent studies with leaf life span data.

Appendix S2 Gaussian mixture density fitting: leaf life span versus other traits to distinguish between evergreen and deciduous species.

Appendix S3 Full results of the mixed model analysis.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be reorganized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCH

The Department of Systems Ecology at the Vrije Universiteit Amsterdam (<http://www.falw.vu.nl/nl/onderzoek/ecological-sciences/systems-ecology/index.asp>) specializes in research revolving around the great diversity in functional traits of plants, animals and microbial species. This particular research team within systems ecology is interested in quantifying underlying patterns of functional diversity, using targeted experiments, meta-analyses of trait databases and process-based modelling. As an ultimate goal we attempt to contribute to the transformation of ecology into a quantitative discipline linked to other components of earth systems sciences.

Author contributions: E.O.K and P.B.R. compiled the data, E.O.K, P.M.B. and J.C.D. ran the models, E.O.K., J.C.D., J.C.O and P.M.B. analysed the data, E.O.K., J.C.D., P.B.R and P.M.B. contributed to the writing, while P.M.B. coordinated and led the writing.

Editor: Martin Sykes