Mechanisms underlying global temperature-related patterns in leaf longevity

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ABSTRACT

Aim At a global scale, the relationship of leaf longevity (LL) to mean annual temperature (MAT) is positive for deciduous species but negative for evergreen species. The aim of this paper is to understand the mechanisms underlying these contrasting patterns of leaf longevity, from a cost–benefit perspective.

Location Global.

Methods We tested our hypothesis that contrasting LL–MAT relationships in evergreen and deciduous species result from differing adaptations to variation in the length of the annual favourable period. We defined *f* as the portion of the year when monthly temperature and water availability were favourable. We examined whether the contrasting LL patterns with MAT can be also seen with *f*. Next, we calculated the optimal LL that maximizes carbon gain per unit time across a range of *f*.

Results The contrasting LL patterns across MAT were also found across *f*. Our optimization model successfully reproduced the contrasting LL patterns across *f* for the evergreen (LL longer than 1 year) and deciduous plants. The model shows that longer LL is required to maximize carbon gain for evergreen plants in shorter *f*, while LL of deciduous plants decreases with decreasing *f*. Without any a priori trait association, the model reproduced the well-known LL–leaf mass per area (LMA) relationship. The model also reproduced observed shifts in LL–LMA relationships across MAT or *f*. Evergreen leaves in long *f* need greater LMA to maintain LL than those in shorter *f*.

Main conclusions Observed contrasting LL–MAT patterns in deciduous and evergreen species can be reproduced via the simple rule of maximizing carbon gain across different lengths of favourable periods. Our model provides a mechanistic explanation for the empirical global patterns of several key leaf traits and their relationships.

Keywords

Adaptive optimization, cost–benefit analysis, deciduous, evergreen, favourable period length, leaf longevity, leaf habit, LMA.

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INTRODUCTION

Understanding the nature of global vegetation patterns is essential for modelling global geochemical cycles and for predicting how climate change will influence vegetation. In the last few decades, plant functional traits such as leaf longevity, leaf mass per leaf area, nutrient concentrations and photosynthetic rate have been studied extensively in various vegetation types, and both their generality and global biogeographic patterns revealed (Reich *et al.*, 1997, 1999; Niinemets, 2001; Reich & Oleksyn, 2004; Wright *et al.*, 2004, 2005a; Ordoñez *et al.*, 2009; Onoda *et al.*, 2011; van Ommen Kloeke *et al.*, 2012). However, analyses of the global biogeographic patterns of plant traits have been empirical for the most part, and mechanistic understanding of the ecological causes and significance of such patterns remains poor.

Leaf longevity (LL) is a key trait related to leaf, plant and ecosystem function and is closely associated with plant phenology, i.e. deciduous and evergreen habits. In general, evergreen species have longer LL than deciduous species (ranging from *c.* 0.2–10 years, and *c.* 0.2–0.8 years, respectively; Wright *et al.*, 2005a; van Ommen Kloeke *et al.*, 2012). It has been known for many years that some vegetation zones such as the wet tropics, areas with infertile soils and the boreal biome are dominated by evergreens, whereas other areas such as the cold temperate and tropical (dry) seasonal climate zones are dominated (or co-dominated) by deciduous species. Several models and explanations have been proposed to account for these patterns of deciduous and evergreen dominance (e.g. Kikuzawa, 1991; Reich *et al.*, 1992; Givnish, 2002). However, one conspicuous pattern that remains poorly understood is that LL increases with increasing mean annual temperature (MAT) across deciduous species, while LL *decreases* with increasing MAT across evergreen species (Wright *et al.*, 2005a). Further analyses and hypotheses (Ordoñez *et al.*, 2009, van Ommen Kloeke *et al.*, 2012) have failed to provide a definitive causal explanation for these trends. Those authors suggested that the pattern in deciduous species is relatively straightforward: LL is attuned to the annual length of the favourable period for growth (*f*), which is shorter at sites with lower MAT. Indeed van Ommen Kloeke *et al.* (2012) found temperature to be the sole best predictor of *f* for deciduous plants, while water availability (i.e. precipitation and evapotranspiration) and soil N availability had only marginal effects on *f*. The bigger challenge is to understand the pattern in evergreen species.

In the present study, we investigate global patterns in LL from a carbon budget perspective. Regardless of environmental differences, leaves need to assimilate enough carbon during the growing season to ensure positive plant growth. At the very least they have to pay back their own construction cost, and presumably also that of physically supporting structures such as stem and root (Givnish, 1988; Kikuzawa & Ackerly, 1999; Reich *et al.*, 2009). With a cost–benefit model, we test a hypothesis that the trend of longer LL of evergreen leaves in low MAT environments reflects the longer pay-back time for construction costs in such places, due to the shorter growing season and/or to suppressed metabolic activity (Kikuzawa, 1991; Kikuzawa & Kudo, 1995); a longer payback time is difficult to achieve in deciduous leaves since the maximum LL is limited by the onset of the unfavourable period.

The question still remains of how to best achieve a positive carbon balance for deciduous species within short growing seasons. In a local-scale study of subarctic and arctic sites, Kudo *et al.* (2001) found that plants growing at sites with shorter *f* had higher leaf N concentration, suggesting higher photosynthetic capacity (A_{max}), than plants growing at sites with longer *f*. This finding is consistent with the generally higher leaf nitrogen concentration per unit mass (N_{mass}) seen in shorter- versus longer-LL deciduous species (Reich *et al.*, 1992, 1999). These local phenomena may also be realized at the global scale. We hypothesize that deciduous-leaved species have an increasingly higher potential photosynthetic rate and nutrient concentration

as MAT or *f* decreases, but such an adjustment may not be required for evergreen plants that can amortize construction costs over multiple seasons.

In many datasets – local, regional and global – a positive relationship has been reported between LL and leaf mass per area (LMA) (Reich *et al.*, 1991, 1992, 1997, 1999; Wright *et al.*, 2004). Presumably this reflects the facts that both greater mechanical protection is necessary to prolong LL and high-LMA leaves require a longer period for payback of construction costs (Chabot & Hicks, 1982; Reich *et al.*, 1991, 1998; Wright & Westoby, 2002; Onoda *et al.*, 2011). That said, there are also intriguing and as yet unexplained MAT-related shifts in global LMA–LL relationships (Fig. 3b in Wright *et al.*, 2005a): at colder sites the slope of the LL–LMA relationship is steeper; the relationship becomes flatter with increasing MAT.

Thus, the aim of this paper is to understand the mechanisms underlying global patterns of several key leaf traits (LL, LMA, A_{max}, N) from a cost–benefit perspective, focusing on LL, and especially (1) the contrasting LL–MAT relations of deciduous and evergreen species, and (2) global shifts in LMA–LL relationships with respect to MAT. In our analyses we use a modified version of the cost–benefit model for LL initially proposed by Kikuzawa (1991) that considers length of the growing season (*f*) as a key variable. We address the following questions: (1) Can we reproduce divergent trends between LL and MAT shown for evergreen versus deciduous taxa by Wright *et al.* (2005a) by replacing MAT with the proportion of the year for favourable growth (*f*) based on monthly temperature and/or water availability? (2) Does the relationship between LL and LMA, which shifted systematically with MAT, also shift across *f*? (3) Does the cost–benefit model of maximizing carbon gain reproduce these trends? And (4), do deciduous species in low MAT have higher photosynthetic efficiency and nutrient concentration than those in high MAT?

MATERIALS AND METHODS

For the study of LL we analysed all 749 species-at-site combinations (657 species from 55 sites) for which LL was available in the dataset of Wright *et al.* (2004). These data cover a wide range of climates such as tropical forest, temperate forest, grasslands, boreal, alpine and desert. We also used data for photosynthetic rate, respiration rate, LMA and leaf N concentration in the same dataset for simulations and associated analyses (see below).

Favourable period length

Based on the latitude, longitude and elevation information for each site, we obtained monthly climate data from the CRU CL 2.0 dataset (climate means from 1961–90; 10′ spatial resolution; New *et al.*, 2002), and monthly estimates of PET from Choudhury (1997) (0.5° resolution). We consider low temperature and low water availability as two major factors that limit the length of the growing season (Chabot & Hicks, 1982; Kikuzawa, 1995). We calculated the proportion of the year for favourable growth (*f*) based on the number of consecutive months that satisfied the following conditions: firstly, that mean 24-h monthly tempera-

ture (MMT) was above 5 °C (Luo *et al.*, 2002; Wright *et al.*, 2005a) and secondly, that mean monthly precipitation (MMP) was more than 10% of mean monthly potential evapotranspiration (PET). Thus we had two different estimates of *f*: f_T and f_{TW}. The threshold of MMP/PET < 0.1 was chosen by examining several studies that reported phenology of dry deciduous species in both tropical (e.g. Kitajima *et al.*, 1997; Lal *et al.*, 2001) and temperate climates (e.g. Escudero & Del Arco, 1987; Mediavilla *et al.*, 2001).

Optimum leaf longevity

Since leaves are essentially photosynthetic organs, one can hypothesize that optimum LL is the longevity that maximizes the lifetime carbon gain per unit time of leaves:

$$g = \frac{1}{t}\left(\int_0^f p(t)\mathrm{d}t + \int_1^{1+f} p(t)\mathrm{d}t + \ldots + \int_{[t]}^t p(t)\mathrm{d}t - \int_0^t m(t)\mathrm{d}t - C\right) \quad (1)$$

where *g* is carbon gain per unit time (*t*), *p(t)* is the photosynthetic rate of a leaf at time *t*, *m(t)* is the respiration rate and *C* is the construction cost of the leaf and associated stem and root tissues needed to support a given leaf (see equation 4). This equation (modified from Kikuzawa, 1991) is equally valid for either mass- or area-basis parameters. In the present simulations we use area-based parameters.

We assumed that photosynthesis was carried out only during the favourable period within each year, whereas maintenance respiration costs were incurred right throughout a leaf's life; but that the respiration rate during the unfavourable period (i.e. cold winter) is considerably lower than that during the favourable season.

Since photosynthetic rate is maximum in young leaves and declines approximately linearly over time (see Reich *et al.*, 2009, for more references), we define it as follows (Kikuzawa, 1991):

$$p(t) = a(1 - t/b) \quad (2)$$

where *a* and *b* are species-specific parameters, *a* being the maximum diurnal photosynthetic gain at the leaf's full expansion (gC m^{-2} day^{-1}) and *b* the potential LL (in years) which determines the rate of decline rate in photosynthesis with leaf age (Kikuzawa, 1991; Ackerly, 1999). The respiration rate (*m(t)*) is defined in a similar manner:

$$m(t) = m(1 - t/b) \quad (3)$$

where *m* is the maximum daily respiration rate of the leaf and associated stem and root tissues needed to support a given leaf, at the leaf's full expansion (gC m^{-2} day^{-1}).

Here, construction cost per unit leaf area (*C*) includes the construction cost of the leaf as well as that of other organs (stem and root) that support the leaf. (Note that capital italic '*C*' denotes construction cost, and capital roman 'C' denotes carbon in this paper.) Leaf construction cost per area is the product of LMA and leaf construction cost per unit mass (*c*, g glucose C g^{-1} drymass C). In the present study, we express *C* as follows:

$$C = \mathrm{LMA}_C \times c \times k \quad (4)$$

where LMA_C is leaf carbon mass per unit area (gC m^{-2}), *c* is construction cost per unit leaf C mass (g glucose C/g drymass C) and *k* is the ratio of construction cost at the whole plant scale (leaf and associated metabolically active stem and root tissues that are constructed to support the leaf) to the construction cost of the leaf. Previous studies reported that leaf construction cost per unit mass was quite conservative (1.29–1.62 g glucose g drymass^{-1}, Williams *et al.*, 1989). Carbon concentration in glucose and leaf tissue is 40% and *c*. 50%, respectively. In this study, we thus approximated *c* as 1.2 gC gC^{-1} (= 1.5 g glucose g drymass^{-1}; e.g. Griffin, 1994, Poorter & Villar, 1997; Villar & Merino, 2001). *k* may depend on plant size, functional groups and habitat conditions (Kikuzawa & Ackerly, 1999) but quantitative knowledge on this is scarce. Accordingly we ran simulations with *k* = 1, 3, 5, 7, 10 and report the result for *k* = 3 in the main text and the other results in Supporting Information.

Parameter settings

We considered two things in choosing parameter settings. First, the range of parameters (*a*, *m*, *b* and *C*) should be realistic. Second, all parameters should be independent of each other in the model. For the latter, in nature, there are correlations among parameters such as a positive correlation between *a* (maximum diurnal photosynthetic gain) and *m* (maximum daily respiration rate), or a negative correlation between *a* and leaf construction cost (*C*) (e.g. Reich *et al.*, 1991; Wright *et al.*, 2005b). However, here we were specifically interested in what the results would be if we did not assume any a priori biological correlations. This approach has two merits: first, we can examine the unbiased pattern of LL without any potential confounding factors (i.e. autocorrelation with other traits); second, we can test what kind of parameter combinations would result in deciduous or evergreen habits, and most importantly we can test how parameter combinations achieve positive carbon balance across different lengths of *f*.

We set parameters *a*, *b*, *C* and *m* based on actual published observations. Daily maximum C gain (*a*, gC m^{-2} day^{-1}; equation 5) was calculated from the maximum instantaneous photosynthetic rate per unit leaf area (A_{area}, μmol m^{-2} s^{-1}). A_{area} has been measured in many studies and was summarized by Wright *et al.* (2004) for 825 species-site combinations. Since leaves do not operate at A_{max} right throughout the day – due to variations in solar angle, cloud cover, mutual/self-shading, humidity, temperature and inactivation of the photosynthetic machinery etc. – we introduced a conversion constant (t_l, 'mean labour time' *sensu* Kikuzawa *et al.*, 2004) to calculate *a* from A_{area}. Kikuzawa *et al.* (2004) found that actual total daily photosynthetic gain, *a*, was equivalent to photosynthetic gain if leaves operated at A_{max} for 5.5 h day^{-1} for a pioneer tree species in Japan. In nature, t_l may vary depending on various factors as mentioned above; hence, here we varied t_l in the simulations:

$$a = A_{area} \times 12 \times 3600 \times t_l \times 10^{-6} \quad (5)$$

Table 1 Mean, standard deviation (SD) and number of observations of net photosynthetic rate (A_{area}), respiration rate (R_{area}), leaf mass per area (LMA) and potential leaf longevity (b). The first three traits are from the GLOPNET database (Wright *et al.*, 2004) and b is from Kikuzawa & Lechowicz (2006).

	Mean	SD	n
$Log_{10}(A_{area})$ (μmol m^{-2} s^{-1})	1.001	0.236	825
$Log_{10}(R_{area})$ (μmol m^{-2} s^{-1})	0.0935	0.218	274
$Log_{10}(LMA)$ (g m^{-2})	1.990	0.301	2370
$Log_{10}(b)$ (year)	0.189	0.597	26

where A_{area} is maximum net assimilation rate per unit area (μmol m^{-2} s^{-1}), 12 is molecular weight of carbon, 3600 is the number of seconds in an hour and t_l is mean labour time. The default t_l was 5.5, but we also ran simulations using $t_l = 2, 4, 7$ and 9 h.

Similarly, the daily maximum respiration rate of leaf and associated stem and root tissues needed to support a given leaf, at the leaf's full expansion (m, gC m^{-2} day^{-1}; equation 6) was converted from the instantaneous leaf respiration rate (μmol m^{-2} s^{-1}). For simplicity we only included night-time leaf respiration (night assumed to be 12 h long), although associated stem and root respiration were considered for the full 24 hour period. Reich *et al.* (2008) showed that the average per-gram respiration rates of root and stem tissues are roughly half that of leaves (for woody plants in the field, median and mean rates for leaves, stems, and roots were 8.0, 2.9, 4.3 and 9.9, 3.4, and 6.8 nmol g^{-2} s^{-1} respectively; $n = 327, 131, 118$). Based on this we assume the rate per gram of leaf of associated stem and root tissue is 0.5 times the leaf rate. Given that stem and root respiration occur twice the hours per day but at half the rate, we can use k from equation 4 for the ratio of stem and root respiration to leaf respiration:

$$m = R_{area} \times 12 \times 3600 \times 12 \times 10^{-6} \times s \times k \qquad (6)$$

where s is the extent of suppression of the respiration rate during the unfavourable season (i.e. cold winter) compared with that during the favourable season. For the favourable season $s = 1$, while for the unfavourable season we ran simulations adopting different s-values (0, 0.1, 0.25, 0.5 and 1).

The parameters a, m and C were randomly produced based on the actual data distribution of A_{area}, R_{area} and LMA, respectively, in the dataset of Wright *et al.* (2004). For the parameter b (maximum potential LL), the data summarized in Kikuzawa & Lechowicz (2006) were used. All these parameters had an approximately log-normal distribution (Wright *et al.*, 2004; see also Appendix S1 in Supporting Information). The mean and SD of log_{10}-transformed variables are summarized in Table 1. We produced 1000 random values for each parameter based on each mean and SD (function 'rnorm' in *R* software package, v. 2.15.0; R foundation for Statistical Computing, Vienna, Austria). The range of a, b, C and m were 0.30–22.2 (gC m^{-2}

day^{-1}), 0.01–68 (year), 17.9–1375 (gC m^{-2}) and 0.20–10.1 (gC m^{-2} day^{-1}), respectively, in a default setting ($k = 3$, $t_l = 5.5$).

Simulation and data analysis

Based on 1000 sets of a, b, C and m, we calculated g under different favourable period lengths (f being from 1 to 12 months per year). Each parameter combination can be regarded, conceptually, as a different 'species'. For each species we defined the t-value showing the highest g (i.e. maximum C gain per unit time) as the optimum leaf longevity (LL_{opt}). Note that some simulated species showed negative g for their entire LL (negative carbon budget). In these cases we considered that such trait combinations would not be successful in nature. LL_{opt} of more than 1 year was considered as evergreen and LL less than 1 year was considered deciduous. Evergreen species with short LL (< 1 year) do exist but are primarily pioneer or early successional tropical trees (Reich *et al.*, 1991) where f is near 1. As they are scarce in number compared with evergreens with long LL, they will be omitted from further consideration.

Ordinary least squares regression was used for the analysis of environmental gradients of leaf traits since our interest was in quantifying the 'driving' influence of climate in this regard. Relationships *between* leaf traits were described using a combination of standardized major axis (SMA) slopes (Warton *et al.*, 2006) and the Pearson correlation test. All analyses were run using the R software package.

RESULTS

The portion of the year when monthly mean temperature was above 5 °C (f_T) strongly correlated with MAT (Fig. 1a, $R^2 = 0.692$). However, there was large variation in MAT at $f_T = 1$. This was mainly due to high-elevation tropical sites with long f_T but low MAT. As would be expected, the correlation between MAT and favourable period became much weaker (Fig. 1b, $R^2 = 0.357$) when we also considered dry season effects (MMP/PET > 0.1) in the calculation of favourable period (f_{TW}).

In the empirical dataset, LL of evergreen plants decreased as f_T increased, while in deciduous species LL was positively correlated with f_T (Fig. 2b). These trends are similar to the relationships between LL and MAT as was found in Wright *et al.* (2005a) (Fig. 2a). Basically similar patterns were observed when water availability was additionally considered in defining f, although the R^2 of the relationships became somewhat lower (Appendix S2). LMA and LL/LMA were also analysed with respect to MAT and f, and similar patterns were observed (Appendix S3).

In deciduous species, N_{mass} increased with decreasing MAT (Fig. 3a). Similarly, N_{mass} increased with decreasing f_T and f_{TW} in deciduous species (Fig. 3b,c). In evergreen species N_{mass} tracked MAT, decreasing towards colder sites, whereas it was unrelated to either f_T or f_{TW}. Photosynthetic rates were also analysed with respect to MAT and f, but the patterns were less clear than that of N_{mass}, perhaps because photosynthetic rates are sensitive to measurement conditions which themselves differ somewhat among studies (Appendix S3).
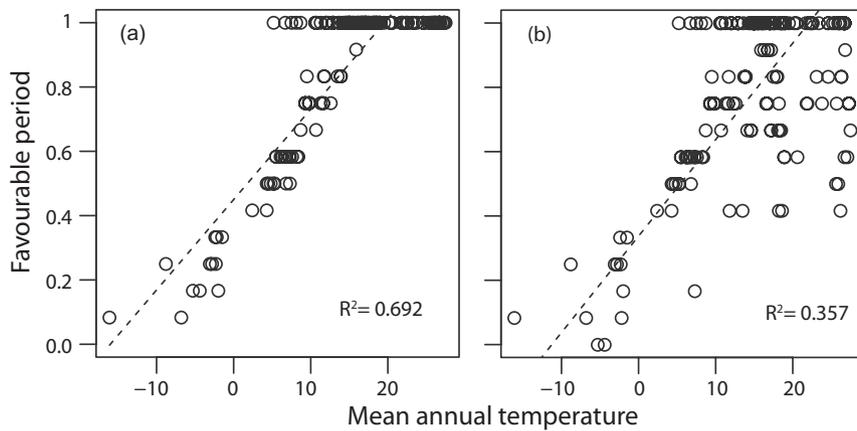
Figure 1 Relationship between mean annual temperature (MAT) and the portion of the year for favourable growth (*f*). (a) The favourable period was calculated first as the number of consecutive months whose mean monthly temperature is above 5 °C (f_T) and (b) secondly with the additional constraint that the ratio of mean monthly precipitation (MMP) to monthly potential evapotranspiration (PET) was above 0.1 (f_{TW}). Regression lines: (a) $y = 0.281x + 0.450$; (b) $y = 0.300x + 0.337$.
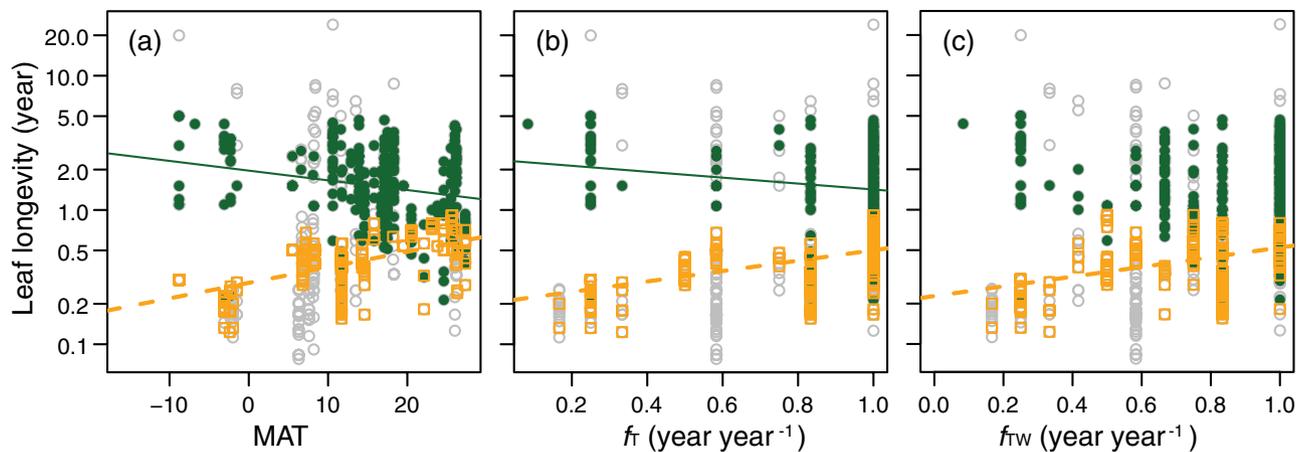

Figure 2 Leaf longevity of actual species (Wright *et al.*, 2004) versus (a) mean annual temperature (MAT), (b) the proportion of the year when the mean monthly temperature is above 5 °C (f_T), and (c) the proportion of the year when the mean monthly temperature is above 5 °C and the ratio of mean monthly precipitation to monthly potential evapotranspiration is above 0.1 (f_{TW}). Filled dark green circles, open orange squares and open grey circles denote evergreen, deciduous and unclassified/variable species, respectively. Type I regression lines (solid and dashed line for evergreen and deciduous species, respectively) are shown when the correlation are significant ($P < 0.05$, Pearson's test). See Appendix S2 for regression coefficients and significance levels.

The overall relationship between LMA and LL was strongly positive ($R^2 = 0.42$; Fig. 4). Furthermore, LL–LMA regression slopes differed systematically among classes of MAT (Fig. 4a) and *f* (Fig. 4bc), decreasing in steepness from the lowest to the highest MAT (as reported by Wright *et al.*, 2005a), or from the shortest to the longest f_T. The shift in scaling slope from the shortest to the longest f_T class was from 2.2 to 1.3 (Appendix S1), which for a five-fold shift in LMA equates to a 37-fold shift in LL at short f_T (1–3 months per year) and an eight-fold shift in LL at longest f_T (10–12 months per year). A similar trend was found across f_{TW}, but the trend in slopes was less clear (Fig. 4c).

We found divergent patterns across the simulated LL (Fig. 5a) when we calculated optimal LL in relation to *f* for each of 1000 parameter combinations (*a*, *b*, *C* and *m*) at $k = 3$ in equation 4 and 6, $t_l = 5.5$ in equation 5 and $s = 0.1$ in equation 6 (see Appendices S4–S6 for other *k*, t_l and *s* settings). Many 'species' (a given set of parameters of *a*, *b*, *C* and *m*) could produce a positive rate of net carbon gain per day when $f = 1$ (373 out of 1000). But, when *f* decreased, it became impossible for some

species to have positive net carbon gain because, while photosynthesis is limited to just part of the year, respiration continues year-round (albeit at a reduced rate during unfavourable periods). In such cases optimal LL was not achieved, which can be seen as truncated lines in Fig. 5(a). Some species showed consistently deciduous habit (LL shorter than 1 year) throughout the entire range of *f* (D type, pale green lines in Fig. 5a), while other species showed consistently evergreen habit across *f* (E type, dark green lines in Fig. 5a). There were also species which 'changed' their leaf habits with decreasing *f*, whether from evergreen to deciduous (ED type, blue line), or from deciduous to evergreen (DE type, red line), or from evergreen to deciduous then back to evergreen (EDE type, orange line). Among the 37% of species that showed a positive C budget using the default parameter settings, 33% were deemed E type, 33% D type, 8% ED type, 5% DE type and 20% EDE type.

Optimal LL increased with decreasing *f* in E type species while optimal LL of D type species was reduced when *f* decreased (Fig. 5a). For deciduous species the maximum LL is limited by *f*
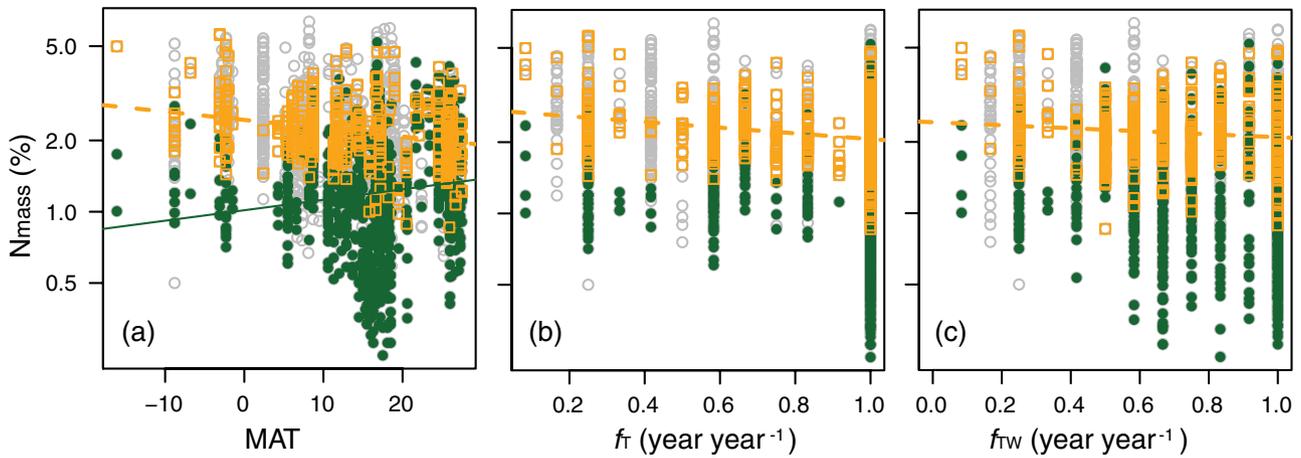
Figure 3 Leaf N concentration per unit mass (N $_{mass}$) of actual species (Wright *et al.*, 2004) versus (a) mean annual temperature (MAT), (b) the proportion of the year when the mean monthly temperature is above 5 °C (f_T), and (c) the proportion of the year when the mean monthly temperature is above 5 °C and the ratio of mean monthly precipitation to monthly potential evapotranspiration is above 0.1 (f_{TW}). Filled dark green circles, open orange squares and open grey circles denote evergreen, deciduous and unclassified/variable species, respectively. A type I regression line is shown when the correlation is significant ($P < 0.05$, Pearson's test). Regression coefficients and the level of significance are summarized in Appendix S2.
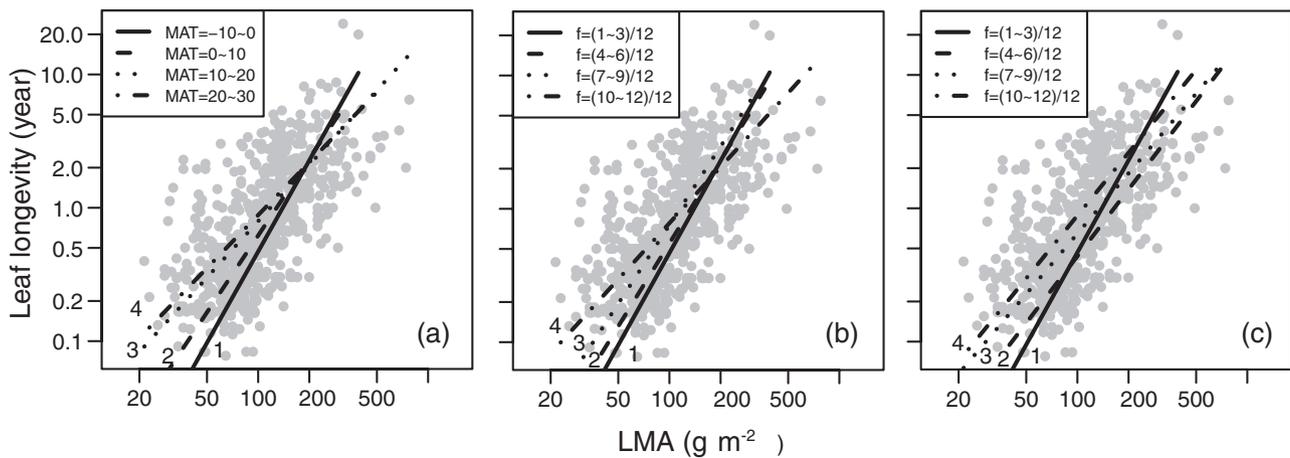

Figure 4 Relationships between field-measured leaf longevity and leaf mass per area (LMA); data from Wright *et al.* (2004). Standardized major axis slopes were fitted to species grouped by (a) mean annual temperature (MAT), (b) the proportion of the year when the mean monthly temperature is above 5 °C (f_T), and (c) the proportion of the year when the mean monthly temperature is above 5 °C and the ratio of mean monthly precipitation to monthly potential evapotranspiration is above 0.1 (f_{TW}). The numbers (1–4) in each figure indicate the four groups, from low to high MAT or *f*. See Appendix S2 for regression coefficients and significance levels.

by definition, therefore the overall trend of LL in deciduous species decreased with *f*. Among deciduous species an increasing number of species had optimal LL equal to *f* when *f* was short (0, 28, 63 and 96% of deciduous species when *f* = 1, 0.75, 0.5 and 0.25, respectively). If optimal LL were averaged for all evergreen types (LL > 1), optimal LL increased with decreasing *f*, while average optimal LL of deciduous types (LL < 1) decreased with decreasing *f* (Fig. 5b). This result is consistent with the trends observed in LL for real plant species (Fig. 2b,c). We also examined the trends of optimal LL with respect to *f* using a range of different assumptions (*k* = 1–10, t_l = 2–9, *s* = 0–1; Appendices S4–S6). In short, with increasing *k* (the ratio of the whole plant

cost to leaf cost) the evergreen habit became more abundant while with increasing t_l (mean labour time) the deciduous habit became more abundant. Varying *s* (suppression of respiration during the unfavourable season) had little effect on the relative abundance of deciduous and evergreen habits, although higher *s* reduced the overall number of species that achieved positive growth, especially in short *f*. Overall, the trends of optimal LL with respect to *f* were similar irrespective of which specific sets of assumptions were chosen.

Figure 6 shows the emergent relationship between optimal LL and LMA from our simulations. Note that these LMA data were randomly produced according to the mean and SD of global
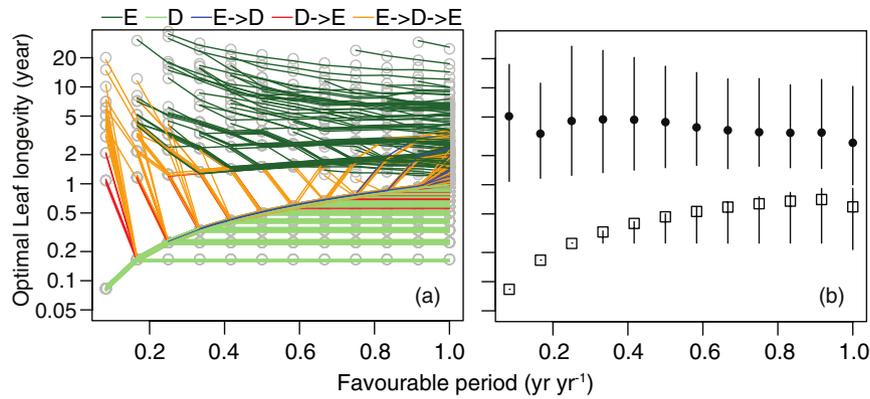
Figure 5 The relationship between predicted optimal leaf longevity (LL) and favourable period (*f*, year year⁻¹) obtained from our simulations. Optimal LL was calculated from equation 1 across different lengths of the favourable period (1–12 months per year) with 1000 sets of randomly produced parameters (*a*, *m*, *b* and *C*, see main text for details). Optimal LL for a given set of parameters across *f* are connected by a line. When simulated leaves did not show a positive carbon budget for the end of their lifespan, optimal LL was not calculated. Therefore some lines are truncated at certain *f* because of the inability to make a positive carbon balance at short values of *f*. LL more than 1 year is denoted as evergreen. (a) Species were grouped into phenological classes depending on their predicted trends in LL with decreasing *f*, Strict evergreen (E, dark green); strict deciduous (D, light green); evergreen changing to deciduous (E– > D, blue); deciduous changing to evergreen (D– > E, red); evergreen changing to deciduous then back to evergreen (E– > D– > E, orange). Marginal noise was added to each line (function 'jitter' in the R software package) in order to better visualize overlapping lines. (b) Mean and 95% confidence intervals of optimal LL across the length of favourable period. Data sorted into either deciduous (open squares) or evergreen phenologies (filled circles).
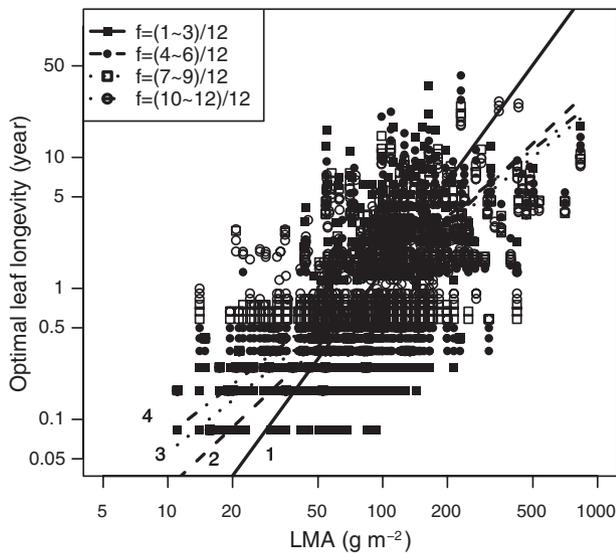

Figure 6 Relationship between predicted optimal leaf longevity (LL) and leaf mass per area (LMA) obtained by the simulation. Optimal LL values were calculated with the same set of parameters used in Fig. 5. LMA data were generated as semi-random numbers satisfying the mean and deviation of the global dataset (see Table 1). Standardized major axis slopes are drawn for 'species' grouped by different length of favourable period (*f*). The numbers (1–4) in each figure indicate four groups from low to high *f*. Regression coefficients and the level of significance are summarized in Appendix S2.

LMA data (Table 1). With increases in LMA, and thus increases in *C*, optimal LL became longer. The relationship between optimal LL and LMA was examined for four *f* classes. Optimal LL was significantly positively correlated to LMA in each *f* class, with relationship slopes becoming flatter with increasing *f* (Fig. 6). This pattern is consistent with the LL–LMA relationships observed in the global dataset of field-measured leaf traits (Fig. 4).

To investigate how the simulated parameter combinations were related to leaf phenology types across *f*, pair-wise scatterplots of parameters are shown with different symbols for different leaf phenology types (Fig. 7). Since we avoided any a priori assumptions in trait correlations, some combinations of parameters did not produce a positive carbon balance (grey crosses in Fig. 7). Most notably, these combinations included: (1) high *m* (maintenance respiration) with low *a* (daily photosynthesis), (2) low *a* and low *b* (potential LL), (3) low *a* and high *C* (leaf construction cost), (4) high *C* and low *b*, and (5) high *m* and low *b*. Strict evergreen type species tended to have relatively low *a*, high *C* and *b*, while strict deciduous type species tended to have the opposite set of parameters.

DISCUSSION

Contrasting patterns of LL against *f*

In this study we showed that the contrasting LL–MAT patterns of evergreen and deciduous species (Wright *et al.*, 2005a) could also be found when we analysed LL with respect to favourable period, *f*. We calculated *f* based firstly on temperature (*f*_T) and secondly on both temperature and water availability (*f*_TW) but

Figure 7 Bivariate scatterplots of parameters used in the simulation. Daily maximum C gain (*a*, gC m^{-2} day^{-1}), daily maximum respiration rate (*m*, gC m^{-2} day^{-1}), potential leaf longevity (*b*, year) and construction cost (*C*, gC m^{-2}) at *k* = 3 *t*$_l$ = 5.5 and *s* = 0.1 (see the main text for details). Combinations of parameters are grouped into six groups; strict evergreen (E, dark green filled circle), strict deciduous (D, light green open circle), evergreen to deciduous with decreased favourable period (E–> D, blue open triangle), deciduous to evergreen with decreased favourable period (D–> E, red cross), evergreen to deciduous and again to evergreen with decreased favourable period (E–> D–> E, orange filled triangle) and no positive C budget in any cases (NC, grey multiplier sign). Correlation coefficients among parameters that produced positive carbon balance are summarized in Appendix S7.
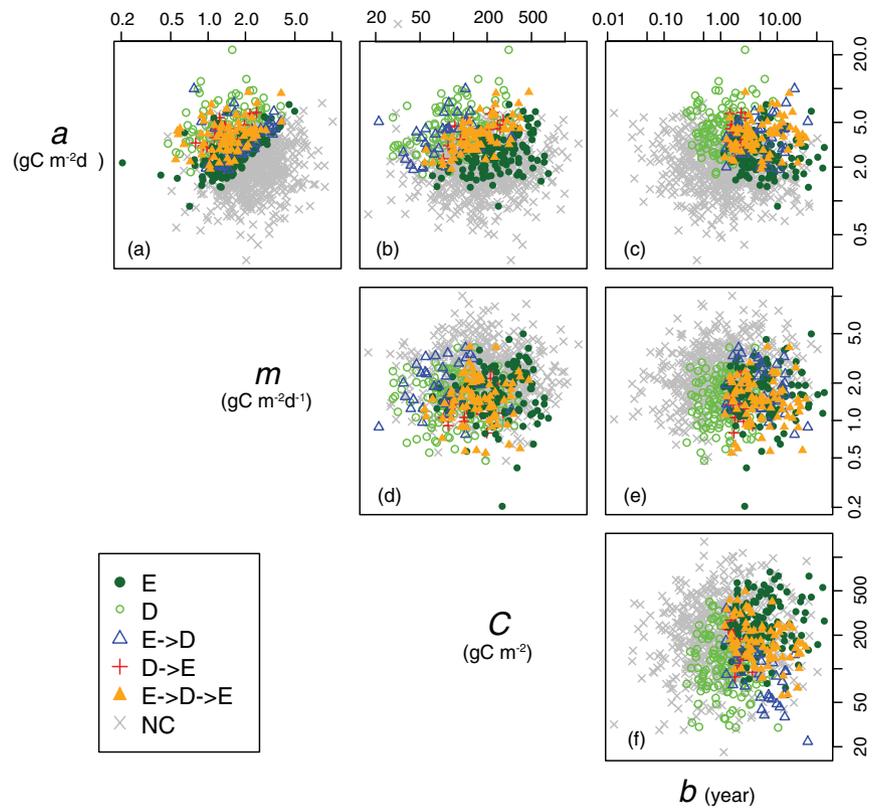
similar patterns in LL were found across each variant (although the R^2 values between MAT and *f* varied markedly, i.e. 0.69 and 0.36, respectively). This suggests that the MAT-related trends can be interpreted, to a considerable extent, as reflecting adaptation to variation in *f*. Of course, the length of the favourable period is not a direct measure of environmental conditions, rather it is a proxy for those. Still, local and regional studies have shown that the length of favourable period strongly influences phenology and associated plant characteristics (e.g. Ehleringer, 1983; Kudo, 1992; Sawada *et al.*, 1994; Kudo *et al.*, 2001; Onoda *et al.*, 2004). Our study showed that this can be realized at the global scale.

In general, cold winter and dry summer seasons are considered as two major factors that limit the length of the growing season. Therefore *f*$_{TW}$, which considered both factors, was expected to have better explanatory power for LL in deciduous species than did MAT. As it turned out the correlation coefficient between LL and *f*$_{TW}$ was not higher than those between LL and *f*$_T$ or MAT. This result is similar to the result of van Ommen Kloeke *et al.* (2012) who found that MAT was the single best predictor of *f* among various environmental factors. While temperature is likely a reasonable indicator of thermal environmental conditions among coexisting species in a given area, water availability may be much more heterogeneous due to spatial differences in distance to water source, topography and the physical properties of soils, or rooting depth. That is, perhaps data from the global gridded climate datasets only poorly capture variation in water availability at local scales. Furthermore, many plants in the dry season are not completely inactive as they flush leaves before the

rainy season starts, and also they often flower and set fruits during the dry season (Gerhardt & Hytteborn, 1992; Lal *et al.*, 2001). Therefore it may not be so surprising that considering precipitation and PET in calculation of *f* does not improve the correlation with LL. Similarly, because there is variation among species in their ability to grow at very low temperatures, our choice of a 5 °C cut-off between favourable and non-favourable months cannot be considered as applying to all species.

Our simple model, which assumes that optimal LL is determined by maximizing photosynthetic gain per unit time, reproduced the observed, contrasting LL patterns across *f* between evergreen and deciduous species (Fig. 5). This result suggests that the divergent LL trends in evergreen and deciduous plants can be interpreted as the outcome of adaptive behaviour of plants to maximize their carbon gain. With decreasing *f* the model predicts that evergreen species need to prolong their leaf longevity in order to compensate for the shorter photosynthetic period within a year. Thus in evergreen species LL is negatively correlated to *f*. Deciduous species could behave similarly, but in doing so, by definition, they would no longer be deciduous (i.e. their LL would become longer than 12 months). Deciduous species could not prolong their LL beyond *f*, thus many deciduous species in nature as well as in our simulation have LL similar to *f* when *f* is short, resulting in the positive correlation between LL and *f* in deciduous plants. Similar contrasting patterns in LL across *f* between deciduous and evergreen species were previously observed in a regional study (Kudo, 1992; Kikuzawa & Kudo, 1995). Here we show that this generalizes far more widely.

On average, deciduous species in short-*f* regions had higher N_{mass} than deciduous plants in longer-*f* regions (and also P_{mass}; data not shown), or than evergreen plants in any region (Fig. 3). The parameter combinations that were associated with deciduous phenology had consistently higher *a* per unit *C* than the combinations for evergreen habits (Fig. 7). These trends could be interpreted as indicating that more nutrients are invested in photosynthetic enzymes at colder sites in order to achieve higher photosynthetic rates, or perhaps that more photosynthetic enzyme is required to achieve a *given* photosynthetic rate at colder sites or sites with only very short growing seasons (Kudo *et al.*, 2001; Onoda *et al.*, 2004).

Modulation of the LL–LMA relationships in relation to *f*

Optimal LL was positively correlated with LMA (Fig. 6), which in turn was proportional to *C* (equation 4). The positive correlation between LL and LMA was predicted by a theoretical model (Kikuzawa, 1991) and well recognized in the comparison of many plants (Reich *et al.*, 1992, 1997; Wright *et al.*, 2004). Wright *et al.* (2005a) found that the slope of LL–LMA relationships varied systematically with MAT. Similar changes were also found when we examined the relationships between LL and LMA with respect to f_T (Fig. 4): i.e. the actual LL–LMA relationship was steeper in the short f_T than that in the longer f_T. These changes in LL–LMA relationship were also realized by our simulation (Fig. 6), indicating that change in slope of LL–LMA relations may be caused by adaptation to different *f*. Evergreen leaves in short *f* need long LL for a given LMA to pay back the construction cost, while deciduous leaves in short *f* have shorter LL for a given LMA due to the limited length of growing season (Fig. 2g–i), which result in steeper slope in shorter *f*. It is worthwhile noting, however, that the change in slope was less clear across f_{TW} than across f_T (and, further, that Wright *et al.*, 2005a found that differences in mean annual precipitation did not change the slope but did change the intercept of LL–LMA relationships). These results indicate that changes in slope may be specifically related to geographical temperature gradients. The empirical global data suggested that leaves in seasonal dry environments had LMA values somewhat higher than that predicted by the optimal LL model. One possible explanation is that maintaining leaves longer in *dry* unfavourable periods is in a sense more costly than maintaining leaves through *cold* unfavourable periods, e.g. because of less supressed respiration rates, higher herbivory pressure or greater water losses in regions with dry unfavourable periods.

Other environmental factors potentially influencing LL

Longer LL has been reported in plants growing in infertile soil (Beadle, 1954; Givnish, 2002; Reich *et al.*, 2004) and in plants persisting in shade (Coley & Aide, 1991; Osada *et al.*, 2003; Reich *et al.*, 2004; Onoda *et al.*, 2011). However, our model did not consider either soil fertility or the light environment. Although these environmental factors are highly variable, even at a local scale, our global LL model can still be used to at least partially explore the potential influence of these factors. For example, on infertile soil nutrient concentrations and thus photosynthetic rate are generally low (low *a*), whereas root-to-shoot ratios are generally high (high *k*). Therefore in such places the model predicts that optimal LL should be longer (see Appendix S4), which is indeed consistent with actual observations. Responses to shade are rather more complicated because shade *acclimation* (i.e. plastic responses) typically involves lower LMA (thus lower *C*) and lower root-to-shoot ratio (lower *k*), while shade *adaptation* (i.e., shade tolerant versus. shade intolerant species) may involve higher LMA (high *C*) and higher root-to-shoot ratio (high *k*) (Kitajima, 1994; Kitajima & Poorter, 2010; Lusk *et al.*, 2010). In general, photosynthetic rate is heavily suppressed by low light (low *a*) while the other parameters, *C* and *k*, are less affected; therefore in either situation the model predicts longer optimal LL.

Trait combinations and evolution of different leaf habits

For the present model we produced random values for each parameter based on the mean and SD of a global leaf trait dataset and purposely did not assume a priori correlations among traits (despite their well-known correlations in many datasets, e.g. Reich *et al.*, 1997; Wright *et al.*, 2004). Thus, we included in our simulations both realistic and unrealistic parameter combinations. As it turned out, unrealistic combinations such as low photosynthetic capacity in combination with high respiration rate could not achieve positive carbon balance, and presumably this is why they do not exist in nature. Similarly, when potential LL (*b*) was short, some parameter combinations such as low photosynthetic rate, high respiration rate or high construction cost did not make positive carbon balance (Fig. 7), as also observed in nature (Wright *et al.*, 2004). Conversely, despite not assuming any a priori trait correlations, a number of known relationships emerged from the simulations among the parameter sets that had positive C balance (Fig. 7; Appendix S6). For example, there was a broad positive correlation between photosynthetic rate (*a*) and respiration rate (*m*), and between construction cost (*C*) and potential LL (*b*); and a negative correlation between *a* and *b* (as reported by Kitajima *et al.*, 1997; Kikuzawa & Lechowicz, 2006, 2011). While there is no doubt that many interacting factors shape what trait combinations are successful in the real world (soil nutrients, light environment, freezing tolerance, wind exposure, etc), our analysis showed that many major correlations among leaf traits can be realized by a simple rule: the need for a positive carbon budget.

Depending on the precise combination of input parameters, some 'species' exhibited an evergreen habit and others a deciduous habit. An interesting finding was that some 'species' changed their leaf habit depending on *f* (Figs 5 & 7, Appendices S4–S6). While facultative deciduousness (phenotypic plasticity) of this kind is not uncommon across local or regional temperature gradients (e.g. Reich & Borcher, 1984), the ED (evergreen →

deciduous) and EDE (evergreen → deciduous → evergreen) types emerged relatively commonly in our analyses. These changes in leaf phenology across *f* provide some prospective explanations for the evolution of plants across latitudes. For example, *Quercus* species are widely distributed in the Northern Hemisphere from tropical to temperate climate. Many *Quercus* species in tropical and warm temperate zones are evergreens (the so-called 'live oaks' such as *Quercus suber, Quercus virginiana* and *Quercus glauca*), but those at high latitudes are often deciduous (such as *Quercus alba, Quercus robur* and *Quercus crispula*). Arguably it can be considered that the evolution of the deciduous habit might have been necessary for *Quercus* species to distribute themselves to high latitudes (ED type). Other ED type genera include *Magnolia, Ficus* and *Symplocos*. Examples of EDE type genera include *Rhododendron* and *Vaccinium* (both Ericaceae) and *Ilex* (Aquifoliaceae): these genera contain evergreen species in the tropics but both deciduous and evergreen species in temperate regions (evergreen in alpine areas, deciduous at lower elevations). Many plant families have both deciduous and evergreen species whereas others are exclusively evergreen or deciduous. Understanding the ecological and genetic basis of the evolution of leaf phenology is key to understand adaptation and distribution of plants. Our analysis provides a potentially useful framework for their future study.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Correlation coefficients and their level of significance of Figures 2, 3, 4 and 6.

Appendix S2 Distribution of data of key parameters.

Appendix S3 LMA, LL/LMA and photosynthetic rates across MAT and f.

Appendix S4 Simulation of optimal leaf longevity with varying k.

Appendix S5 Simulation of optimal leaf longevity with varying t_l.

Appendix S6 Simulation of optimal leaf longevity with varying s.

Appendix S7 Correlation coefficients of parameters that have positive C balance.

BIOSKETCH

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