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Measurement of leaf longevity of 14 species of grasses and forbs using a novel approach

J. M. CRAINE[1]*, D. M. BERIN[2], P. B. REICH[3], D. G. TILMAN[4] AND J. M. H. KNOPS[4]

[1] *Deparment of Integrative Biology, University of California Berkeley, Berkeley, CA 94720, USA*
[2] *Department of Biology, Oberlin College, Oberlin, OH 44074, USA*
[3] *Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, USA*
[4] *Department of Ecology, Evolution, and Biology, University of Minnesota, St. Paul, MN 55108, USA*

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SUMMARY

Grasses and forbs are often classified into separate functional types, although systematic differences between the types have only been verified for a few functional traits. Since leaf longevity has been shown to be a key trait linking plant ecophysiology, whole-plant growth and ecosystem resource cycling, we compared the leaf longevity of 14 species to determine if there were consistent differences between grasses and forbs or other functional classifications, such as persistence of leaves into winter. Leaf longevity was assessed in 6-yr-old monoculture plots in central North America by tagging and sequentially monitoring the phenological states of whole forb leaves and sections of grass leaves. This new approach enables a calculation of leaf longevity unbiased by the manner in which grass leaves grow and provides a more accurate comparison between grasses and forbs. *Lupinus perennis* had the shortest leaf longevity (4 wk) and *Koeleria cristata*, *Poa pratensis*, and *Solidago rigida* the longest (13–14 wk). Average leaf longevity for the 14 species was *c.* 9 wk, with no significant differences between grasses and forbs nor between current alternative functional classifications.

Key words: Cedar Creek, forb, grass, leaf longevity, phenology, plant functional type.

INTRODUCTION

Classifying plant species into functional types is a strategy for representing species in a manner that reduces the complexity of models of ecosystem functioning while still representing critical functional traits. Grasses and forbs are often separated into different functional types because they have been shown to differ systematically in positioning of meristems, rooting depth (Sala *et al.*, 1997), leaf architecture (Anten *et al.*, 1995), content of certain cations and silicon, and leaf toughness (Cornelissen & Thompson, 1997). These traits are asssociated with differences in tolerance of removal of aboveground biomass (Langer, 1966), decomposition rate of leaf biomass (Cornelissen & Thompson, 1997) and leaf and stand-level light acquisition (Anten *et al.*, 1995; Turner & Knapp, 1996).

Differences in a few traits does not imply that grasses and forbs differ in all important functional traits. Leaf longevity, an important plant trait linking leaf ecophysiology, whole-plant growth and ecosystem processes, has been shown to correlate with other ecophysiological parameters such as photosynthetic rate, tissue N concentration and RGR (Reich *et al.*, 1992, 1997). In cost–benefit analyses, longevity of the leaf is important for determining net carbon (C) gain, an important component of whole-plant growth and competitive superiority (Chabot & Hicks, 1982; Aerts & Berendse, 1989). In addition, leaf fall constitutes a major pathway for nutrient cycling; the rate of leaf biomass turnover can drastically alter estimates of net primary production and is a major determinant of ecosystem nutrient cycling rates (Son & Gower, 1991).

Models of resource exchange at the organ, whole-plant, and ecosystem levels are best parameterized with leaf biomass longevity for a plant or stand, yet most studies estimate the longevity of individual leaves, likely to be similar for species such as trees and forbs, in which all parts of individual leaves tend to be produced and senesced synchronously, but not

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*Author for correspondence (tel + 001 510 642 1054; fax +001 510 643 6264; e-mail jcraine@socrates.berkeley.edu).

for species such as grasses, in which production and/or senescence is asynchronous within a leaf (Sims & Coupland, 1977). In these species, an individual leaf can live markedly longer than the biomass that constitutes the leaf, because older sections of a leaf senesce before the younger; the individual leaf lives on as its biomass is replaced. For example, the leaves of *Welwitschia* have a much longer life span than any unit of leaf length or biomass (Chabot & Hicks, 1982).

Leaf longevity has been quantified for many different species of trees and forbs (Reich *et al.*, 1997), but we know of only a few studies that have attempted to quantify the longevity of grass leaves (Coupland & Abouguendia, 1974; Sydes, 1984; Cornelissen & Thompson, 1997). In these studies, the longevity of grass leaves was estimated for entire leaves rather than per unit leaf length, the latter being more likely to represent biomass turnover rates. Thus, comparison of leaf longevity of grass and other species with different forms of growth might not accurately compare leaf longevity. In this study, we compared the biomass longevity of six grasses and eight forbs by tagging and periodically assessing the phenological states of individual forb leaves and sections of grass leaves, to provide a more accurate comparison of leaf longevity. In addition, we examined alternative functional classification of the 14 species based on leaves that lived into winter. Although our replication was low, we also examined whether there were obvious differences between C_3 and C_4 grasses and nonleguminous forbs and legumes.

MATERIALS AND METHODS

The study was conducted at Cedar Creek Natural History Area, MN, USA, situated on a glacial outwash sandplain (Tilman, 1988). The 14 species surveyed were part of the experimental monoculture study (LTER experiment E111) established in fall 1992 in a portion of an abandoned agricultural field, weeded each year to maintain monoculture status. Species names and current functional classifications of the species are contained in Table 1. Authorities for species follow Moore (1973). Plots were 2.4×1.5 m for most species, 1.2 m $\times$ 1.5 m for the remainder. Adjacent plots were separated by sheet metal sunk 25 cm into the ground. When necessary, plots were watered weekly during the 1997 growing season to ensure at least 2.5 cm of weekly precipitation, thereby minimizing water stress.

Census

Census of leaves began 25 June 1997 and continued at least every 2 wk until 12 October 1997. Five individuals per grass plot and three individuals per forb plot were censused in each of three or four plots per species. A grass individual was defined as a set of leaves appearing to share the same basal meristem; a forb individual was defined as leaves sharing the same emergent stem. Individuals with leaves damaged by herbivory or other factors were removed from the data set, which finally comprised 199 individual plants, 1868 forb leaves and 95.2 m of grass leaf.

On each census date the 'birth' date of each approximately fully expanded forb leaf was recorded and a numbered 1×2 cm paper tag was attached to its base with floss. We estimate that average expansion time of forb leaves was *c.* 2 wk. During the census, previously tagged leaves were checked and recorded as either green, or considered senesced when the leaf was mostly yellow to fully brown and/or had fallen. All leaves present at the beginning of the experiment or subsequently produced on the selected individual during the census period were tagged and quantified in this manner, except for *Asclepias syriaca*, for which only one leaf of each pair was tagged, and *Lespedeza capitata* and *Desmodium canadense*, for which every third leaf was tagged and senescence was assessed per leaflet of tripartate leaves. There were signs of disease on some of the leaves, but these were coincident with the pattern of senescence. The causal or resultant role of the disease in the senescence process could not be distinguished. No obvious effect of the presence of the tag on longevity was seen.

For most species, the sampling scheme adequately spans the relevant period of the phenology of leaf dynamics for an average area of ground in the plots during the observation period, except *Rudbeckia serotina*, *Agropyron repens*, and *Lupinus perennis*. Individual plants of *R. serotina* seen in June, having overwintered as basal rosettes, were tagged as described, but new rosettes produced late in the year were not censused. Neither were those leaves of *A. repens* which overwinter green, because they grew on new individuals produced during the year. Leaves of *L. perennis* individuals that had germinated in previous growing seasons were fully senesced by early July, whereas leaves of seedlings from seeds produced in June which had germinated by July were not included in the census. This does not indicate any error in measurement of leaf longevity, but reflects the time of the census.

At each census date, the bases of new grass leaves were permanently marked. There was no observed difference between the longevity of marked and unmarked leaves on adjacent plants. At each census date, total leaf length and senesced length were recorded. Senesced length was determined as leaf length from the leaf tip to the interface of the green nonsenescent tissue and the brown, sensecent tissue. If senescence was noncontinuous, total senesced length was recorded.

Table 1. *Mean longevity and quantity ($\pm SE$) of forb and grass leaves were produced and senesced mid-May–mid-October 1997*

Species	Functional type	Over-winters green?	No. of plots	Longevity (wk)	No. leaves or length (cm) measured per plot
Agropyron repens	C_3 grass	Yes	4	7.5 ± 0.1	64.9 ± 4.6
Ambrosia artemisiifolia elatior	Annual forb	No	4	6.5 ± 0.3	18.8 ± 1.4
Andropogon gerardi	C_4 grass	No	4	10.4 ± 0.2	94.9 ± 14.3
Anemone cylindrica	Perennial forb	Yes	4	9.1 ± 0.5	8.6 ± 0.9
Asclepias syriaca	Perennial forb	No	4	6.1 ± 0.3	13.6 ± 0.7
Desmodium canadense	Legume	No	4	10.6 ± 0.6	31.6 ± 0.7
Koeleria cristata	C_3 grass	Yes	4	13.5 ± 0.9	68.2 ± 3.0
Lespedeza capitata	Legume	No	4	6.8 ± 0.2	50.3 ± 3.3
Lupinus perennis	Legume	No	3	4.1 ± 0.9	5.6 ± 0.8
Poa pratensis	C_3 grass	Yes	4	13.1 ± 0.4	41.7 ± 3.8
Rudbeckia serotina	Perennial forb	Yes	3	6.7 ± 0.4	8.9 ± 0.3
Schizachyrium scoparium	C_4 grass	No	4	10.4 ± 1.2	54.4 ± 9.5
Solidago rigida	Perennial forb	Yes	4	13.1 ± 3.5	14.3 ± 4.1
Sorghastrum nutans	C_4 grass	No	4	8.5 ± 0.5	84.3 ± 9.1

Included are the functional type classifications for the species as commonly used at Cedar Creek LTER and whether a species has leaves that overwinter green. For each species, the standard error is based on the number of plots sampled that had leaf production during that period. Three to five individuals were sampled in each plot.

Calculation of leaf longevity

Since censuses did not begin until late June, longevities were calculated for an unextended data set, consisting of only the June–October measurement period, and an extended data set including an early-season census. The results of both these measurements were qualitatively similar ($r = 0.84$, $P < 0.001$) and we present only the results for the extended set. Because some species had produced most of their leaves before the first census date, we believe that the extended data set provides a truer estimate of leaf longevity. For those species whose leaves were assumed not to remain unsenesced through winter (winterbrown) (Table 1), the phenology observations provided a date of emergence at which it was assumed that individuals had neither green nor senesced leaves. All individuals had begun to grow by 13 May and we assumed that leaf production began on 6 May, using this date as the equivalent of the first census for all species except *Lespedeza capitata*, which did not emerge until 20 May. For those species that are assumed to have leaves that live through winter (wintergreen), we assumed that at the beginning of the growing season there were no senesced leaves and as many green leaves as at the end of the growing season. For the reasons already given, we did not count the green leaves on individuals of *R. serotina* and *A. repens*, assuming that individuals of these two species began the year with no green leaves.

Division of the total number of days lived by all leaves (leaf days) both born and senesced during the census period by the number of leaves both born and senesced during the census period gives the average longevity of these leaves. Using data on the total number or length of leaves present at each census, leaf longevity was determined by this equation:

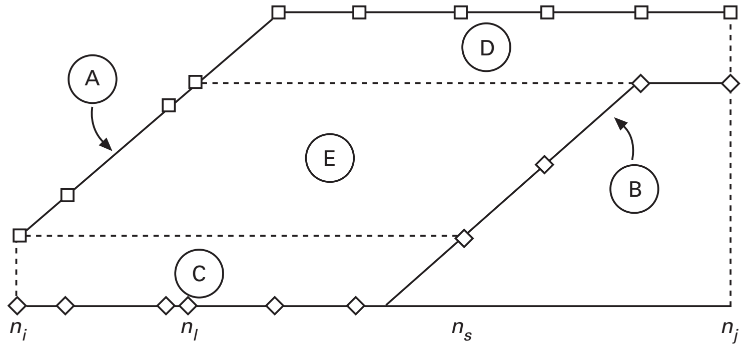
$$\left(\sum_{n=i}^{j}\left(\frac{L_{n+1}+L_n}{2}\right)\times k_n\right)- \qquad \text{Eqn 1a}$$

$$\left(\sum_{n=i}^{j}\left(\frac{S_{n+1}+S_n}{2}\right)\times k_n\right)- \qquad \text{Eqn 1b}$$

$$\left(((n_s-n_i)\times L_i)-\left(\sum_{n=i}^{s}\left(\frac{S_{n+1}+S_n}{2}\right)\times k_n\right)\right)- \qquad \text{Eqn 1c}$$

$$\left(((n_j-n_l)\times L_i)-\left(\sum_{n=i}^{j}\left(\frac{L_{n+1}+L_n}{2}\right)\times k_n\right)\right) \qquad \text{Eqn 1d}$$

($i =$ first census date, $j =$ last census date, $L_n =$ cumulative number or length of leaves observed or produced by census date n, $L_{n+1} =$ cumulative number or length of leaves observed or produced by the census following census n, $S_n =$ cumulative number or length of leaves senesced by census date n, $S_{n+1} =$ cumulative number or length of leaves senesced by the census following census n, $k_n =$ time interval between census n and $n+1$, $n_S =$ the date at which $S = L_i$, $n_l =$ the date at which $L = S_j$,and $n_s =$ the date at which $S = L_i$) The first two parts of the equation represent the total number of leaf days for all leaves tracked during the census, calculated as the difference between the total number of leaf days for total (Eqn 1a, Fig. 1A) and senesced leaves (Eqn 1b, Fig. 1B) and is equivalent to the area between the curves for the census period used. The second part of the equation (Eqn 1c, Fig. 1C) represents the number of leaf days for leaves that might have been present at the beginning of the census period, and the third part of the equation (Eqn 1d, Fig. 1D)



A: Cumulative total (green and senesced) leaf-days (Eqn 1a).
B: Cumulative senesced leaf-days (Eqn 1b).
C: Leaf-days of leaves that were present at the first sample period (birthdate unknown) (Eqn 1c).
D: Leaf-days of leaves that did not senesce within the census period (deathdate unknown) (Eqn 1d).
E: Leaf-days of leaves that were born and senesced within the census period.

Fig. 1. Calculation of average leaf and leaf length longevity of a species. Curve A represents the cumulative number of days that leaves (green or senesced) were observed (leaf days) during the census period (Eqn 1a). Curve B represents the total number of leaf days for senesced leaves (Eqn 1b). The difference between these two curves represents the total number of leaf days for unsenesced leaves. Area C represents the total number of leaf days for leaves that were present at the beginning of the census (birthdate unknown) (Eqn 1c). Area D represents the total number of leaf days for leaves that did not senesce during the census period (deathdate unknown) (Eqn 1d). Subtracting these two quantities from the difference between curves A and B provides the total number of leaf days for leaves that were both born and senesced within the census period (E). Dividing this by the total number (or length) of leaves in quantity E provides the estimate of leaf longevity, equivalent to the average horizontal distance of Area E. Also represented are the first (n_i) and last (n_j) census dates and the interpolated 'census dates' n_l and n_s (see text for details).

represents the number of leaf days for leaves that had not senesced by the end of the census period. These two quantities are subtracted from the total number of leaf days to provide the total number of leaf days for those leaves both born and senesced within the census period (Fig. 1E). Leaf longevity is equivalent to the average horizontal distance between the two curves. The dates n_l and n_s were calculated by a linear interpolation method based on the relevant census measures and dates. All analyses were computed with JMP-IN v. 3.1.5 for the Apple Macintosh (SAS Institute, Cary, NC, USA). Each plot served as a replicate for a species in determining the average longevity and standard error for a species. Differences between species and groups were determined by ANOVA.

RESULTS

Charts of the patterns of leaf production and mortality are contained in Fig. 2. Where senescent leaf values are equivalent to total leaf values, all tagged leaves had senesced. For example, *A. syriaca* had fully senesced by week 15 (Fig. 2). Wintergreen species, such as *Poa pratensis* and *Solidago rigida* are characterized by a difference in the total leaf and senescence values by the last census, whereas winterbrown species, such as *Desmodium canadense* are equivalent. Although the measurements for *Schizachyrium scoparium* show that at the last census date green leaves were still present, it is known not to be wintergreen and considered winterbrown in our statistical analyses. Similarly, *Rudbeckia serotina* and *Agropyron repens* are considered wintergreen although individuals present at the beginning of the growing season had no green leaves at the end of the year.

Estimates of leaf longevity for the different species of grass were 6.5–13.5 wk (Table 1). Estimates of longevity for forbs were 4.1–13.1 wk for the extended data set (Table 1). There were significant differences between species, yet no significant differences between any of the functional type classifications. The difference in leaf longevity between the grasses and forbs was 2–3 wk (10.6 wk and 7.9 wk, respectively; $P = 0.09$) (Table 2). There was no significant difference between wintergreen and winterbrown species (10.5 wk vs 7.9 wk; $P = 0.10$) (Table 2). There were also no significant correlations between the number of leaves (forbs) or length of leaves (grasses) and leaf longevity for either the unextended or extended data sets ($P > 0.3$ for all comparisons, data not shown).

DISCUSSION

Longevities of forbs observed in our experiment were similar to those recorded by Diemer *et al.* (1992), which ranged from 41 to 95 d, but the longevity of *Lupinus perennis* was *c.* 29 ± 6 d, less than that of any forb in that study. It is possible the apparently low leaf longevity of *L. perennis* might be a result of our assumption of the time of greening of the species. Yet extending the emergence date for the species to 2 wk earlier would only have increased the longevity measured by *c.* 5 d.

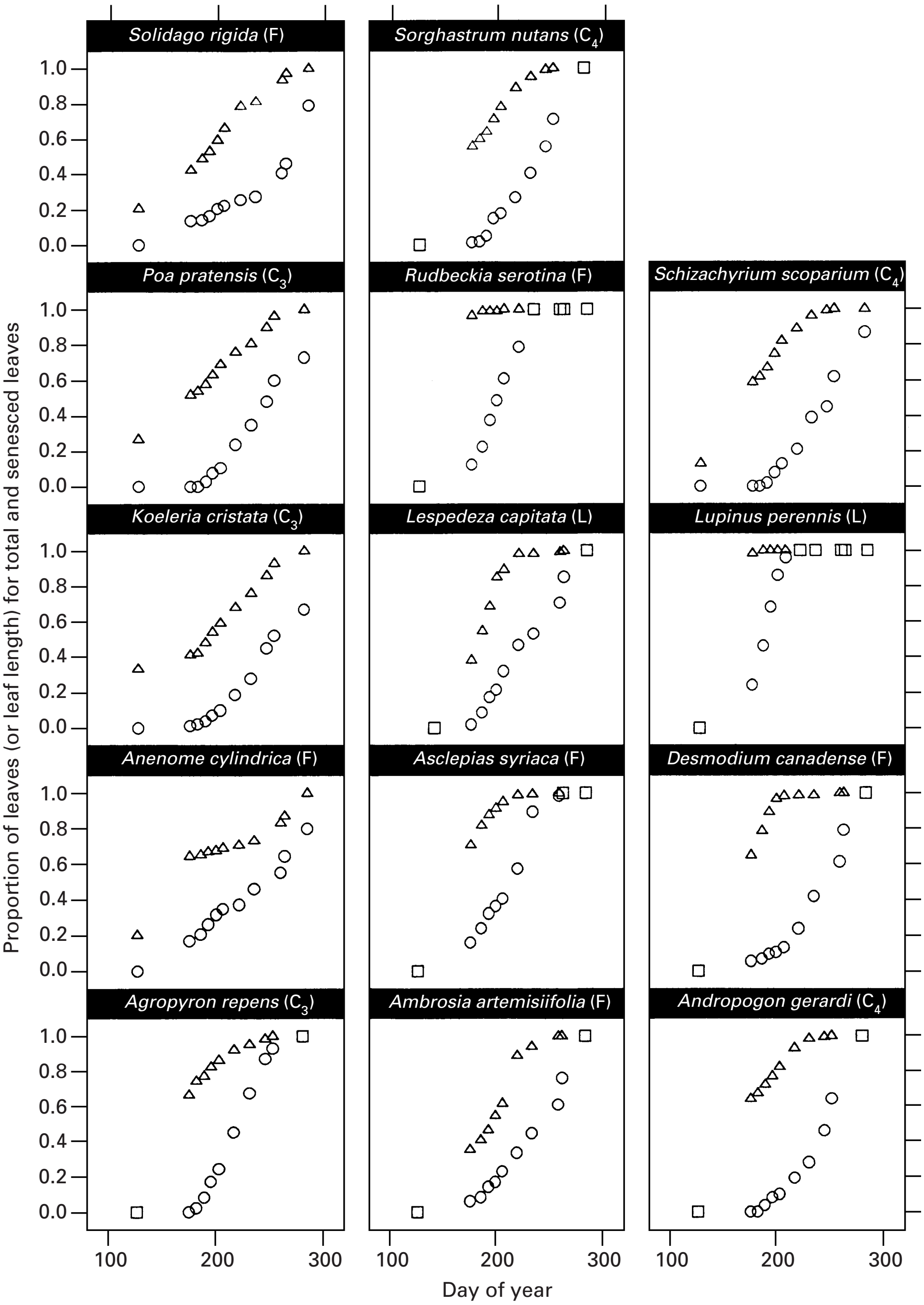


Fig. 2. Measured values for total (open triangle) and senesced (open circle) leaves averaged for all individuals in a plot for 14 species of forbs (F, L) and grasses (C_3, C_4); no leaves present or all leaves senesced (open square). These data were used for determining the leaf longevities in Table 1.

Sims & Coupland (1977) report that Coupland & Abougendia (1974) tracked leaves of *Agropyron dasystachyum* and categorized the leaves as 'dying from the tip', 'yellow', or 'brown'. The longevity of these leaves ranged from a few days to 4 wk, much lower than our estimates of grass longevity. Although we could not obtain the original reference and the authors were not explicit about the conditions for inclusion in these categories, it appears that these estimates are a form of individual leaf longevity and have been biased by the conditions for 'birth' and 'death' of leaves. Reanalysis of data presented in Sims & Coupland (1977) reveals that a given unit of grass length appears to have lived for approx. 1–2 months, closer to our estimate of longevity.

The longevities of leaves of grasses and forbs presented in Cornelissen & Thompson (1997) were approx. twice those in our study. Cornelissen & Thompson followed leaves from a 'recently emerged, but not fully expanded' state until full senescence. This method has the potential to exaggerate the longevity of a given length of leaf equivalent to the time of linear growth of the leaf, assuming that the longevity of a unit of length is

Table 2. *Mean leaf longevity for all species and the functional classifications*

	n	Mean ± SE	df	F ratio	P
C_3 grass	3	11.4 ± 1.9			
C_4 grass	3	9.7 ± 0.6	4	0.66	0.46
Non-leguminous forb	5	8.3 ± 2.9			
Legume	3	7.2 ± 3.2	6	1.3	0.63
Grass	6	10.6 ± 1.0			
Forb	8	7.9 ± 1.0	12	3.4	0.09
Wintergreen	6	10.5 ± 1.1			
Winterbrown	8	7.9 ± 1.0	12	3.1	0.10
All species	54	9.0 ± 2.2	13	6.5	<0.001

Also reported are the results of ANOVA's that compared all the average leaf longevity for the 14 species and different levels of functional type classification (C_3 grass, C_4 grass, non-leguminous forb, legume; grass, forb; wintergreen, winterbrown).

constant within a leaf. In comparing grasses and forbs, Cornelissen & Thompson (1997) found no difference in RGR and specific leaf area between grasses and forbs, yet longevity of grass leaves was *c.* 25% greater than that of forbs, although broadly similar in range. We observed that the length of grass leaves in our study extended for *c.* 25–33% of the entire life span of the leaves, equivalent to the difference in longevity measured by Cornelissen & Thompson (1997). This is a potential cause of the differences between the functional types in their study. Although we considered this source of bias in estimates of leaf longevity, leaf longevity of grasses in the species studied tended to be greater than that of forbs by a similar proportion. More work is necessary for an understanding of the bias associated with different measurement techniques and differences between floras in patterns of leaf longevity.

Our observations of leaf longevity in other fields at Cedar Creek revealed that leaves (and leaf biomass) of a species tended to live longer at other sites. The plots for the E111 experiment were established on soils of lower N availability than most of Cedar Creek (D. Wedin, unpublished). While there is good evidence for increased leaf longevity among species that inhabit less fertile sites (Monk, 1966; Escudero *et al.*, 1992; Reich *et al.*, 1992), there is also evidence of decrease in leaf longevity associated with nutrient stress (Turner & Olson, 1976; Fife & Nambiar, 1982). Further research is necessary to find whether this relationship between leaf longevities in the two classifications changes at different nutrient availabilities.

In some forbs, difference in the size of leaves produced at different stages of the season could skew the relation between the average longevity of a given leaf and the average longevity of a given unit of leaf area or biomass. For example, individuals of *Solidago rigida* begin as a basal rosette with large leaves that live longer than the smaller, more numerous leaves produced later in the season after the plant has bolted. Therefore, the average longevity of a leaf is less than that of a unit of leaf area or biomass, the more important measurement in resource cycling. Moreover, measurements of the longevity of leaves that might overwinter had been included, average leaf longevity would have been greater, but the average difference between forbs and grasses would not have been affected, because wintergreen species were well represented in both types.

It is common to consider grasses and forbs as different functional types (Lauenroth *et al.*, 1997; Tilman *et al.*, 1997), yet in grasses and forbs, leaf longevity, a key trait linking plant ecophysiology, whole-plant growth, and plant interaction with ecosystem resource cycling, was not significantly different. There ar two possible explanations of this similarity. First, grass leaves live longer (on average 34%) than forb leaves, which might be ecologically significant. The lack of statistical significance was simply a result of the small sample size (14 species). Second, there was greater than threefold variation in leaf longevity among the 14 species sampled, yet that of grasses and forbs only differed on average by *c.* 30%. Although the leaves of an average grass might consistently live longer than the leaves of an average forb, different functional classifications might be appropriate for maximum representation of variation in leaf longevity among species. A similar dual approach can be taken with alternative functional types, such as the wintergreen habit, or more specific functional type classifications such as C_3 and C_4 grass species and N-fixing and nonN-fixing forbs. Although it is possible that leaf longevity of forbs was reduced by seasonal patterns of leaf size or that leaves of forbs and grasses were differentially affected by the low-nutrient conditions of this study, the major differences in leaf longevity among species were not congruent with any current functional classification.

Although the species of two functional classifications do not necessarily differ in every trait, the importance of leaf longevity in C and nutrient dynamics of plants (Reich *et al.*, 1992, 1997) suggests that there should at least be functional classifications congruent with patterns of leaf longevity. Grasses and forbs are probably not the best functional classifications for this purpose: there are clear differences between species, but there are weak patterns between currently ascribed functional types. Further research is necessary to find whether factors such as tissue N (Reich *et al.*,1997) can better explain the patterns of leaf longevity described in this study and to delineate new classifications that encompass variation in leaf longevity.

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