Leaf life spans in wild perennial herbaceous plants: a survey and attempts at a functional interpretation

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Summary. Leaf longevity in 29 herbaceous plant species of Central Europe was studied by inspecting tagged leaves at weekly intervals. About half of the species are elements of the lowland meadow flora, the other half comprises a representative sample of species from the highest sites where vascular plants grow in the Alps. Shaded and water-stressed sites were avoided. Overall mean leaf longevity did not differ significantly between sites and amounted to 71 ± 5 days at low and 68 ± 4 days at high altitude. Leaf life spans ranged (with no clear altitudinal trend) from 41 to 95 days. Low-altitude forbs and grasses produced several leaf cohorts during their growth period, while most alpine species produced only one. Correlations were found between leaf duration and percent nitrogen content and carbon-cost/carbon-gain ratios, but not with leaf dry mass per unit leaf area and photosynthetic capacity alone. As leaf life spans increase, more C tends to be invested per unit CO_2 uptake and less N is invested per unit invested C. Thus, mass relationships rather than area relationships seem to be linked to leaf life span in these species, suggesting that leaf duration is associated with properties other than the efficiency of light utilization (e.g. mechanical strength, herbivory or pathogen resistance). It seems that the explanations of leaf duration that have been developed for evergreen/deciduous plants and for plants along steep light gradients do not apply to the variable life spans in leaves of perennial herbaceous plants of open habitats.

Key words: Altitude – Longevity – Nitrogen – Photosynthesis – Specific leaf area

Leaf construction costs, leaf metabolic activity and functional duration are the three determinants of a leaf's net carbon gain. Besides its influence on carbon gain, leaf duration encompasses a number of other significant functions. For instance, leaves represent a reserve pool for nutrients (Chapin et al. 1990); leaf longevity also determines the duration of soil coverage and mutual shading of neighbour plants, affects rainfall interception losses, soil moisture depletion, influences microbial and herbivory life in the canopy and is a key component of air pollution sensitivity of species and cultivars (Reich 1987). The significance of leaf life span is quite obvious when deciduous and evergreen plants are compared, and this field has received much attention in the literature (e.g. Larcher 1963; Schulze et al. 1977; Miller and Stoner 1979; Mooney and Gulmon 1982; Chabot and Hicks 1982; Karlsson 1985). Variations of leaf duration within deciduous woody and herbaceous plants, including grasses, are not so obvious, since they do not necessarily correspond to the length of periods favourable for growth in terms of temperature and moisture. Even under similar light regimes and adequate moisture and nutrient supply substantial interspecific differences in leaf longevity are found. This was documented by Koike (1988) for 30 deciduous woody species in Japan. In herbaceous species previous studies have addressed leaf longevity either in a demographic context (Bazzaz and Harper 1977; Peters 1980; Sydes 1984; Mitchley 1988) or as part of carbon balance considerations (Jurik 1983; Jurik and Chabot 1986). Here we intend to combine both approaches in an interspecific comparison.

The purpose of this paper was thus threefold: We wanted (1) to provide an overview of the range of leaf life spans in common grassland species, (2) to test whether these patterns change if comparable taxa from extreme high altitudes in the Alps are considered, and (3) to investigate relationships between leaf life spans and leaf properties such as photosynthetic capacity, dry matter and nitrogen investment per unit leaf area and tissue nitrogen concentration.

Material and methods

The study was conducted in the vicinity of Innsbruck (47° N 11° E, Austria) in 1987. However, additional data from subsequent years

are provided in some instances. Four species were also sampled in the subarctic environment in N Sweden (Abisko research station, 68° N, 19° E). We took care to select open and moist sites in order to avoid the confounding effects of shade or water stress on leaf life span (cf. Jurik and Chabot 1986). The lowland site (600 m) was a semi-natural fen, south of the village of Arzl, that was mowed at irregular intervals, but usually once in August. Growth of new leaves can occur at any time of the year, but the main growing period begins by late March and ends in November. During the study season the area was fenced and not mowed. A few additional species were investigated in a meadow and in weeded plots located in the Botanical Garden of the University of Innsbruck (same altitude and exposure). The mountain site (10 km SE of the lowland site) was situated at the upper alpine belt and included scree and rockfield communities near a permanent snowfield on Mt. Glungezer, 2600 m, Tuxer Alps, Tyrol. Both sites had the same general weather pattern. Mean daytime air temperatures during the growth period in 1987 (April to mid-June at low altitude and June to mid-September at high altitude) were 15.3° C at 600 m and 5.5° C at 2600 m elevation. Monthly means of air temperature and precipitation during 1987 generally lie within 1–2 K of long term records for Innsbruck (Fliri 1975), with the exception that the mean for May 1987 was 2.8 K below average (low temperatures at the beginning of the month). Further details of the climate and experimental plants of the two areas are described by Körner and Diemer (1987) and Bahn and Körner (1987). Taxonomic nomenclature follows the Flora Europaea check list (Moore 1982).

Determination of leaf life spans roughly followed the procedure described by Bazzaz and Harper (1977). Leaves from about 10 individuals per species were observed from the time of appearance ("birth") until death throughout a full season. As soon as leaves attained a length of approximatively 5 mm at high and 10 mm at low altitude, coloured loops of telephone wire (diameter 0.6 mm) where placed around the petioles for identification. Loops were wide enough to permit further petiole expansion without constraints. At weekly intervals each leaf was inspected and its length and overall appearance were recorded. For the purpose of this analysis, whenever possible, leaves that arose concurrently were grouped into discrete cohorts. Although the number of leaves per cohort varies according to the number of individual plants censored and the number of leaves subject to herbivory or mechanical damage, the frequency of observations in Table 1 roughly represents the number of leaves produced within a given ground area and a particular time period. Hence, mean leaf life span, calculated for the period considered here, incorporates the range of observed leaf longevities as well as their relative abundance during the months

covered by the survey. Since the time between the onset of senescence and final leaf death is quite variable, the end of the functional life span was defined here as the age when more than 25% of the leaf blade was chlorotic (yellow) or 10% necrotic (senescence-induced). Total life span, which includes full senescence (i.e. 100% necrosis or leaf abscission), is on average 10–30 days longer than the functional life span defined and employed here. Leaf death and damage by herbivores were recorded, but such leaves were disregarded for the present purpose. Likewise individuals that lost part of their leaves to herbivores were excluded. Leaves which did not complete their life cycle within the growth period, i.e. overwintering leaves, were also excluded. The total number of leaves whose life history entered the statistics was 297 at low and 192 at high altitude (ca. 5000 records in total). In some of the high-altitude species we missed the first leaves that flushed prior to or during snow-melt. Thus, we may have underestimated life spans by several days (e.g. in *Polygonum, Pedicularis, Ranunculus*). Surprisingly the time period between birth of a leaf and full expansion of the lamina did not vary significantly with altitude. The mean expansion times for all species were 27 ± 2 days at low and 29 ± 3 days at high altitude, although final leaf size differed by a factor of 10 (Körner et al. 1989). Thus, the life spans reported here are roughly proportional to the life span of fully expanded leaves at both sites.

Data for leaf nitrogen content (Kjeldahl), specific leaf area and photosynthetic capacity (maximum rate of net photosynthesis at ambient CO_2 partial pressure per unit projected leaf area) were obtained from studies conducted on the same species and sites between 1985 and 1988 (Körner and Diemer 1987; Körner et al. 1989; Körner 1989; Körner and Pelaez Mendendez-Riedl 1989, Diemer 1990). Since these data were gathered in similar screening efforts, thus including numerous individuals and leaves, they are assumed to be representative for the purposes of present survey. However, some of the interspecific variation in the correlations given here may be associated with intraspecific variations introduced by the combination of these data sets.

Results

The mean leaf life span of the species investigated was 71 ± 5 days at low and 68 ± 4 days at high altitude, and not significantly different ($P = 0.64$, t-test). Mean leaf life spans of the individual species ranged from 41 to 95 days irrespective of elevation (Tables 1 and 2). Life spans

Table 1. Leaf life span of herbaceous plants at low altitude (Innsbruck, 600 m, means in days ± SE, number of leaves per cohort in brackets)

Plant species	Site	Mean leaf life span (n)	Life span for leaves of various cohorts			
			March	April	May	June
Achillea millefolium	A	42 ± 3 (12)	44 ± 3 (10)	35 ± 4 (2)	–	–
Ranunculus acris	A	55 ± 2 (44)	59 ± 3 (15)	50 ± 4 (20)	–	–
Potentilla anserina	B	57 ± 2 (27)	–	52 ± 3 (6)	51 ± 3 (17)	80 ± 3 (4)
Trifolium repens	B	61 ± 3 (17)	48 ± 2 (5)	65 ± 3 (12)	–	–
Carum carvi	B	61 ± 1 (28)	58 ± 2 (11)	65 ± 1 (17)	–	–
Chrysanthemum leucanthemum	A	66 ± 3 (5)	66 ± 3 (5)	–	–	–
Taraxacum officinale s.l.	B	66 ± 2 (41)	65 ± 2 (29)	74 ± 3 (8)	61 ± 3 (8)	60 ± 8 (5)
Bellis perennis	B	75 ± 3 (23)	90 ± 4 (3)	81 ± 2 (15)	49 ± 4 (5)	–
Caltha palustris	A	78 ± 4 (18)	68 ± 4 (8)	88 ± 5 (9)	78 (1)	–
Plantago lanceolata	A	83 ± 3 (22)	84 ± 5 (7)	89 ± 5 (9)	73 ± 6 (4)	73 ± 12 (2)
Geum rivale	A	87 ± 3 (18)	81 ± 5 (13)	101 ± 5 (5)	–	–
Primula elatior	A	94 ± 3 (25)	97 ± 3 (22)	70 ± 5 (3)	–	–
Luzula campestris	A	95 ± 4 (17)	–	94 ± 4 (15)	105 ± 0 (2)	–
Mean ± SE (no. of species)		71 ± 4 (13)				

A Seminatural fen community
B Meadow (Botanical Garden)

Table 2. As Table 1 but for high altitude (Mt. Glungezer, 2600 m)

Plant species	Mean leaf life span (n)	Life span for leaves of various cohorts		
		June	July	August
Polygonum viviparum	41 ± 8 (6)	–	41 ± 8 (6)	–
Oxyria digyna	48 ± 3 (14)	–	48 ± 4 (12)	48 ± 15 (2)
Doronicum clusii	54 ± 4 (11)	42 ± 3 (5)	65 ± 4 (6)	–
Luzula alpino-pilosa	58 ± 2 (24)	–	60 ± 2 (18)	51 ± 3 (6)
Bartsia alpina	59 ± 4 (6)	–	66 ± 3 (3)	52 ± 6 (3)
Pedicularis asplenifolia	61 ± 1 (9)	–	61 ± 1 (9)	–
Geum montanum	64 ± 5 (6)	–	64 ± 5 (6)	–
Taraxacum alpinum	66 ± 4 (13)	–	66 ± 4 (13)	–
Achillea erba-rotta	70 ± 4 (10)	–	70 ± 4 (10)	–
Potentilla crantzii	73 ± 3 (22)	72 ± 4 (16)	76 ± 3 (6)	–
Primula glutinosa	76 ± 4 (12)	92 ± 6 (3)	70 ± 4 (8)	57 ± 4 (2)
Ligusticum mutellina	77 ± 4 (5)	–	77 ± 4 (5)	40 ± 7 (4)
Erigeron uniflorus	78 ± 2 (9)	–	78 ± 2 (9)	–
Leucanthemopsis alpina	80 ± 6 (5)	–	80 ± 6 (5)	–
Geum reptans	91 ± 2 (22)	91 ± 2 (22)	–	–
Ranunculus glacialis	93 ± 4 (18)	95 ± 4 (14)	82 ± 8 (4)	–
Mean ± SE	68 ± 4 (16)			

Table 3. Comparison of leaf life spans of temperate zone and sub-arctic zone populations of herbaceous perennial species (means ± SE, number of leaves in brackets)

	Temperate zone		Subarctic zone	
Low altitude species:				
Ranunculus acris	55 ± 2	(44)	85 ± 7	(8)
Geum rivale	87 ± 3	(18)	83 ± 2	(13)
High altitude species:				
Ranunculus glacialis	93 ± 4	(18)	72 ± 3	(11)
Potentilla crantzii	73 ± 3	(22)	74 ± 4	(5)

varied within species as well. Leaf cohorts which emerged during the middle of the main growth period tended to have slightly longer life spans than those of earlier or subsequent cohorts, but in a few cases the reverse was observed. Leaf longevity determined for some species in the following year (1988) fluctuated by up to 10 days compared to 1987 at low altitude. The alpine *Ranunculus glacialis* and *Geum reptans* attained life spans 20 days longer in 1988 as result of earlier snow melt.

A comparison of leaf life spans of *Ranunculus acris* and *Geum rivale* from the natural fen habitat with individuals that were maintained in weeded plots in garden soil of the Botanical Garden showed that rich soil and the absence of competition decreased life spans by only 12%. Within the same period the weeded individuals produced on an average 72% more leaves, thus suggesting that the rate of leaf initiation is more sensitive to such environmental variations than leaf duration. The leaf life spans of these and two alpine species obtained in N. Sweden (1989) are listed in Table 3. While leaves of *Geum rivale* and *Potentilla crantzii* achieved similar life spans, those of *Ranunculus acris* lasted substantially longer in the Subarctic than in Central Europe. The 20-day shorter life span of *Ranunculus glacialis* in the arctic-alpine zone is
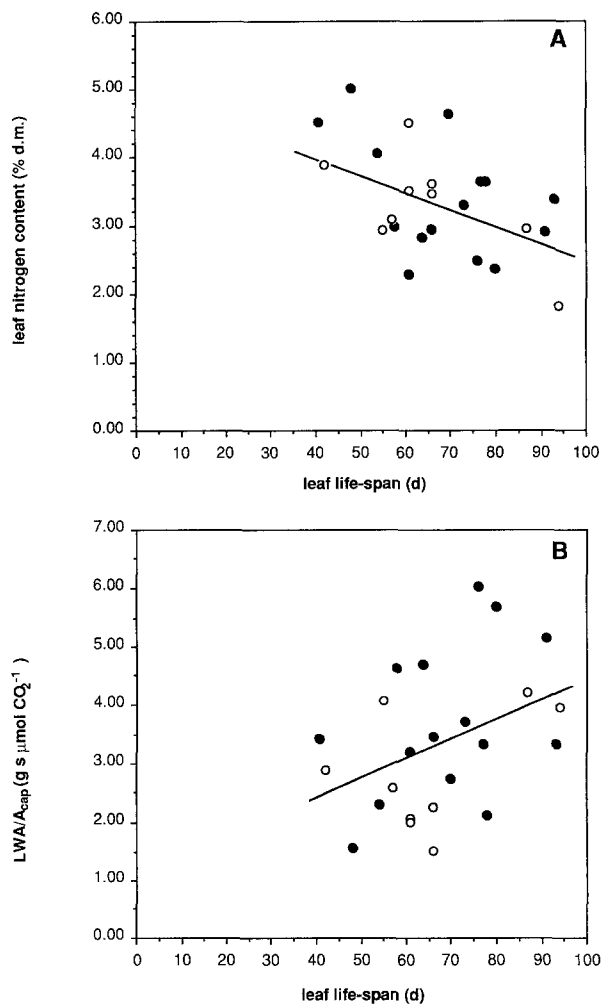

Fig. 1A, B. Linear regression of the relationship between leaf longevity and **A** nitrogen content on a weight basis (% d.w.) and **B** the ratio of dry matter investment per unit leaf area and photosynthetic capacity (LWA/A_{cap}). Low elevation species are shown as *open symbols*, while alpine taxa are depicted as *closed symbols*. Regression parameters are presented in Table 4

Table 4. Leaf life span and leaf properties for a subsample of the species listed in Table 1 and 2

Plant species	Longevity (d)	LWA (g m^{-2})	Nitrogen content (% d.m.)	Nitrogen content (mmol m^{-2})	A_{cap}[a]	LWA/A_{cap}[b]
Low altitude:						
A.m.	42	51.8	3.88	193	17.9	2.89
R.a.	55	65.4	2.93	–	16.1	4.06
P.a.	57	52.3	3.09	116	20.2	2.59
T.r.	61	33.9	4.50	109	16.3	2.08
C.c.	61	37.9	3.50	95	19.0	1.99
C.l.	66	51.6	3.46	156	22.8	2.26
T.o.	66	34.4	3.60	81	22.7	1.51
C.p.	78	32.4	–	–	–	–
G.r.	87	52.6	2.96	91	12.5	4.21
P.e.	94	42.3	1.82	54	10.7	3.96
High altitude:						
P.v.	41	69.0	4.51	193	20.2	3.41
O.d.	48	25.4	5.00	129	16.4	1.55
D.c.	54	48.8	4.04	141	21.1	2.31
L.a.-p.	58	68.0	2.98	145	14.7	4.63
P.a.	61	64.5	2.27	136	20.2	3.19
G.m.	64	69.9	2.81	175	14.9	4.69
T.a.	66	36.5	2.94	77	10.6	3.44
A.e.	70	45.0	4.62	168	16.4	2.75
P.c.	73	60.6	3.28	168	16.4	3.70
P.g.	76	74.1	2.47	139	12.3	6.02
L.m.	77	79.4	3.62	200	23.9	3.32
E.u.	78	47.6	3.63	138	22.5	2.12
L.a.	80	62.5	2.36	111	11.0	5.68
G.r.	91	70.4	2.89	152	13.7	5.14
R.g.	93	64.5	3.37	173	19.4	3.32

[a] A_{cap} μmol m^{-2} s^{-1}; [b] LWA/A_{cap} g s μmol^{-1}

Statistical data:
Dependent variable: mean leaf life span (Spearman rank correlation)

Independent variable	r	R^2	n	P	sign.
LWA	0.09	0.01	25	0.336	n.s.
N (% d.m.)	−0.45	0.20	24	0.043	*
N (mmol m^{-2})	−0.17	0.03	23	0.228	n.s.
A_{cap}	−0.29	0.08	24	0.086	n.s.
LWA/A_{cap}	0.38	0.14	24	0.034	*

Linear regression: $y = a+b$ (life span), see Fig. 1

y	a	b	R^2	P of b	sign.
N (% d.m.)	5.23	−0.03	0.28	0.004	**
LWA/A_{cap}	1.05	0.03	0.17	0.020	*

* $P \leq 0.05$, ** $P \leq 0.01$, n.s. not significant

associated with the later date of snow melt in its northerly habitat.

In an effort to explain the variation in leaf life span, we attempted to correlate it with various leaf properties (Table 4). Leaf life spans correlate significantly with percent leaf nitrogen content when high-and low-altitude data sets are combined ($P = 0.043$, Spearman rank test, Fig. 1A). Neither photosynthetic capacity (on an area basis, A_{cap}) nor leaf weight per area (LWA) are significantly correlated with longevity. The ratio of dry matter investment per unit leaf area and photosynthetic capacity (carbon cost/gain ratio) is correlated with leaf life span ($P = 0.034$), although the relationship is weaker than with percent nitrogen content (Fig. 1B). If data sets are segregated according to altitudinal origin, these significant relationships disappear. Only nitrogen content, on an area basis, is significantly correlated to leaf life span in a subsample of lowland taxa ($P = 0.013$, $n = 8$). Restriction of the data set to only the April cohort, when most leaf properties were determined, does not change results of the analysis appreciably. In the high-elevation group leaf longevity is not correlated with any of the leaf properties included.

Discussion

The results of this survey show that leaves of common herbaceous perennials generally function for 2–2.5 months. Since lamina expansion requires on average 27–29 days, leaves from both high and low altitudes function for about 60% of their life span (according to our definition) while fully expanded. The 1988 data indicate that some high-altitude specialists can initiate growth at various dates depending on snow melt, but senescence occurs roughly at the same time. Hence longer life spans occur in years with an early spring. Mountain plants keep those leaves that are produced active for approximatively the same period of time as lowland plants, but do not produce additional cohorts. Exceptions are members of the Rosaceae *(Geum, Potentilla)* that show continuous production of new leaves even towards the end of the season. Some of these leaves overwinter and complete their growth in the next year (not included in this analysis). Since no altitudinal trends in leaf longevity were observed, we will now concentrate on interspecific differences.

Comparisons of leaf longevity with literature data are

difficult, due to variations in the definition of leaf death and in measurement intervals. We observed that the period between the onset of decay (necrosis) and death or abscission is extremely variable and weather-dependent. The inclusion of this part of the leaf life span thus masks species-specific behaviour, when leaf longevity is viewed in connection with leaf carbon gain. If the total turgid life span (including the chlorotic phase) is considered, our data for *Ranunculus acris* (65 ± 3 days, not shown in Tables) roughly correspond to those obtained by Peters (1980). Total leaf life span of *R. acris* measured by Peters decreased from 55 days in March cohorts to only 32 in May cohorts. Schmid (1985) investigated the dynamics of *Bellis perennis* leaves in a permanent pasture. Mean total life spans of 90 days (March cohorts) and 55 (June) determined in Wales are in agreement with our findings (94 ± 4 days for March and 57 ± 5 for May cohorts). Although leaf longevity of English limestone grassland species was quite variable, Sydes (1984) concluded that most leaves produced between April and July had half-lives (time until 50% of leaves were dead) of approximately 65 days. Mitchley (1988) determined half-lives of 75–143 days in a similar dry grassland. These results suggest that life spans of leaves of herbaceous plants in water-stressed pastures may be longer than those of the non-water stressed communities investigated here. Leaf life span of *Fragaria virginiana* varies between 55 and 150 days (Jurik and Chabot 1986).

Fast growing agricultural crops tend to have shorter leaf life spans. For example, Hodanova (1981) reports spans of 17–67 days for *Beta vulgaris* cv. and values from 27 to 60 days are reported for wheat (e.g. Maillette 1986; Van Keulen et al. 1989).

Considering the subsample of 24 species included in Table 4, neither carbon investment per unit leaf area (leaf weight per leaf area), nor nitrogen per unit leaf area seem to play a significant role in connection with longevity of leaves of these species. In the high altitude group, this may be related to the generally high levels of nitrogen and mineral nutrients in the leaves (Körner 1989), which were explained by limited nutrient dilution due to developmental constraints rather than carbon limitation of plant growth (Körner 1989; Körner and Pelaez Menendez-Riedl 1989). The correlation of leaf life span with N content per unit dry matter rather than N and C investments per unit leaf area or photosynthetic capacity (all of which are co-determined by mesophyll thickness) may indicate that leaf duration is associated with tissue qualities which are not directly linked to assimilatory potential. Food quality for herbivores has many times been stated to correlate with mean leaf life expectancy (e.g. Mooney and Gulmon 1982). Southwood et al. (1986) showed a strong correlation between the life expectancy of a leaf and its palatability to insect herbivores. Their results are not directly comparable to our data, since we excluded leaves subject to herbivory, but our field observations at the alpine site intuitively support these findings: the alpine *Oxyria digyna*, with a mean life span of only 48 days and N content of almost 5% was heavily damaged by snow mice *(Microtus nivalis)*, while the

long-lived leaves of Rosaceae species of the same area with low N contents were never touched. However, without information concerning chemical defence, such interpretations remain speculative.

Perhaps we would have found stronger correlations between gas exchange properties and leaf life span if the integrated life span carbon gain under the real light conditions of individual leaves was known. These parameters, however, tend to be autocorrelated. From their work in tropical *Piper* species that occupy different positions along a steep light gradient, Williams et al. (1989) concluded that only the ratio of carbon cost to carbon gain is a meaningful determinant of leaf life span when species of contrasting ecology are compared. We have only instantaneous cost/maximum gain ratios, but the correlation with leaf duration (although not studied along a light gradient) seems to support this hypothesis. The greater the dry matter (carbon) investment per unit of photosynthetic capacity, the greater the life span. This relationship holds only if dry matter investment in leaf structure is not inherently linked to leaf longevity.

Hypotheses that suggest a relationship between leaf carbon gain and longevity employ lifetime carbon gain as the independent variable. Harper (1989) suggests that carbon returns to a plant may be maximized at an early age, i.e. within a brief portion of the entire (or functional) life span. Control of leaf longevity in this case would be closely attuned to patterns of leaf growth (determinate vs. indeterminate) or mineral nutrition. An example of the latter is the increase in leaf turnover within individuals of the same species, when reallocation of resources from shaded to sunlit plant parts is required under light competition in growing stands with closed canopies, as illustrated by Hirose and Werger (1987). In our survey competition for light did occur at low altitude, but was negligible at high altitude, which may explain why a trend of life span with N per area exists among a subsample of the low-altitude species, but not at high altitude. On the other hand, life spans were not different between the two groups, hence the light effect could not have been very pronounced.

Although growth rate was not studied here, our data intuitively suggest that leaf duration declines with increasing vigor of growth of a species (with some exemptions). It is known that intraspecific variations in growth rate are accompanied by variations in leaf turnover. This is also supported by the increased leaf turnover that we found in lowland *Ranunculus* and *Geum* when vigorously growing in isolation on garden soil, compared to the meadow community. Lower leaf life spans as a result of fertilizer treatment were observed by several authors (e.g. Shaver 1983; Körner 1984; Karlsson 1985) and similar observations were obtained in many other experiments. The survey of deciduous woody species by Koike (1988) is particularly illustrative in this respect. He found a clear trend of decreasing life span under fertilizer treatment. In the insectivorous *Drosera*, however, leaf longevity is positively related to plant nutrition (Schulze and Schulze 1990).

The obvious difficulties we had in detecting significant

functional relationships between duration and quality of leaves within that large group of species may also reflect the conceptual weakness of our traditional views of optimization theory that focus primarily on growth and (carbon) budgets. Fitness in the sense of genetic persistence in space and time may be achieved along very different routes. Persistence is a quality not necessarily related to the most efficient utilization of certain resources, which is the paradigm under which leaf function is commonly seen – unless light, moisture or the duration of the growth period significantly impair carbon gain (cf. Schulze et al. 1977; Jurik and Chabot 1986; Williams et al. 1989). Data from Diemer (1990) indicate that the success of herbaceous plants at very high altitudes is possibly not related to their leaf carbon budgets. Körner and Pelaez Menendez-Riedl (1989) examined the developmental constraints that become predominant under such conditions.

Conclusions

The overall impression drawn from this survey is that environmental changes associated with an altitudinal increase of 2000 m do not appear to alter patterns of leaf life spans of the herbaceous species that commonly grow at these elevations. In addition, climatic differences between Central Europe and the sub-arctic zone do not fundamentally alter leaf duration. Compared to the interspecific variation in leaf life span, the differences between field- and garden-grown individuals of the same species are also relatively small. Thus, genetic control of leaf life span seems to be stronger than effects induced by these environmental differences. At least for the environmental conditions encountered here, leaf duration, unlike the rate of leaf initiation, is a relatively conservative parameter and strongly species-specific.

Leaf longevity appears to respond more slowly than structural or metabolic parameters (e.g. LWA, photosynthetic capacity or nitrogen content). Hence correlations between these functional attributes and life span are likely to take effect only when limitations are imposed that are drastic enough to influence leaf longevity. For example, under light limitation longevity increases concurrently with SLA while photosynthetic capacity and N content decline. If light-versus shade-adapted plants are compared (as with *Piper* by Williams et al. 1989) then correlations between life span and carbon gain rates are likely to be found.

Here we studied leaves representing a common life form, namely herbaceous taxa, that were neither water, shade, nor nutrient-stressed. We found no correlation between life span and leaf costs in terms of nitrogen or carbon per unit area, or photosynthetic capacity. On a mass basis we find significant correlations both with nitrogen content and carbon cost versus carbon gain. We take that as an indication that – within a certain range of life forms and leaf morphotypes – leaf longevity is more likely to be related to properties such as herbivore pressure, stress resistance or intraplant requirements for

resource allocation (growth rate, reproductive strategy), than to the efficiency of light utilization and associated plant processes. The results of this study question the validity of a general theory of leaf duration.

References

Bahn M, Körner Ch (1987) Vegetation und Phänologie der hochalpinen Gipfelflur des Glungezer in Tirol. Ber Nat-Med Ver Innsbruck 74:61–80

Bazzaz FA, Harper JL (1977) Demographic analysis of the growth of *Linum usitatissimum*. New Phytol 78:193–208

Chabot BF, Hicks DJ (1982) The ecology of leaf life spans. Annu Rev Ecol Syst 13:229–259

Chapin FS, Schulze ED, Mooney HA (1990) The ecology and economics of storage in plants. Annu Rev Ecol Syst 21:423–447

Diemer MW (1990) Die Kohlenstoffbilanz von Blättern krautiger Pflanzen aus dem Hochgebirge und der Niederung. PhD thesis, Univ Innsbruck

Fliri F (1975) Das Klima der Alpen im Raume von Tirol. Univ Verlag Wagner, Innsbruck

Harper JL (1989) The value of a leaf. Oecologia 80:53–58

Hirose T, Werger MJA (1987) Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. Oecologia 72:520–526

Hodanova D (1981) Photosynthetic capacity, irradiance and sequential senescence of sugar beet leaves. Biol Plant (Prag) 23:58–67

Jurik TW (1983) Reproductive effort and dynamics of wild strawberry populations. Ecology 64:1329–1342

Jurik TW, Chabot BF (1986) Leaf dynamics and profitability in wild strawberries. Oecologia 69:296–304

Karlsson PS (1985) Effects of water and mineral nutrient supply on a deciduous and an evergreen dwarf shrub: *Vaccinium uliginosum* L. and *V. vitis-idea* L. Holarct Ecol 8:1–8

Koike T (1988) Leaf structure and photosynthetic performance as related to the forest succession of deciduous broad-leaved trees. Plant Spec Biol 3:77–87

Körner Ch (1984) Auswirkungen von Mineraldünger auf alpine Zwergsträucher. Verh Ges Ökol 12:123–136

Körner Ch (1989) The nutritional status of plants from high altitudes. A worldwide comparison. Oecologia 81:379–391

Körner Ch, Diemer M (1987) In situ photosynthetic responses to light, temperature and carbon dioxide in herbaceous plants from low and high altitude. Funct Ecol 1:179–194

Körner Ch, Pelaez Menendez-Riedl S (1989) The significance of developmental aspects in plant growth analysis. In: Lambers H et al. (eds) Causes and consequences of variation in growth rate and productivity of higher plants. SPB Acad Publ, The Hague, pp 141–157

Körner Ch, Neumayer M, Pelaez Menendez-Riedl S, Smeets-Scheel A (1989) Functional morphology of mountain plants. Flora 182:353–383

Larcher W (1963) Die Leistungsfähigkeit der CO_2-Assimilation höherer Pflanzen unter Laboratoriumsbedingungen und am natürlichen Standort. Mitt Florist-Soziol Arbeitsgem N.F. 10:20–33

Maillette L (1986) Canopy development, leaf demography and growth dynamics of wheat and three weed species growing in pure and mixed stands. J Appl Ecol 23:929–944

Miller PC, Stoner WA (1979) Canopy structural and environmental interactions. In: Solbrig OT et al. (eds) Topics in plant population biology, Columbia Univ Press, New York, pp 428–458

Mitchley J (1988) Control of relative abundance of perennials in chalk grassland in Southern England. III. Shoot phenology. J Ecol 76:607–616

Mooney HA, Gulmon SL (1982) Constraints on leaf structure and function in reference to herbivory. BioScience 32:198–206

Moore DM (1982) Flora Europaea check-list and chromosome index. Cambridge Univ Press, Cambridge

Peters B (1980) The demography of leaves in a permanent pasture. PhD thesis, Univ of Wales

Reich PB (1987) Quantifying plant response to ozone: a unifying theory. Tree Physiol 3:63–91

Schmid B (1985) Clonal growth in grassland perennials. II. Growth form and fine-scale colonizing ability. J Ecol 73:809–818

Schulze ED, Fuchs M, Fuchs MI (1977) Spatial distribution of photosynthetic capacity and performance in a mountain spruce forest of Northern Germany. Oecologia 30:239–248

Schulze W, Schulze ED (1990) Insect capture and growth of the insectivorous *Drosera rotundifolia* L. Oecologia 82:427–429

Shaver GR (1983) Mineral nutrition and leaf longevity in *Ledum palustre:* the role of individual nutrients and the timing of leaf mortality. Oecologia 56:160–165

Southwood TRE, Brown VK, Reader PM (1986) Leaf palatability, life expectancy and herbivore damage. Oecologia 70:544–548

Sydes CL (1984) A comparative study of leaf demography in limestone grassland. J Ecol 72:331–345

Van Keulen H, Goudriaan J, Seligman NG (1989) Modelling the effects of nitrogen on canopy development and crop growth. In: Russell G, Marshall B, Jarvis PG (eds) Plant canopies: their growth, form and function. (soc Exp Biol Sem Ser 31) Cambridge Univ Press, pp 83–104

Williams K, Field CB, Mooney HA (1989) Relationships among leaf construction cost, leaf longevity, and light environment in rain-forest plants of the genus *Piper*. Am Nat 133:198–211