OIKOS 98: 308–322, 2002

How perennial are perennial plants?

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Ehrlén, J. and Lehtilä, K. 2002. How perennial are perennial plants? – Oikos 98: 308–322.

Trade-offs involving life span are important in the molding of plant life histories. However, the empirical examination of such patterns has so far been limited by the fact that information on life span is mainly available in terms of discrete categories; annuals, semelparous perennials and iteroparous perennials. We used transition matrix models to project continuous estimates of conditional life spans from published information on size- or stage-structured demography for 71 perennial plant species. The projected life span ranged from 4.3 to 988.6 years and more than half of the species had a life span of more than 35 years. Woody plants had on average a projected life span more than four times as long as non-woody plants. Life spans were higher in forests than in open habitats and individuals of non-clonal species tended to have a longer life span than ramets of clonal species. Self-incompatible plants on average lived longer than self-compatible plants. There were no clear relations between life span and geographical region, dispersal syndrome, pollination mode, seed size or the presence of a seed bank. We conclude that accurate estimates of life span are central to understand how longevity is correlated to other traits within the group of perennial plants.

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Longevity is a fundamental component of life histories (Roff 1992, Stearns 1992). The realized life span of an organism depends on the environment, on the particular set of traits that the organism possesses, and how these traits change with age. In plants, estimates of maximum longevity range from a few weeks in some annuals to over 1000 years in many conifers and clonal plants (Molisch 1938, Schulman 1958, Wangermann 1965, Ogden 1978, Leopold 1980, Cook 1983, Noodén 1988, Bender et al. 2000). Whereas some plant species have extreme maximum life spans (Leopold 1980, Watkinson and White 1985, Noodén 1988, Pedersen 1999), semelparous plants constitute dramatic examples of rapid senescence (Watkinson 1992, Pedersen 1999). Moreover, closely related species often have different patterns of senescence (Wangermann 1965, Roach 1993).

In the absence of any constraints, individuals should act to increase their fitness by developing traits that maximize their longevity, given that older plants continue to produce seeds. However, there are several reasons why we should expect that other traits, which are important fitness components, should decrease life span (Williams 1957, Blarer et al. 1995). For example, reproduction early in life may exhaust the resources of an organism, thereby making it more prone to stress-related sources of mortality. In plants, several consequences of such trade-offs have been suggested (Eriksson 1996, Ehrlén and van Groenendael 1998). Clonal growth and a long life span of physiological individuals constitute alternative strategies for genet survival. Provided that there are some costs associated with ramet longevity, we would therefore expect ramets of clonal species to have a shorter life span than individuals of non-clonal species. Similarly, persistence of genetic individuals can be achieved either by a long life span of established individuals or by a long-lived seed bank. Rees (1993, 1996) found that for herbaceous

Accepted 8 March 2002

ISSN 0030-1299

species, seed dormancy was inversely correlated to longevity in the non-seed phase. At the gene level, maintenance can be secured either by persistence of established individuals or by sexual reproduction. Short-lived species are more dependent than more long-lived species on a reproductive system that ensures some reproduction every year. Life-history traits that increase the risk of reproductive failure, such as self-incompatibility or unpredictable pollination service systems, are therefore not expected among short-lived plants (Frankel and Galun 1977, Sutherland 1986). In a spatial context, persistence can be achieved either by survival at one site or by dispersal to other sites. If dispersal is costly we would thus expect species that have morphological or chemical attributes that favor dispersal to have a shorter life span. Empirical evidence appears to be contradictory and there is support for a negative (Grime et al. 1988), a positive (Venable and Levin 1983) and no (Rees 1993) correlation between life span and dispersal ability. It is important to recognize that the trade-offs discussed above refer to the level of genetic individuals and the arguments do not necessarily apply to ramets of clonal plants.

Trade-offs between life span and other plant traits have been examined empirically primarily by comparative studies. One severe limitation with such studies is that they have only considered the discrete differences in life span between annuals, biennials (semelparous perennials) and iteroparous perennials (Venable and Levin 1983, Fitter 1986, Grime et al. 1988, Wilson and Thompsson 1989, Rees 1993). This is problematic because the category "perennials" is likely to entail a variation in longevity that is at least as large as the range of variation within many animal groups, such as birds and mammals. Similarly, we know that "biennials" include considerable variation in longevity (van der Meijden et al. 1992). Estimates of life span in plants that go beyond the simple classification into annuals, biennials and perennials come primarily from trees where counting of the number of annual growth rings is a convenient way to determine age. For perennial herbs evidence is limited and estimates of life spans are usually based on counting of scars on perennial rootstocks (Flamm 1922, Garcia and Antor 1995), long-term studies (Inghe and Tamm 1985), and examinations of clonal size and growth (Oinonen 1967, Cook 1983).

In contrast to the scarcity of information on plant life spans there is an increasing body of information on stage-structured demography, in particular for perennial herbs. Demographic models usually use size categories instead of age classes as stages, since size is often a far better predictor of the future survival and reproduction rates of plants than age (Menges 2000). Although plant demographic studies have mainly focused on size or reproductive stage rather than age, the accumulating demographic data could be used to increase our knowledge about the life spans of perennial plants. This is because age is implicit in stage-structured models (Cochran and Ellner 1992). Cochran and Ellner suggested methods to derive age-based measures from stage-structured models. The analysis of demographic data would thus provide a basis for testing relationships between life span and other traits also within perennials. Franco and Silvertown (1996) used such methods to examine the relationship between different age-based measures derived from stage-structured models but so far estimates of life spans derived in this way have been presented only for a few species.

In this study we used size- and stage-structured population matrix models for 71 perennial plant species to address the following questions: (1) What are the life spans of vascular plants as calculated from size- and stage-based demographic data? (2) How reliable are these values as judged by agreement with other estimates of plant life span and by within-species variation in model estimates? (3) How is life span related to other plant traits? More specifically, we tested whether ramets of clonal plants have a shorter life span than non-clonal individuals and, for non-clonal species, whether species with a seed bank have a shorter carbon-fixing life span. Furthermore, we examined whether self-incompatible species and wind-pollinated species have a longer life span than self-compatible and animal-pollinated species, respectively, and whether species with morphological attributes that favor dispersal or with small seeds have a shorter life span. The benefits of investments towards an increased life span will increase with decreased community disturbance rates. We therefore tested whether species in forests had a higher average life span than species from open habitats, assuming that disturbance frequency is higher in open habitats. We also compared life spans between semelparous and iteroparous species, between woody and non-woody species and between plants from different climatic zones.

Methods

The data set comes from studies on demography in 71 species. Most of these studies are published up to 1998, but we also included unpublished material for 5 species to which we had access (Appendix 1). We excluded studies for which it was impossible to distinguish between survival and sexual reproduction, or between survival and fission (= one individual splitting into two or more individuals). For clonal species we examined data for ramets (19 species) or groups of ramets (3 species). We also had to exclude two species for which the studies reported no mortality in the largest size-classes. As our objective was to examine life span in perennial plants we did not include annuals.

A population matrix model was projected using standard methods of population matrix analysis and age-based techniques (Caswell 1989, Cochran and Ellner 1992). The model yielded the dominant eigenvalue of each matrix, λ, and the conditional total life span (equation 6 in Cochran and Ellner 1992). This equation actually gives life span estimates that are one year too large, which can easily be checked by calculating life spans of annuals or obligate biennials. We therefore subtracted one year from the estimated life span. In a few cases matrices were reducible (Caswell 1989) because a transition involving growth from seedlings or the smallest stage was recorded as zero. In these cases we added a small value (10^{-20}) to the matrix to achieve irreducible matrices (Appendix 1). Before calculation of conditional life spans special care was taken to remove all types of reproduction and fission from the matrices. Consequently, life spans of clonal plants were clearly referring to ramets or clonal fragments. If a matrix included a seed stage, we checked that it referred to seed bank. In cases where the incorporation of the seed stage caused an incorrect one-year delay in the life cycle, the stage was removed and the remaining vital rates were corrected (Caswell 1989, Silvertown et al. 1993) (Appendix 1).

In a stage-structured population, an individual is born to one of the stages. In many plant population models, the offspring enter the stage of seedlings or juveniles, but they can in principle enter the stage of flowering individuals or any other of the stages in species having rapid growth in the first year of life. The offspring entering different stages are called different newborn types. The conditional total life span is defined as the average age of death for individuals that survive to a certain stage. Hence, for each newborn type, there are usually as many life span values as there are stages in the matrix, and each newborn type has its own series of life span values. For instance, in one of the populations of *Primula veris*, the newborn type of seedlings had the following life span values: 6.9 years (seedlings), 14.4 years (small vegetative individuals), 29.1 years (middle-sized vegetative individuals), 38.9 years (large vegetative individuals) and 33.6 years (flowering individuals). This means that a randomly chosen seedling will have an expected total life span of 6.9 years, a randomly chosen small vegetative individual lives on average 29.1 years and so on, all of which started their life as seedlings and were not, for example, vegetative daughter ramets or seeds that stay in the seed bank for the first years of their life.

Typically, the conditional total life span of individuals that survive to the seedling stage was low, as the average life span of seedlings is low, although some of the seedlings may grow up and eventually survive for tens or hundreds of years. Conditional total life span was higher for plants that survived to mature stages because mortality during the seedling and juvenile stages are not affecting these estimates. Since conditional total life spans of seedlings and juveniles are more strongly affected by juvenile mortality rate than by potential maximal longevity of the species, we chose to use the life span of the mature stage that had the highest value as the longevity measure. In the Primula veris example above, we chose the life span of large vegetative individuals, 38.9 years, to represent the population. Differences in conditional life spans between newborn types were small and we chose to use the highest value irrespective of newborn type. Time spent in the seed bank was not regarded as a part of the life span. The effect of seed bank was always small, because seed bank mortality was high.

Several of the included studies contained information from more than one year or more than one population. In these cases we calculated λ-values and conditional life spans for each available matrix. When there were data for multiple years we computed the harmonic mean of the life spans for all matrices representing different years within one population as a measure of the average life span for the species at that site. The logic behind using harmonic means is that life span is inversely related to mortality and that mortality rates ultimately determine life spans. For example, if we have two matrices from successive years and project a life span of 10 years from the first matrix and 100 year from the second matrix, the expected life span is 18 years rather than 55 years, assuming that the two years are representative. Harmonic means enabled us to also incorporate infinite life spans, that can emerge if there is no mortality at all in some years. For species where we had information from several populations we took the arithmetic mean of all population estimates (single values or harmonic means). In these calculations infinite values were assigned the maximum value obtained in any other population of that species. The estimated value of the conditional life span is hereafter referred to as the ‘‘projected life span’’.

We collected data on plant traits from the studies used as a source for demographic models as well as all other sources of information that we were able to find. With regard to the number of reproductive events, species were categorized as semelparous or iteroparous. Four facultatively semelparous plants were included in the semelparous category. Woody and non-woody plants were used as life form categories. Distribution was categorized as subarctic/arctic/alpine, temperate or subtropical/tropical. Only species with distinct morphological features for clonal growth were considered clonal. This is a potentially difficult distinction to make and in a few difficult cases we followed the categorization used in the demographic study on which we based our calculations. We classified species for which seeds have been demonstrated to survive more than one year in the seed bank as having a seed bank and species for which some kind of negative evidence in this respect have been published as not having a seed bank. For the analysis we placed hermaphroditic and self-compatible species in one group whereas the other group included both self-incompatible plants and species with other means to avoid self-fertilization or decrease the selfing rate (7 monoecious, 5 dioecious and 2 sequentially hermaphroditic species). We used two categories for pollination syndrome, animal or wind, and three for dispersal mode, animal, wind or unassisted. We followed the categorization used in the literature although we are aware that, especially with regards to dispersal, assessments based on morphology may be unreliable. The extremely small seeds of orchids were considered wind-dispersed. Habitat was divided into forests, including woodland, or open. All classifications are shown in Appendix 1.

To examine how the estimates of conditional life span calculated from stage-transition models agree with estimates of longevity from other sources we scanned the literature for the latter type of information. Information was usually available as maximum recorded age (mainly trees) or as lower limits or half-lives recorded during demographic studies (mainly herbs). Half-lives were transformed into average life spans by dividing half-lives with ln 2 (Pedersen 1999).

We used ordinary one-way ANOVA to examine the relationship between projected plant life span from stage-transition models, two distribution parameters (habitat and geographical distribution) and eight life-history traits (life-form, dispersal syndrome, pollination syndrome, parity, clonality, compatibility, presence of a seed bank, seed size). Many of the traits under investigation are correlated and the relationship between life span and one trait may be influenced by simultaneous correlations with other traits. Information on life form was available for all species and we were thus able to examine the effects of other traits also in the presence of life form by two-way ANOVAs. We did not use more advanced multi-way analyses, since the trait matrix we were able to assemble often had missing values for each species. For tests of dispersal syndrome, pollination syndrome, compatibility, presence of a seed bank and seed size we included only non-clonal species. Three clonal species for which estimates of life span were based on groups of tillers were excluded from contrasts between single ramets of clonal plants and individuals of non-clonal plants. Projected life spans approximately followed a log-normal distribution (Fig. 1) and were log-transformed before statistical analyses.

Any comparative study should consider that observed patterns are influenced by phylogenetic relationships (Harvey 1996). Life history characteristics vary at a relatively low phylogenetic level and in our data set species belonged to 37 different families. Assuming that families represent different phylogenetic branches, our sample of species thus still represents a considerable amount of replication. Moreover, in our data set phylogenetic independent contrasts (Harvey and Pagel 1991) would have been based on a relatively weak phylogeny as species are scattered among different families (Donoghue and Ackerly 1996). Hence, we did not use phylogenetic independent contrasts in our analyses but examined the distribution of variation in life span among different taxonomic levels.

Results

Life span estimates

The projected life spans of the 71 investigated perennial plant species ranged from 4.3 years for *Anthyllis vulneraria* to 988.6 years for the shrub *Eremophila forrestii* (the results for all species are given in Appendix 1). More than half of the species had a projected life span exceeding 35 years and a quarter of the species had a life span of more than 80 years. The distribution of projected life span was approximately log-normal (Fig. 1). The geometric average life span for the investigated perennial plants was 36.0 year (95% C.I. = 26.9–48.1).

An examination of the across-species variance in life span estimates showed that 54.7% of the variation occurred at the level of genus and above but that 45.3% of the variation occurred at the among-species, within-genus level (nested ANOVA). Also a comparison of the relative variation in terms of coefficients of variation showed that the variation among species within genera sometimes is in the same order of magnitude as the variation for the total data set (Table 1).

Reliability and within-species variation

Values of projected life span derived from stage-transition matrices in this study agreed well with previous estimates derived from other sources (Fig. 2). However, for species with previously reported values that were

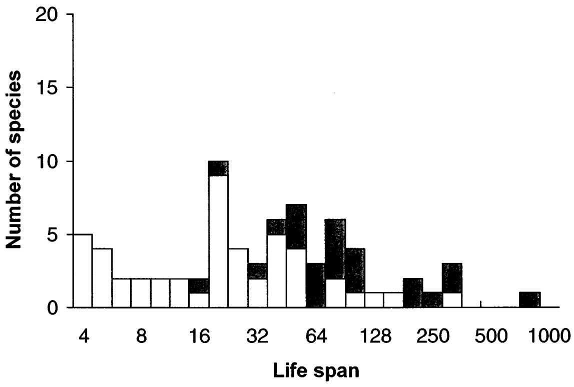

Fig. 1. Distribution of average conditional life spans for 71 species. Stippled sections of bars show woody plants and open sections non-woody.

Table 1. Coefficient of variation in life span (log-transformed values) in different taxonomic groups.

Level of analysis	N	CV
Across families		
All species	71	1.75
All iteroparous	63	1.64
Iteroparous woody	23	1.30
Iteroparous herbs	40	1.28
Within families		
Asteraceae	4	1.71
Fabaceae	5	1.00
Liliaceae	7	0.32
Arecaceae	7	1.91
Pinaceae	4	0.18
Within genera		
Calochortus	4	0.21
Pinguicula	3	1.01
Primula	3	0.41
Silene	3	1.35

lower than 40 years matrices yielded on average higher values. In contrast, for previous estimates of more than 40 years matrix estimates suggested lower values.

There was a considerable variation in the estimates of projected life span also within species suggesting that single estimates may not be sufficient to assess the potential life span of a species. For the eleven species for which we had information for at least two populations during at least two years, the within-species variation was of the same magnitude as between-species differences (Table 2). Obviously, infinite values do not mean that plants have eternal life but that study plants did not experience any mortality in some years. Friedman test with exact significances for nine species (all except *Panax* and *Arisaema* in Table 2) showed that projected life span differed significantly between years for only one species (*Primula vulgaris*, $P = 0.031$) and between sites for no species. Calculated life span was positively correlated to the λ-value of the matrix for all species, and significantly so for five species (Table 2).

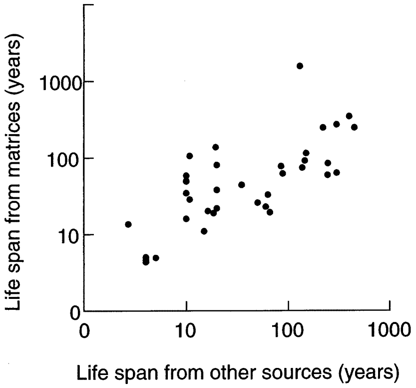

Fig. 2. Relationship between estimates of life span from size- or stage-based matrices calculated in this study and life span estimates derived by other means gathered from the literature. Matrix estimate = 1.71 (SE = 0.32) + 0.57 (SE = 0.08) previous estimate, adjusted squared multiple $R = 0.56$, $P < 0.001$, linear regression on log values, $N = 37$).

Life span and other plant traits

Life span differed between woody and non-woody plants (Table 3). Woody plants had on average more than four times as long projected life span as non-woody plants, although non-woody plants sometimes grow very old and may even outlive woody plants. The highest recorded value in this study, 988.6 years, was for the shrub *Eremophila forrestii*. The highest value for a herb was 337.2 years in *Silene acaulis*, which is very close to the second highest value for a woody species (346.0 years in *Araucaria cunninghamii*).

Plant life spans did not differ between geographical regions. One-way tests showed that life spans were significantly longer in forests than in open habitats and, expectedly, that iteroparous plants grew older than semelparous plants (Table 3). These differences remained significant also when taking differences in life form into account (Habitat: $F_{1,65} = 4.05$, $P = 0.048$, Parity: $F_{1,68} = 16.81$, $P < 0.001$, two-way ANOVA with life form as the second main factor). However, some semelparous plants had a projected life span of more than 16 years whereas the most short-lived iteroparous plant had a life span of 4.5 years. Average life span of iteroparous woody and non-woody plants was 98.6 ($N = 23$) and 28.3 years ($N = 40$), respectively. Non-clonal plant species had a longer projected life span than ramets of clonal species (Table 3). This difference was clearly significant when examined in a one-way test but only marginally significant when accounting also for life form ($F_{1,65} = 3.63$, $P = 0.061$, two-way ANOVA with life form as the second main factor).

We examined the relationship between projected life span and dispersal syndrome, pollination syndrome, compatibility, presence of a seed bank and seed size only for non-clonal species. Species that lacked a permanent seed bank had a longer life span than species that possessed a seed bank (Table 3) but this difference disappeared when differences in life form were taken into account ($F_{1,30} = 1.83$, $P = 0.186$, two-way ANOVA with life form as the second main factor). There was no difference between species with different dispersal syndromes (Table 3). Seed size and life span were positively correlated but this relation appeared to be due to differences in seed size between woody and non-woody plants (Seed size (covariate): $F_{1,18} = 0.94$, $P = 0.346$, ANCOVA with life form as the main factor). Self-incompatible plants, including dioecious and monoecious, grew on average older than self-compatible plants and this difference remained significant also when taking differences in life form into account ($F_{1,33} = 14.97$, $P < 0.001$, two-way ANOVA with life form as the second main factor). Lastly, wind-pollinated species had on

Table 2. Variation in life span within species and correlation between estimates of conditional life span (CLS) and lambda. Presented values for correlations are Spearman rank correlation coefficients based on both infinite and finite values. Infinite values were given the highest rank.

Species	Years	Populations	Matrix number	CLS – Harmonic mean	Range	Correlation CLS – lambda
Arabis fecunda	6	4	18	7.2	3.5–∞	0.179 ^{NS}
Asarum canadense	4	5	20	6.4	3.6–35.3	0.754 ***
Panax quinquefolium	2	4	6	22.8	13.8–∞	0.429 ^{NS}
Primula vulgaris	2	8	14	31.8	16.1–929.1	0.916 ***
Astragalus scaphioides	5	2	10	15.9	7.0–∞	0.387 ^{NS}
Saxifraga cotyledon	4	2	8	16.6	8.2–∞	0.383 ^{NS}
Plantago media	4	2	8	24.7	14.9–226.1	0.952 **
Arisaema triphyllum	2	2	4	21.8	15.3–31.3	0.800 ^{NS}
Calathea ovandensis	4	4	16	23.2	10.4–∞	0.706 **
Lathyrus vernus	3	11	32	44.1	21.7–∞	0.726 ***
Danthonia sericea	2	5	10	55.6	8.9–∞	0.478 ^{NS}

*** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$, ^{NS} = $P>0.05$.

average a longer life span than insect-pollinated plants (Table 3), but this effect seemed to be the result of that many trees are wind pollinated ($F_{1,35} = 0.03$, $P = 0.886$, two-way ANOVA with life form as the second main factor).

There was no significant relationship between the projected life span and the variance in lambda values (Spearman $r = 0.145$, $N = 11$, $P > 0.5$) among the eleven species for which we had information for several populations during several years (Table 2).

Discussion

This study used stage- and size-structured matrix population models to address the questions of how old perennial plants grow and how life span is related to other plant life history traits. Our analyses show that half of the perennial vascular plants had a projected life span exceeding 35 years and a quarter of the species had a life span of more than 80 years. The projected life spans among species most closely agreed with a log-normal distribution with a geometric mean of 36 years. This probably means that plants as a group on average have a longer life span than all investigated animal groups (Stearns 1992 and references therein). This conclusion is likely to hold true even if one takes into account that the flora includes a proportion of annual plants that were not incorporated in this study. The proportion of annual species in the North American and European flora has been estimated to 10–28% (Hart 1977, Silvertown 1983). The results of this study are thus in agreement with several previous studies suggesting that plants in general have relatively long life spans (Wangermann 1965, Inghe and Tamm 1985, Watkinson 1992, Bender et al. 2000). The life span of plants relative to other groups of organisms is important. If plants and interacting organisms, such as pollinators and herbivores, have different life spans, it imposes important restrictions on coevolutionary processes, in an analogous way as generation time (Thompson 1994).

Previous estimates of plant life span, except for trees, have been available for relatively few species and have been estimated from few individuals with many different methods. Previous examinations of life history correlations invoking life span have mainly used the trichotomy annuals, biennials and perennials. By contrast, our study provides estimates of life span for many species with a wide range of life histories and is based on large number of individuals in every species. As any investigation based on published information, our comparisons across species suffer from sampling errors. However, we still believe that the continuous estimates calculated in this study is the best information available and that it allows better assessment of how life span is related to other life history traits than previously used data. The values of projected life span agreed reasonably well with previously published information derived from other sources. There was a tendency that our results were higher than previous estimates for relatively short life spans, and lower for longer life spans. A possible explanation for this pattern is that yearly growth rings in long-lived woody plants provide a relatively reliable estimate but that maximum life spans of exceptionally long-lived individuals are often reported whereas a typical life span will be considerably shorter (Loehle 1987). In contrast, estimates for most short-lived herbs previous are based on long-term observations and provide estimates of the lower range of the potential life span.

For species where we had information from several populations and years it was clear that demographic parameters vary considerably. Several other studies with plants have also demonstrated large variations in demographic parameters (Moloney 1988, Bengtsson 1993, Horvitz and Schemske 1995, Ehrlén 1995, Oostermeijer et al. 1996). Our analyses suggest that projections of conditional life spans are very sensitive to such variation in demographic parameters. In extreme cases simulations project an eternal life span because the conditions at the particular site that particular year were so favorable that mortality was zero. However, among-year variation in life span is artificial as the actual longevity integrates conditions over the entire life span. This illustrates the important fact that matrix simulations cannot say anything about what will happen if the environment changes but only projects the expected life span during present conditions. This is analogous with the projection of population growth rates in stationary matrices (cf. Caswell 1989). The observed among-population variation in life spans illustrates that although species-specific life histories set the ultimate limits for life spans, they are largely the product of the environment and not an inherent property of the individual. The notion that the realized life span depends on how beneficial the environment is, gains further support from the positive correlation between population growth rate and life span within species found in this study. Because conditions vary and mortality may even occur only in some years, single values may sometimes be non-representative of a species. For example, if mortality is low except during disturbance events then short studies that do not include such events will overestimate life span. Integrated estimates based on information from more years (e.g. harmonic mean values used in this study) will be more reliable. However, the good agreement with life span estimates derived by other means suggests that variation of estimates should not be a major concern. With respect to the examination of across-species patterns, within-species variance in projected life span results in a unsystematic sampling error that may obscure, but not bias, existing patterns.

When within-species variance was removed by using one joint value for each species, nearly half of the remaining variance in the calculated conditional life span occurred at the among-species, within-genus level. This suggests that a considerable part of the variation is uncoupled from phylogenetic constraints. The variance component at the highest taxonomic level can be interpreted both in terms of phylogenetic constraints and niche conservatism (Lord et al. 1995). One obvious example of variance that is most appropriately explained at high taxonomic levels is the difference between long-lived coniferous trees and short-lived angiosperm herbs. In any case, it seems likely that much of the variation in life span should be interpreted at the species level.

The life span of individuals will have important effects for population dynamics and community structure (Schoener 1983, Eriksson 1996). A basic assumption in hypotheses on how life span of individuals is correlated to population and community dynamics is that a longer life span is associated with a smaller variation in population growth rates and consequently smaller probability of population extinction. Schoener (1983) showed for terrestrial vertebrates, plants and arthropods that the annual extinction rate of populations declined approximately linearly with the generation length of individuals. Fischer and Stöcklin (1997) examined extinction rates of plant populations in rem-

Table 3. Summary statistics of the relationship between ten plant traits and the expected life span of species. For tests including dispersal syndrome, pollination syndrome, compatibility, presence of a seed bank and seed size only non-clonal species were included. Relationships were tested statistically by Spearman rank correlation (seed size) or one-way ANOVA (all other traits). Statistical tests were carried out on log-transformed values and presented values for each category are back-transformed means least-square means from respective ANOVA.

					P
Life form	Non-woody (N = 48) 22.2 years	Woody (N = 23) 98.6 years		F = 33.5	< 0.001
Distribution	(Sub-)Arctic/alpine (N = 8) 19.0 years	Temperate (N = 48) 34.4 years	(Sub-)Tropical (N = 14) 61.6 years	F = 2.5	0.089
Habitat	Open (N = 39) 22.2 years	Forest/Woodland (N = 29) 63.6 years		F = 14.6	< 0.001
Parity	Itero (N = 63) 44.6 years	Semel (N = 8) 6.6 years		F = 22.4	< 0.001
Clonality	Clonal (N = 19) 17.3 years (ramets)	Non-clonal (N = 49) 46.2 years		F = 9.8	0.003
Seed bank	Present (N = 22) 24.8 years	Absent (N = 11) 73.2 years		F = 5.3	0.029
Dispersal syndrome	Animal (N = 10) 41.8 years	Wind (N = 8) 69.0 years	Unassisted (N = 17) 28.3 years	F = 1.72	0.195
Seed size (N = 21)				r = 0.502	0.020
Compatibility	Self-compatible (N = 20) 16.4 years	Self-incompatible (N = 16) 91.7 years		F = 26.3	< 0.001
Pollination syndrome	Animal (N = 31) 33.7 years	Wind (N = 7) 110.7 years		F = 5.4	0.026

nant sites of nutrient poor calcareous grasslands in the Swiss Jura mountains and found that populations that went extinct from 1950 to 1985 tended to be small in 1950 and to represent habitat specialist species with a short life cycle. However, our study provided no direct evidence of that a longer life span of individuals is translated into a more stable population dynamics. There was no significant relationship between the conditional life span and the variance in λ values among species. This suggests that the causal link from individual life spans to stable population dynamics may not be straightforward. On the other hand, we found that species in forests had a higher average life span than species in more open habitats. If disturbances occur with a lower frequency in forests than in open habitats, this may indicate that disturbances select for shorter life spans.

Our results also agree with the common notion that woody plants have a longer life span than non-woody plants. However, several authors have previously pointed out that also herbs sometimes can have very long life spans (Inghe and Tamm 1985, Bender et al. 2000). In support of this view, our results suggest that non-woody plant species may reach considerable ages and outlive the surrounding trees. Not surprisingly, we found higher estimates of life span in iteroparous than semelparous plants, but there was a considerable overlap. In contrast, Franco and Silvertown (1996) using stage-structured models found no relationship between longevity and age at first reproduction.

We found support for some, but not all, of previously suggested trade-offs between life span of established plant individuals, and clonality, seed longevity, self-compatibility and dispersal ability. Tanner (2001) found that expected remaining life span increased with size in clonal species whereas it was highest at intermediate sizes in aclonal species. He suggested that this indicates that whereas aclonal species experience senescence, it is less common for clonal species even at the ramet level. In contrast, we found that ramets of clonal plant individuals have a shorter expected life span compared with non-clonal individuals, suggesting instead that ramification and longevity of physiological individuals constitute alternative strategies for genet survival. However, this relationship was only marginally significant when correcting for life form.

In contrast to Rees (1993, 1996) we found no evidence that seed dormancy in perennials is associated with a shorter life span in the vegetative phase when differences in life form are taken into account. We examined variation among perennial plants whereas Rees based his study only on the trichotomy of annuals, biennials and perennials. Hence, the differences in seed longevity demonstrated between the discrete categories of annuals, biennials and perennials, is not evident when considering continuous estimates of life span within the biennial-perennial group. This suggests that at some threshold a decrease in seed longevity cannot be balanced by increased adult life span.

Self-incompatibility, including monoecy and dioecy, was associated with a longer life span than self-compatibility. Other studies have found that self-compatibility is very common in annual plants (Frankel and Galun 1977, Sutherland 1986). These results support the notion that short-lived species are more dependent on a reproductive system that decreases the risk of reproductive failure, such as self-compatibility.

Similar to Rees (1993) we found no support for a trade-off between dispersal syndrome and longevity. Although empirical evidence of the hypothesized trade-off between longevity and dispersability still seems to be lacking, it is not clear whether this relates to the basic hypothesis or whether it has to do with the relation between dispersal syndrome and seed size, and the actual dispersal distance of seeds (Eriksson and Jakobsson 1999). In any case, we found a positive correlation between life span and seed size but this relation apparently was the result of that woody plants grew older and had larger seeds than non-woody.

This study provides support for the notion that important trade-offs between plant life span and other means of persistence, such as clonal propagation and a predictable sexual reproduction, exist also among perennial plants. Thus trade-offs involving life span are important in the molding of plant life histories. To further our understanding of plant evolution, as well as population and community dynamics, accurate estimates of life spans for perennial plants will be indispensable.

Acknowledgements – We are grateful to L. Allphin-Woolstenhulme, B. Carlsson, P. Lesica, A. Jakobsson, R. Lindborg, B. Svensson and A. Tolvanen for access to unpublished data, to P. Jokela and R. Lindborg for help with the data collection, to O. Eriksson for comments on the manuscript, and to the Swedish Natural Science Research Council for financial support (J.E. and K.L.).

References

Abrams, M. D. and Copenheaver, C. A. 1999. Temporal variation in species recruitment and dendroecology of an old-growth white oak forest in the Virginia Piedmont, USA. – Forest Ecol. Manage. 124: 275–284.

Ackerman, J. D., Melendez-Ackerman, E. J. and Salguero-Faria, J. 1997. Variation in pollinator abundance and selection on fragrance phenotypes in an epiphytic orchid. – Am. J. Bot. 84: 1383–1390.

Akashi, N. 1997. Dispersion patterns and mortality of seeds and seedlings of *Fagus crenata* (Blume) in a cool temperate forest in western Japan. – Ecol. Res. 12: 159–165.

Allphin, L. and Harper, K. T. 1997. Demography and life history characteristics of the rare Kachina daisy (*Erigeron kachinensis*, Asteraceae). – Am. Midland Nat. 138: 109–120.

Alvarez-Buylla, E. R. 1994. Density dependence and patch dynamics in tropical rain forests: matrix models and applications to a tree species. – Am. Nat. 143: 155–191.

Andersson, P. D. 1983. The dynamics of longevity of *Viola fimbriatula* seeds in the soil. – Ph.D. thesis. Harvard Univ., Cambridge Mass. USA.

Baker, K., Richards, A. J. and Tremayne, M. 1994. Fitness constraints on flower number, seed number and seed size in the dimorphic species *Primula farinosa* L. and *Armeria maritima* (Miller) Willd. – New Phytol. 128: 563–570.

Bastrenta, B., Lebreton, J.-D. and Thompson, J. D. 1995. Predicting demographic change in response to herbivory: a model of the effects of grazing and annual variation on the population dynamics of *Anthyllis vulneraria*. – J. Ecol. 83: 603–611.

Batista, W. B., Platt, W. J. and Macchiavelli, R. E. 1998. Demography of a shade-tolerant tree (*Fagus grandifolia*) in a hurricane-disturbed forest. – Ecology 79: 38–53.

Bender, M. H., Baskin, J. M. and Baskin, C. C. 2000. Age of maturity and life span in herbaceous polycarpic perennials. – Bot. Rev. 66: 311–349.

Bengtsson, K. 1993. *Fumana procumbens* on Öland-population dynamics of a disjunct species at the northern limit of its range. – J. Ecol. 81: 745–758.

Bernal, R. 1998. Demography of the vegetable ivory palm *Phytelepas seemannii* in Colombia, and the impact of seed harvesting. – J. Appl. Ecol. 35: 64–74.

Bierzychudek, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. – Ecol. Monogr. 52: 335–351.

Blarer, A., Doebeli, M. and Stearns, S. C. 1995. Diagnosing senescence: inferring evolutionary causes from phenotypic patterns can be misleading. – Proc. R. Soc. Lond. B 262: 305–312.

Bornbusch, A. H., Swender, L. A. and Hoogerwerf, D. L. 1994. Genetic variation in Massachusetts populations of *Cypripedium arietinum* R. Brown in Ait. and *C. acaule* Ait. (Orchidaceae). – Rhodora 96: 354–369.

Boucher, D. H. and Mallona, M. A. 1997. Recovery of the rain forest tree *Vochysia ferruginea* over 5 years following Hurricane Joan in Nicaragua: a preliminary population projection matrix. – Forest Ecol. Manage. 91: 195–204.

Boyd, M., Silvertown, J. and Tucker, C. 1990. Population ecology of heterostyle and homostyle *Primula vulgaris* – growth, survival and reproduction in field populations. – J. Ecol. 78: 799–813.

Bullock, S. H. 1980. Demography of an undergrowth palm in littoral Cameroon. – Biotropica 12: 247–255.

Burrows, C. J. and Lord, J. M. 1993. Recent colonization by *Nothofagus fusca* at Cass, Canterbury, South Island, New Zealand. – N.Z. J. Bot. 31: 139–146.

Byers, D. L. 1995. Pollen quantity and quality as explanations for low seed set in small populations exemplified by *Eupatorium* (Asteraceae). – Am. J. Bot. 82: 1000–1006.

Byers, D. L. 1998. Effect of cross proximity on progeny fitness in a rare and a common species of *Eupatorium* (Asteraceae). – Am. J. Bot. 85: 644–653.

Byers, D. L. and Meagher, T. R. 1997. A comparison of demographic characteristics in a rare and a common species of *Eupatorium*. – Ecol. Appl. 7: 519–530.

Cain, M. L., Damman, H. and Muir, A. 1998. Seed dispersal and the Holocene migration of woodland herbs. – Ecol. Monogr. 68: 325–327.

Calvo, R. N. 1993. Evolutionary demography of orchids: intensity and frequency of pollination and the cost of fruiting. – Ecology 74: 1033–1042.

Caswell, H. 1989. Matrix population models: construction, analysis, and interpretation. – Sinauer.

Charron, D. and Gagnon, D. 1991. The demography of northern populations of *Panax quinquefolium* (American ginseng). – J. Ecol. 79: 431–445.

Cochran, M. E. and Ellner, S. 1992. Simple methods for calculating age-based life history parameters for stage-structured populations. – Ecol. Monogr. 62: 345–364.

Cook, R. E. 1983. Clonal plant populations. – Am. Sci. 71: 244–253.

Damman, H. and Cain, M. L. 1998. Population growth and viability analysis of the clonal woodland shrub, *Asarum canadense*. – J. Ecol. 86: 13–26.

Degreef, J., Baudoin, J.-P. and Rocha, O. J. 1997. Case studies on breeding systems and its consequences for germplasm. 2. Demography of wild Lima bean populations in the central valley of Costa Rica. – Genet. Resour. Crop Evol. 44: 429–438.

Delph, L. F., Bailey, M. F. and Marr, D. L. 1999. Seed provisioning in gynodioecious *Silene acaulis* (Caryophyllaceae). – Am. J. Bot. 86: 140–144.

Desmet, P. G., Shackleton, C. M. and Robinson, E. R. 1996. The population dynamics and life-history attributes of a *Pterocarpus angolensis* DC. Population in the Northern Province, South Africa. – S. Afr. J. Bot. 62: 160–166.

Dinnetz, P. and Nilsson, T. 2001. Population viability analysis of *Saxifraga cotyledon*, a perennial plant with semelparous rosettes. – Plant Ecology in press.

Doak, D. F. 1991. The consequences of herbivory for dwarf fireweed: different time scales, different morphological scales. – Ecology 72: 1397–1407.

Doak, D. F. 1992. Lifetime impacts of herbivory for a perennial plant. – Ecology 73: 2086–2099.

Donoghue, M. J. and Ackerly, D. D. 1996. Phylogenetic uncertainties and sensitivity analysis in comparative biology. – Phil. Trans. R. Soc. Lond., Ser. B 351: 1241–1249.

Ehrlén, J. 1995. Demography of the perennial herb *Lathyrus vernus*: II. Herbivory and population dynamics. – J. Ecol. 83: 297–308.

Ehrlén, J. and van Groenendael, J. 1998. Colonization and extinction processes in plant communities. – J. Appl. Veget. Sci. 1: 29–36.

Enright, N. J. 1992. Factors affecting reproductive behaviour in the New Zealand nikau palm, *Rhophalostylis sapida* Wendl. et Drude. – N.Z. J. Bot. 30: 69–80.

Enright, N. J. and Ogden, J. 1979. Applications of transition matrix models in forest dynamics: *Arucaria* in Papua New Guinea and *Nothofagus* in New Zealand. – Aust. J. Ecol. 4: 3–23.

Enright, N. J. and Watson, A. D. 1992. Population dynamics of the nikau palm, *Rhopalostylis sapida* (Wendl. et Drude), in a temperate forest rainforest remnant near Auckland, New Zealand. – N.Z. J. Bot. 30: 29–43.

Eriksson, O. 1988. Ramet behaviour and population growth in the clonal herb *Potentilla anserina*. – J. Ecol. 76: 522–536.

Eriksson, O. 1996. Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. – Oikos 77: 248–258.

Eriksson, O. and Jakobsson, A. 1999. Recruitment trade-offs and the evolution of dispersal mechanisms in plants. – Evol. Ecol. 13: 411–423.

Fiedler, P. L. 1987. Life history and population dynamcis of rare and common mariposa lilies (*Calochortus* Pursh: Liliaceae). – J. Ecol. 75: 977–995.

Fischer, M. and Stöcklin, J. 1997. Local extinctions of plants in remnants of extensively used calcareous grasslands 1950–1985. – Conserv. Biol. 11: 727–737.

Fitter, A. H. 1986. Acquisition and utilization of resources. – In: Crawley, M. J. (ed.), Plant ecology. Blackwell Scientific Publications, pp. 375–405.

Flamm, E. 1922. Zur Lebensdauer und Anatomie einiger Rhizome. – Akademie der Wissenschaften in Wien, Sitzungsberichte, Mathematisch-naturwissenschaftliche Klasse, Abteilung 1 131: 7–22.

Ford, B. A., Ball, P. W. and Ritland, K. 1991. Allozyme diversity and genetic relationships among North-American members of the short-beaked taxa of *Carex* sect. Vesicariae (Cyperaceae). – Syst. Bot. 16: 116–131.

Franco, M. and Silvertown, J. 1996. Life history variation in plants: an exploration of the fast-slow continuum hypothesis. – Philos. Trans. R. Soc. Lond., Ser. B 351: 1341–1348.

Frankel, R. and Galun, E. 1977. Pollination mechanisms, reproduction and plant breeding. – Springer-Verlag.

Garcia, M. B. and Antor, R. J. 1995. Age and size structure in populations of a long-lived dioecious geophyte: *Borderea pyrenaica* (Dioscoreaceae). – Int. J. Plant Sci. 156: 236–243.

Grime, J. P., Hodgson, J. G. and Hunt, R. 1988. Comparative plant ecology. – Unwin Hyman Ltd, London, UK.

Hamilton, M. B. and Mitchell-Olds, T. 1994. The mating system and relative performance of selfed and outcrossed progeny in *Arabis fecunda* (Brassicaceae). – Am. J. Bot. 81: 1252–1256.

Harper, J. L. and White, J. 1974. The demography of plants. – Annu. Rev. Ecol. Syst. 5: 419–463.

Hart, R. 1977. Why are biennials so few? – Am. Nat. 111: 792–799.

Harvey, P. H. 1996. Phylogenies for ecologists. – J. Anim. Ecol. 65: 255–263.

Harvey, P. H. and Pagel, M. D. 1991. The comparative method in evolutionary biology. – Oxford Univ. Press.

Hiura, T., Koyama, H. and Igarashi, T. 1996. Negative trend between seed size and adult leaf size throughout the geographical range of *Fagus crenata*. – Ecoscience 3: 226–228.

Horvitz, C. C. and Schemske, D. W. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. – Ecol. Monogr. 65: 155–192.

Horvitz, C. C. and Schemske, D. W. 1988. A test of the pollinator limitation hypothesis for a neotropical herb. – Ecology 69: 200–206.

Huenneke, L. F. and Marks, P. L. 1987. Stem dynamics of the shrub *Alnus incana* spp. *rugosa*: transition matrix models. – Ecology 68: 1234–1242.

Hultén, E. and Fries, M. 1986. Atlas of North European vascular plants – North of the Tropic of Cancer. – Koeltz Scientific Books, Königstein.

Huxley, A., Griffiths, M. and Levy, M. 1992. The new RHS dictionary of gardening. – Macmillan Press.

Inghe, O. and Tamm, C. O. 1985. Survival and flowering of perennial herbs. IV. – Oikos 45: 400–420.

Johansson, T. 1999. Site index curves for common alder and grey alder growing on different types of forest soil in Sweden. – Scand. J. Forest Res. 14: 441–453.

Jones, V. and Richards, P. W. 1962. Biological flora of the British Isles: *Silene acaulis* (L.) Jacq. – J. Ecol. 50: 475–487.

Karlsson, P. S. 1986. Seasonal patterns of biomass allocation in flowering and non-flowering specimens of three Pinguicula species. – Can. J. Bot. 64: 2872–2877.

Kawano, S., Takada, T., Nakayama, S. and Hiratsuka, A. 1987. Demographic differentiation and life history evolution in temperate woodland plants. – In: Urbanska, K. M. (ed.), Differentiation patterns in higher plants. Academic Press, pp. 153–181.

Kephart, S. R. and Paladino, C. 1997. Demographic change and microhabitat variability in a grassland endemic, *Silene douglasii* var. *oraria* (Carophyllaceae). – Am. J. Bot. 84: 179–189.

Kephart, S. R., Brown, E. and Hall, J. 1999. Inbreeding depression and partial selfing: evolutionary implications of mixed-mating in a coastal endemic, *Silene douglasii* var. *oraria* (Caryophyllaceae). – Heredity 82: 543–554.

Kinoshita, E. 1987. Sex change and population dynamics in Arisaema (Araceae) I. *Arisaema serratum* (Thunb.) Schott. – Plant Species Biol. 2: 15–28.

Kitamura, K., Okuizumi, H., Seki, T., Niiyama, K. and Shiraishi, S. 1992. Isozyme analysis of mating system in natural populations of *Fagus crenata* and *F. japonica*. – Jpn J. Ecol. 42: 61–69.

Kubota, Y. 1997. Demographic traits of understory trees and population dynamics of a *Picea abies* forest in Taisetsuzan National Park, northern Japan. – Ecol. Res. 12: 1–9.

Kubota, Y., Konno, Y. and Hiura, T. 1994. Stand structure and regeneration strategy of a coniferous forest in Taisetsuzan National Park, Japan. – Ecol. Res. 9: 333–341.

Leopold, A. C. 1980. Aging and senescence in plant development. – In: Thimann, K. V. (ed.), Senescence in plants. CRC Press, pp. 1–12.

Lesica, P. 1995. Demography of *Astragalus scaphoides* and effects of herbivory on population growth. – Great Basin Nat. 55: 142–150.

Lesica, P. and Shelly, J. S. 1995. Effects of reproductive mode on demography and life history in *Arabis fecunda* (Brassicaceae). – Am. J. Bot. 82: 752–762.

Lesica, P. and Shelly, J. S. 1996. Competitive effects of *Centaurea maculosa* on the population dynamics of *Arabis fecunda*. – Bull. Torrey Bot. Club 123: 111–121.

Loehle, C. 1987. Tree life history strategies: the role of defences. – Can. J. Forestry Res. 18: 209–222.

Löfgren, P., Eriksson, O. and Lehtilä, K. 2000. Population dynamics and the effect of disturbance in the monocarpic herb *Carlina vulgaris* (Asteraceae). – Ann. Bot. Fenn. 37: 183–192.

Lord, J., Westoby, M. and Leishman, M. R. 1995. Seed size and phylogeny in six temperate floras: constraints, niche conservatism and adaption. – Am. Nat. 146: 349–364.

Martinez-Ramos, M. and Alvarez-Byulla, E. R. 1995. Seed dispersal and patch dynamics in tropical rain forests: a demographic approach. – Ecoscience 2: 223–229.

Maschinski, J., Frye, R. and Rutman, S. 1996. Demography and population viability of an endangered plant species before and after protection from trampling. – Conserv. Biol. 11: 990–999.

Meagher, T. M. 1980. The population biology of *Chamaelirium luteum*, a dioecious member of the lily family. I. Spatial distributions of males and females. – Evolution 34: 1127–1137.

Meagher, T. M. 1982. two-sex population projections and stable population structure. – Ecology 63: 1701–1711.

Meagher, T. M. and Antonovics, J. 1982. The population biology of *Chamaelirium luteum*, a dioecious member of the lily family: life history studies. – Ecology 63: 1690–1700.

Menges, E. S. 1990. Population viability analysis for an endangered plant. – Conserv. Biol. 4: 52–62.

Menges, E. S. 2000. Population viability analysis in plants: challenges and opportunities. – Trends Ecol. Evol. 15: 51–56.

Menges, E. S. and Dolan, R. W. 1998. Demographic viability of populations of *Silene regia* in midwestern prairies: relationships with fire management, genetic variation, geographic location, population size, and isolation. – J. Ecol. 86: 63–78.

Molau, U. 1993. Reproductive ecology of the three Nordic *Pinguicula* species (Lentibulariaceae). – Nordic J. Bot. 13: 149–157.

Molisch, H. 1938. The longevity of plants. – Science Press.

Moloney, K. 1988. Fine-scale spatial and temporal variation in the demography of a perennial bunchgrass. – Ecology 69: 1588–1598.

Morris, W. F. and Doak, D. F. 1998. Life history of the long-lived gynodioecious cushion plant *Silene acaulis* (Carophyllaceae), inferred from size-based population projection matrices. – Am. J. Bot. 85: 784–793.

Nakashizuka, T. 1991. Population dynamics of coniferous and broad-leaved trees in a Japanese temperate mixed forest. – J. Veg. Sci. 2: 413–418.

Nantel, P., Gagnon, D. and Nault, A. 1996. Population viability analysis of American ginseng and wild leek harvested in stochastic environments. – Conserv. Biol. 10: 608–621.

Nault, A. and Gagnon, D. 1993. Ramet demography of *Allium tricoccum*, a spring ephemeral, perennial forest herb. – J. Ecol. 81: 101–119.

Noodén, L. D. 1988. Whole plant senescence. – In: Noodén, L. D. and Leopold, A. C. (eds), Senescence and aging in plants. Academic Press, pp. 391–439.

Ogden, J. 1978. On the dendrochronological potential of Australian trees. – Aust. J. Ecol. 3: 339–356.

Oinonen, E. 1967. The correlation between the size of Finnish bracken (*Pteridium aquilinum* (L.) Kuhn.) clones and certain periods of site history. – Acta Forestalia Fenn. 83: 1–51.

Olmsted, I. and Alvarez-Buylla, E. R. 1995. Sustainable harvesting of tropical trees: demography and matrix models of two palm species in Mexico. – Ecol. Appl. 5: 484–500.

Oostermeijer, J. G. B., Dennis, J. C. M., Reijmann, L. E. L. and Menken, S. B. J. 1992. Population biology and management of the marsh gentian (*Gentiana pneumonanthe* L.), a rare species in the Netherlands. – Bot. J. Linn. Soc. 108: 117–130.

Oostermeijer, J. G. B., Brugman, M. L., de Boer, E. R. and den Nijs, H. C. M. 1996. Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. – J. Ecol. 84: 153–166.

Pascarella, J. B. 1997. Breeding systems of *Ardisia* Sw (Myrsinaceae). – Brittonia 49: 45–53.

Pascarella, J. B. and Horvitz, C. C. 1998. Hurricane disturbance and the population dynamics of a tropical, understory shrub: megamatrix elasticity analysis. – Ecology 79: 547–563.

Pedersen, B. 1999. Senescence in plants. – In: Vuorisalo, T. O. and Mutikainen, P. K. (eds), Life history evolution in plants. Kluwer Academic Publishers, pp. 239–274.

Pinard, M. 1993. Impacts of stem harvesting on populations of *Iriartea deltoidea* (Palmae) in an extractive reserve in Acre, Brazil. – Biotropica 25: 2–14.

Platt, W. J., Evans, G. W. and Rathbun, S. L. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). – Am. Nat. 131: 491–525.

Price, O. and Bowman, D. M. J. S. 1994. Fire-stick forestry: a matrix model in support of skilful fire management of *Callitris intratropica* R. T. Baker by north Australian Aborigines. – J. Biogeogr. 21: 573–580.

Primack, R. B. and Hall, P. 1990. Costs of reproduction in the lady slipper orchid: a four-year experimental study. – Am. Nat. 136: 638–656.

Raijmann, L. L., van Leeuwen, N. C., Kersten, R. et al. 1994. Genetic variation and outcrossing rate in relation to population size in *Gentiana pneumonanthe* L. – Conserv. Biol. 8: 1014–1026.

Randall, P. M. 1991. A one-year pollen trapping study in Westland and Canterbury, South Island, New Zealand. – J. R. Soc. N.Z. 21: 201–218.

Rees, M. 1993. Trade-offs among dispersal strategies in British plants. – Nature 366: 150–152.

Rees, M. 1996. Evolutionary ecology of seed dormancy and seed size. – Philos. Trans. R. Soc. Lond., Ser. B 351: 1299–1308.

Roach, D. A. 1993. Evolutionary senescence in plants. – Genetica 91: 53–64.

Roff, D. A. 1992. The evolution of life histories: theory and analysis. – Chapman and Hall.

Sagar, G. R. and Harper, J. L. 1964. Biological flora of the British Isles: *Plantago major* L., *P. media* L. and *P. lanceolata* L. – J. Ecol. 52: 205–210.

Saito, H., Imai, H. and Takeoka, M. 1991. Pecularities of sexual reproduction in *Fagus crenata* forests in relation to annual production of reproductive organs. – Ecol. Res. 6: 277–290.

Sato, H. and Hiura, T. 1998. Estimation of overlapping seed shadows in a northern mixed forest. – Forest Ecol. Manage. 104: 69–76.

Schoener, T. W. 1983. Rate of species turnover declines from lower to higher organisms: a reviwe of the data. – Oikos 41: 372–377.

Schulman, E. 1958. Bristlecone pine, oldest living thing. – Nat. Geogr. Mag. 113: 354–372.

Shykoff, J. 1988. Maintenance of gynodioecy in *Silene acaulis* (Carophyllaceae): stage-specific fecundity and viability selection. – Am. J. Bot. 75: 844–850.

Silva, J. G., Raventos, J., Caswell, H. and Trevisan, M. C. 1991. Population responses to fire in a tropical savanna grass *Andropogon semiberbis*: a matrix model approach. – J. Ecol. 79: 345–356.

Silvertown, J. 1983. Why are biennials sometimes not so few? – Am. Nat. 121: 448–453.

Silvertown, J., Franco, M., Pisanty, I. and Mendoza, A. 1993. Comparative plant demography- relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. – J. Ecol. 81: 465–476.

Solbrig, O. T., Sarandón, R. and Bossert, W. 1988a. A density-dependent growth model of a perennial herb, *Viola fimbriatula*. – Am. Nat. 131: 385–400.

Solbrig, O. T., Curtis, W. F., Kincaid, D. T. and Newell, S. J. 1988b. Studies on the population biology of the genus *Viola*. VI. The demography of *V. fimbriatula* and *V. lanceolata*. – J. Ecol. 76: 301–319.

Stahle, D. W., Mushove, P. T., Cleaveland, M. K. et al. 1999. Management implications of annual growth rings in *Pterocarpus angolensis* from Zimbabwe. – Forest Ecol. Manage. 124: 217–229.

Stearns, S. C. 1992. The evolution of life histories. – Oxford Univ. Press.

Sterk, A. A. 1975. Demographic studies of *Anthyllis vulneraria* L. in the Netherlands. – Acta Bot. Neerlandica 24: 315–337.

Sterk, A. A., Van Duijkeren, A., Hogervorst, J. and Verbeek, A. D. M. 1982. Demographic studies of *Anthyllis vulneraria* L. in the Netherlands, II. Population density fluctuations and adaptions to arid conditions, seed populations, seedling mortality, and the influence of the biocenosis on demographic features. – Acta Bot. Neerlandica 31: 11–40.

Sutherland, S. 1986. Patterns of fruit-set: what controls fruit-flower ratios in plants? – Evolution 40: 117–128.

Suzuki, E., Ota, K., Igarashi, T. and Fujiwara, K. 1987. Regeneration process of coniferous forests in mothern Hokkaido. I *Abies Sachalinensis* forest and *Picea glehnii* forest. – Ecol. Res. 2: 61–75.

Svensson, B. M., Carlsson, B. Å., Karlsson, P. S. and Nordell, O. 1993. Comparative demography of three species of Pinguicula. – J. Ecol. 81: 635–645.

Takahashi, K. and Kohyama, T. 1999. Size-structure dynamics of two conifers in relation to understorey dwarf bamboo: A simulation study. – J. Veg. Sci. 10: 833–842.

Tanner, J. E. 2001. The influence of clonality on demography: patterns in expected longevity and survivorship. – Ecology 82: 1971–1981.

Thompson, J. N. 1994. The coevolutionary process. – The Univ. of Chicago Press.

Travis, S. E., Maschinski, J. and Keim, P. 1996. An analysis of genetic variation in *Astragalus cremnophylax* var. *cremnophylax*, a critically endangered plant, using AFLP markers. – Mol. Ecol. 5: 735–745.

Valverde, T. and Silvertown, J. 1998. Variation in the demography of a woodland understorey herb (*Primula vulgaris*) along the forest regeneration cycle: projection matrix analysis. – J. Ecol. 86: 545–562.

van der Meijden, E., Klinkhamer, P. G., de Jong, T. J. and van Wijk, C. A. M. 1992. Metapopulation dynamics of biennial plants: how to exploit temporary habitats. – Acta Bot. Neerlandica 41: 249–270.

Venable, D. L. and Levin, D. A. 1983. Morphological dispersal structures in relation to growth habit in the Compositae. – Plant Syst. Evol. 143: 1–16.

Verkaar, H. J. and Schenkeveld, A. J. 1984. On the ecology of short-lived forbs in chalk grasslands: life-history characteristics. – New Phytol. 98: 659–672.

Wangermann, E. 1965. Longevity and ageing in plants and plant organs. – Encycl. Plant Physiol. 15: 1026–1057.

Watkinson, A. R. 1992. Plant senescence. – Trends Ecol. Evol. 7: 417–420.

Watkinson, A. R. and White, J. 1985. Some life-history consequences of modular construction in plants. – Philos. Trans. R. Soc. Lond., Ser. B 313: 31–51.

Watson, I. W., Westoby, M. and Holm, A. McR. 1997a. Continuous and episodic components of demographic change in arid zone shrubs: models of two *Eremophila* species from Western Australia compared with published data on other species. – J. Ecol. 85: 833–846.

Watson, I. W., Westoby, M. and Holm, A. McR. 1997b. Demography of two shrub species from an arid grazed ecosystem in Western Australia. – J. Ecol. 85: 815–832.

Werner, P. A. and Caswell, H. 1977. Population growth rates and age versus stage-distribution models for teasel (*Dipsacus sylvestris* Huds.). – Ecology 58: 1103–1111.

Williams, G. C. 1957. Pleiotropy, natural selection and the evolution of senescence. – Evolution 11: 398–411.

Wilson, A. M. and Thompsson, K. 1989. A comparative study of reproductive allocation in 40 British grasses. – Funct. Ecol. 3: 297–302.

www.arboretum.harvard.edu/kalimantan

www.bids.ac.uk/ecoflora.html

www.greed.isc.tamu.edu/flora/328fall96/legll.html

www.nps.gov/bela/html/fireweed.htm

Appendix 1. Life-history traits and projected conditional life spans for 71 perennial species. The reference for the demographic data on which projections of conditional life span were based are given with the species name. Other references refer to respective traits. Classification of pollination and dispersal syndrome was in some cases based on the authors' general knowledge of flower and fruit morphology, or on personal communication with colleagues. Lambda are arithmetic means. Distribution: AA = alpine, arctic or subarctic, TE = temperate, ST = subtropical or tropical; Habitat: O = open, F = forest or woodland; Life form: W = woody, NW = non-woody; Parity: I = iteroparous, S = semelparous; Clonality: C = clonal, NC = non-clonal; Compatibility: SC = self-compatible, SI = self-incompatible or else with other means to avoid self-fertilization or decrease selfing-rate (monoecy, dioecy or sequential hermaphroditism); Pollination: W = wind, A = animal; Dispersal syndrome: W = wind, A = animal, U = unassisted (including one species with ballistic seed dispersal); Seed bank: P = present, A = absent; and Conditional life span: (A) = A small value (10^{-20}) added to the original matrix to achieve irreducible matrices, (B) = Error in the original matrix corrected.

Species	Family	Distribution	Habitat	Life form	Parity	Clonality	Compatibility	Pollination	Seed size (mg)	Dispersal syndrome	Seed bank	Life span, previous estimate (yrs)	Lambda (arit. mean)	Conditional life span – mean (yrs)
Abies homolepis[1]	Pinaceae	TE[1]	F[1]	W[1]	I[1]	NC[1]	SI[2]	W[2]			P[2]			83.92
Abies sachalinensis[3]	Pinaceae	TE[3]	F[3]	W[3]	I[3]	NC[3]	SI[2]	W[2]	10.4[4]	W	P[2]	245[5]		84.37
Allium tricoccum[6]	Liliaceae	TE[6]	F[6]	NW[6]	I[6]	C[6]	SC[6]	A[6]		U	P[6]		1.091	41.46
Alnus incana ssp *rugosa*[7]	Betulaceae	TE[7]	O[7]	W[7]	I[7]	C[7]	*SC*[2]	W[2]		W		66[8]	0.961	22.36
Andropogon semiberbis[9]	Poaceae	TE[9]	O[9]	NW[9]	I[9]	C[9]		W					1.346	35.28
Anthyllis vulneraria[10]	Fabaceae	TE[10]	O[10]	NW[10]	S[10]	NC[10]	SC[10]	A	3.31[11]	*U*[12]	P[10, 13]	4[12]	0.699	4.34
Arabis fecunda[14]	Brassicaceae	AA[15]	O[15, 16]	NW[15]	S[15]	NC[15]	SC[15, 16]	A[16]	0.24[16]		P[14]		1.311	8.67
Araucaria cunninghamii[17]	Araucariaceae	ST[17]	F[17]	W[17]	I[17]	NC[17]						400[17]	0.989	345.70 (B)
Ardisia escallonioides[18]	Myrsinaceae	ST[18]	F[18]	W[18]	I[18]	NC[18]	SC[19]	A[19]	50.3[19]		A[18]		1.500	62.51
Arisaema serratum[20]	Araceae	TE[20]	F[20]	NW[20]	I[20]	C[20]	SI[20]	A[20]			A[20]		0.991	22.92
Arisaema triphyllum[21]	Araceae	TE[21]	F[21]	NW[21]	I[21]	C[21]	SI[21]	A[21]		A[21]	A[21]	25[21]	1.105	22.02
Asarum canadense[22]	Aristolochiaceae	TE[22]	F[22]	NW[22]	I[22]	C[22]	SC[22]	A[2]	13.7[23]	A[23]	A[22]		0.910	6.67
Astragalus cremnophylax var. *cremonophylax*[24]	Fabaceae	TE[24]	O[24]	NW[24]	I[24]	NC[24]	SC[25]	A[25]		U[24]	A[24]			21.04
Astragalus scaphoides[26]	Fabaceae	TE[26]	O[26]	NW[26]	I[26]	NC[26]		A[27]		U[27]	P[26]	10[26]	1.414	20.78
Calathea ovandensis[28]	Marantaceae	ST[28]	F[28]	NW[28]	I[28]	NC[28]	SC[29]	A[28]		A[28]	P[28]		1.003	24.36
Callitris intratropica[30]	Cupressaceae	ST[30]		W[30]	I[30]	NC[30]					A[30]		0.824	53.86
Calochortus albus[31]	Liliaceae	TE[31]	O[31]	NW[31]	I[31]	C[31]	SC[31]	A[31]	1.81[31]	U[31]	A[31]	10[31]	1.527	32.54
Calochortus obispoensis[31]	Liliaceae	TE[31]	O[31]	NW[31]	I[31]	C[31]	SC[31]	A[31]	1.54[31]	U[31]	A[31]	10[31]	0.995	50.19
Calochortus pullchellus[31]	Liliaceae	TE[31]	F[31]	NW[31]	I[31]	C[31]	SC[31]	A[31]	3.90[31]	U[31]	A[31]	10[31]	1.035	49.17 (A)
Calochortus tiburnonensis[31]	Liliaceae	TE[31]	O[31]	NW[31]	I[31]	C[31]	SC[31]	A[31]	3.38[31]	U[31]	A[31]	10[31]	1.147	58.48
Carex distans[32]	Cyperaceae	AA[32]	O[32]	NW[32]	I[32]	C[32]		W					1.061	6.14
Carex membranacea[32]	Cyperaceae	AA[32]	O[32]	NW[32]	I[32]	C[32]	SI[33]	W					1.059	6.16
Carlina vulgaris[34]	Asteracae	TE[35]	O[34]	NW[34]	S[34]	NC[34]	SC[36]	A[36]	1.53[36]	U[34]	P[34]	4[37]	0.869	5.25
Cecropia obtusifolia[38]	Cercropiaceae	ST[38]	F[39]	W[38]	I[38]	NC[38]	SI[38]	A[38]		A[38]	P[39]		0.941	49.64
Chamaelirium luteum[40]	Liliaceae	TE[41]	F[42]	NW[42]	I[42]	NC[42]	SI[42]	*A*					1.014	81.00
Coccothrinax readii[43]	Arecaceae	ST[43]	O[43]	W[43]	I[43]	NC[43]						150[43]	1.055	114.80
Cypripedium acaule[44]	Orchidaceae	TE[44]	F[44]	NW[44]	I[44]	NC[44]	SI[45]	A[45]		W	P[44]	50[46]	1.113	25.80 (A)
Danthonia sericea[47]	Poaceae	TE[47]		NW[47]	I[47]	C[47]	SC[47]	W[47]			P[47]		1.084	158.52 (A)
Daucus carota[37]	Apiaceae	TE[35]	O[37]	NW[37]	S[37]	NC[37]	*SC*[36]	*A*[36]	0.88[36]	A[36]	P[37]	4[37]	0.923	4.61 B
Dipsacus sylvestris[48]	Dipsacaceae	*TE*[48]	O[48]	NW[48]	S[48]	NC[48]		*A*[2]		U[48]	P[48]	5[48]	1.932	4.96
Epilobium latifolium[49]	Onagraceae	TE[50]	O[50]	NW[49]	I[49]	C[49]		A[2]		W[51]		35[49]		44.17

Appendix 1 (Continued).

Species	Family	Distribution	Habitat	Life form	Parity	Clonality	Compatibility	Pollination	Seed size (mg)	Dispersal syndrome	Seed bank	Life span, previous estimate (yrs)	Lambda (arit. mean)	Conditional life span – mean (yrs)
Eremophila forrestii[52]	Myoporaceae	TE[52]	O[52]	W[52]	I[52]	NC[53]							1.002	988.65
Eremophila maitlandii[52]	Myoporaceae	TE[52]	O[52]	W[52]	I[52]	NC[53]							0.984	84.49
Erigeron kachinensis[54]	Asteraceae	TE[54]	O[54]	NW[54]	I[54]	NC[54]	SI[55]	A[55]		W[55]	P[55]	20[54]		138.28
Eriophorum triste[32]	Cyperaceae	AA[32]	O[32]	NW[32]	I[32]	C[32]							1.052	6.06
Erythronium japonicum[56]	Liliaceae	TE[56]	F[56]	NW[56]	I[56]	NC[56]	SI[56]	A[56]		U	A[56]	20[56]	1.055	80.56
Eupatorium perfoliatum[57]	Asteraceae	TE[57]	O[57]	NW[57]	I[57]	C[57]	SI[57]	A[58]	160[59]	W[57]			0.881	4.52
Eupatorium resinosum[57]	Asteraceae	TE[57]	O[57]	NW[57]	I[57]	C[57]	SI[57]	A[58]	220[59]	W[57]			1.172	7.37
Fagus crenata[1]	Fagaceae	TE[1]	F[1]	W[1]	I[1]	NC[1]	SI[60]	W[61]	101[62]	U[63]				115.64
Fagus grandifolia[64]	Fagaceae	TE[64]	F[64]	W[64]	I[64]	NC[64]	*SI*[2]	W		A		300[65]	1.001	270.66
Fumana procumbens[66]	Cistaceae	TE[66]	O[66]	W[66]	I[66]	NC[66]	SC[66]	A[66]	3.4[66]	A[66]		18.6[66]	0.987	18.90
Gentiana pneumonanthe[67]	Gentianaceae	TE[67]	O[67]	NW[67]	I[67]	NC[67]	SC[68]	A[68]	0.05[69]	U	A[67, 69]	15[69]	1.039	11.00
Iriartea deltoidea[70]	Arecaceae	ST[70]	F[70]	W[70]	I[70]	NC[70]						88[70]	0.946	62.05
Lathyrus vernus[71]	Fabaceae	TE[71]	F[71]	NW[71]	I[71]	NC[71]	SC[71]	A[71]	12.0[71]	U[71]	P[71]		0.995	57.69 (A)
Nothofagus fusca[17]	Fagaceae	TE[17]	F[17]	W[17]	I[17]	NC[17]	SI[72]	W[73]		W[72]	P[2]	450[17]	1.004	246.92
Panax quinquefolium[74]	Araliaceae	TE[74]	F[74]	NW[75]	I[75]	NC[75]	SC[74]			*A*	P[74]	60[74]	1.032	30.83
Pedicularis furbishiae[76]	Scrophulariaceae	*TE*[76]	O[76]	NW[76]	I[76]	NC[76]		A		U[76]	A[76]		1.275	24.72
Phaseolus lunatus[77]	Fabaceae	ST[78]	O[77]	NW[77]	S[77]	NC[77]	SC[77]				P[77]		0.707	4.55 (B)
Phytelephas seemannii[79]	Palmae	ST[79]	F[79]	W[79]	I[79]	NC[79]	SI[79]	A[79]		A[79]	P[79]	85[79]	1.059	77.47
Picea jezoensis/glehnii[3]	Pinaceae	TE[3]	F[3]	W[3]	I[3]	NC[3]	SI[2]	W	3[80]	*W*		300[81]		63.23
Pinguicula alpina[82]	Lentibulariaceae	AA[84]	O[83]	NW[83]	I[83]	NC[83]	SI[84]	A[84]	0,015[85]	U		10.8[83]	1.062	106.12
Pinguicula villosa[82]	Lentibulariaceae	AA[84]	O[83]	NW[83]	I[83]	NC[83]	SC[84]		0,029[85]	U		2.7[83]	1.041	13.54
Pinguicula vulgaris[82]	Lentibulariaceae		O[83]	NW[83]	I[83]	NC[83]	SC[84]	A[84]	0,024[85]	U		10.8[83]	1.027	28.50
Pinus palustris[86]	Pinaceae	TE[86]	F[86]	W[86]	I[86]	NC[86]	SI[2]	*W*		W[86]	A[86]	244[86]	0.899	59.10
Plantago media[87]	Plantaginaceae	TE[88]	O[88]	NW[88]	I[88]	C[88]	*SI*[88]	A[88]	0.35[88]	U[88]	P[88]		0.939	28.07
Podococcus barteri[89]	Arecaceae	ST[89]	F[89]	W[89]	I[89]	C[89]	SI[89]	A[89]	600[89]	A[89]		63[89]	1.013	32.94 (B)
Potentilla anserina[90]	Rosaceae	TE[35]	O[90]	NW[90]	I[90]	C[90]	SI[90]	A[90]	0.8[91]	U	P[91]		0.890	10.96
Primula farinosa[92]	Primulaceae	TE[92]	O[92]	NW[92]	I[92]	NC[92]	*SI*[93]	A[92]	0.09[92]	U[92]	P[92]			21.75
Primula veris[91]	Primulaceae	TE[36]	O[36]	NW[36]	I[36]	NC[36]	*SI*[91]	A[36]	0.69[36]	U[36]	P[36]	90[94]	0.960	52.33
Primula vulgaris[95]	Primulaceae	TE[95]	F[95]	NW[95]	I[95]	NC[95]	SI[96]	A[96]	0.63[96]	A[95]	P[96]	20[96]	1.128	48.03
Pterocarpus angolensis[97]	Fabaceae	ST[97]	F[97]	W[97]	*I*[97]	NC[97]		A[98]		W[98]	A[97]	137[99]	0.971	73.89
Rhopalostylis sapida[100]	Arecaceae	TE[100]	F[100]	W[100]	I[100]	NC[100]				A[100]		220[101]		246.66
Saxifraga cotyledon[102]	Saxifragaceae	AA[102]	O[102]	NW[102]	S[102]	C[102]		A[102]	0.016[91]	W[102]	P[102]		1.092	17.87
Scabiosa columbaria[37]	Dipsacaceae	TE[36]	O[37]	NW[37]	I[37]	NC[37]		*A*[36]	1.32[36]		P[37]		1.076	9.88
Silene acaulis[103]	Caryophyllaceae	AA[103]	O[103]	NW[103]	I[103]	NC[103]	SI[104]	A[105]	0.23[105]	U[106]			1.013	337.16
Silene douglasii var. *oraria*[107]	Caryophyllaceae	TE[107]	O[107]	NW[107]	I[107]	C[107]	SC[107]	A[108]	1.00[108]				0.976	15.27
Silene regia[109]	Caryophyllaceae	TE[109]	O[109]	NW[109]	I[109]	NC[109]	SC[109]	A[109]		U[109]	A[109]		1.6986	43.41
Thrinax radiata[43]	Palmae	ST[43]		W[43]	I[43]	NC[43]						145[43]	1.127	92.81

Appendix 1 (Continued).

Species	Family	Distribution	Habitat	Life form	Parity	Clonality	Compatibility	Pollination	Seed size (mg)	Dispersal syndrome	Seed bank	Life span, previous estimate (yrs)	Lambda (arit. mean)	Conditional life span – mean (yrs)
Tolumnia variegata[110]	Orchidaceae	ST[110]	F[110]	NW[110]	I[110]	NC[110]	SI[110]	A[111]		W[110]				25.03
Viola fimbriatula[112]	Violaceae	TE[113]	O[112]	NW[113]	I[113]	NC[113]	SC[112]	A[112]	0.831[114]	A[112]	P[115]	16.4[113]		20.03
Vochysia ferruginea[116]	Vochysiaceae	ST[116]	F[116]	W[116]	I[116]	NC[116]					A[116]		1.155	322.96

References: [1] – Nakashizuka 1991. [2] – Huxley et al. 1992. [3] – Kubota 1997. [4] – Sato and Hiura 1998. [5] – Suzuki et al. 1987. [6] – Nault and Gagnon 1993. [7] – Huenneke and Marks 1987. [8] – Johansson 1999. [9] – Silva et al. 1991. [10] – Bastrenta et al. 1995. [11] – Jakobsson, A., unpubl. data. [12] – Sterk 1975. [13] – Sterk et al. 1982. [14] – Lesica and Shelly 1996. [15] – Lesica and Shelly 1995. [16] – Hamilton and Mitchell-Olds 1994. [17] – Enright and Ogden 1979. [18] – Pascarella and Horvitz 1998. [19] – Pascarella 1997. [20] – Kinoshita 1987. [21] – Bierzychudek 1982. [22] – Damman and Cain 1998. [23] – Cain et al. 1998. [24] – Maschinski et al. 1996. [25] – Travis et al. 1996. [26] – Lesica 1995. [27] – Lesica, P., pers. comm. [28] – Horvitz and Schemske 1995. [29] – Horvitz and Schemske 1988. [30] – Price and Bowman 1994. [31] – Fiedler 1987. [32] – Tolvanen, A., Schroderus, J. and Henry, G. H. R., unpubl. data. [33] – Ford et al. 1991. [34] – Löfgren et al. 2000. [35] – Hultén and Fries 1986. [36] – Grime et al. 1988. [37] – Verkaar and Schenkeveld 1984. [38] – Alvarez-Buylla 1994. [39] – Martinez-Ramos and Alvarez-Byulla 1995. [40] – Meagher 1982. [41] – Meagher 1980. [42] – Meagher and Antonovics 1982. [43] – Olmsted and Alvarez-Buylla 1995. [44] – Cochran and Ellner 1992. [45] – Bornbusch et al. 1994. [46] – Primack and Hall 1990. [47] – Moloney 1988. [48] – Werner and Caswell 1977. [49] – Doak 1992. [50] – Doak 1991. [51] – www.nps.gov/bela/html. [52] – Watson et al. 1997a. [53] – Watson et al. 1997b. [54] – Allphin and Harper 1997. [55] – Allphin-Woolstenhulme, L., pers. com. [56] – Kawano et al. 1987. [57] – Byers and Meagher 1997. [58] – Byers 1995. [59] – Byers 1998. [60] – Kitamura et al. 1992. [61] – Saito et al. 1991. [62] – Hiura et al. 1996. [63] – Akashi 1997. [64] – Batista et al. 1998. [65] – Abrams and Copenheaver 1999. [66] – Bengtsson 1993. [67] – Oostermeijer et al. 1996. [68] – Raijmann et al. 1994. [69] – Oostermeijer et al. 1992. [70] – Pinard 1993. [71] – Ehrlén 1995. [72] – Burrows and Lord 1993. [73] – Randall 1991. [74] – Charron and Gagnon 1991. [75] – Nantel et al. 1996. [76] – Menges 1990. [77] – Degreef et al. 1997. [78] – www.greed.isc.tamu.edu/flora. [79] – Bernal 1998. [80] – Takahashi and Kohyama 1999. [81] – Kubota et al. 1994. [82] – Svensson, B. and Carlsson, B., unpubl. data. [83] – Svensson et al. 1993. [84] – Molau 1993. [85] – Karlsson 1986. [86] – Platt et al. 1988. [87] – Eriksson, Å., unpubl. data. [88] – Sagar and Harper 1964. [89] – Bullock 1980. [90] – Eriksson 1988. [91] – Lehtilä, K and Ehrlén, J., unpubl. data. [92] – Lindborg, R. and Ehrlén, J., unpubl. data. [93] – Baker et al. 1994. [94] – Harper and White 1974. [95] – Valverde and Silvertown 1998. [96] – Boyd et al. 1990. [97] – Desmet et al. 1996. [98] – www.arboretum.harvard.edu/kalimantan. [99] – Stahle et al. 1999. [100] – Enright and Watson 1992. [101] – Enright 1992. [102] – Dinnetz and Nilsson 2001. [103] – Morris and Doak 1998. [104] – Shykoff 1988. [105] – Delph et al. 1999. [106] – Jones and Richards 1962. [107] – Kephart and Paladino 1997. [108] – Kephart et al. 1999. [109] – Menges and Dolan 1998. [110] – Calvo 1993. [111] – Ackerman et al. 1997. [112] – Solbrig et al. 1988b. [113] – Solbrig et al. 1988a. [114] – www.bids.ac.uk. [115] – Andersson 1983. [116] – Boucher and Mallona 1997.