Evolution of senescence in iteroparous perennial plants

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ABSTRACT

We applied four tests to detect evidence of the evolution of senescence in life tables and fecundity schedules for 65 species of iteroparous perennial plants. Test 1 determined the pattern of variation in age-specific mortality with age (μ_x). Fifty-five percent of species showed an increase in, or maximum value of, μ_x at the end of life. In test 2, we tried to separate mortality into initial or baseline mortality and senescent mortality by fitting the survival data of these 65 species to Weibull functions. Unlike published results with animals, the rate of senescence was independent of initial mortality rate. However, a positive relationship was found between rate of senescence and reproductive lifespan, suggesting increasing risk of death with successive reproductive events. It has been suggested that a decline in reproductive value with age is a better diagnostic of senescence, but (in test 3) this occurred in only 9% of species (6/65). Our fourth test detected a positive correlation between age at first reproduction (a) and mean reproductive lifespan (L_a), as predicted by the theory that senescence is due to a trade-off between adult survival and reproduction. Comparing species within the two largest families present in the data set, we found a correlation between a and L_a among the Liliaceae, which was largely represented by ramet life tables, but not among the Poaceae, which was largely represented by genet life tables. Clonal growth, which is common in plants, is a necessary but not a sufficient condition to prevent the evolution of senescence. We predict that clones that fragment are more likely to escape the evolution of senescence at the genet level than clones that remain physiologically integrated.

Keywords: age at first reproduction, mortality rate, perennial plants, reproductive lifespan, reproductive value, senescence, Weibull function.

INTRODUCTION

The variety of modern theories for the evolution of senescence have in common the axiom that the force of natural selection declines with age (Rose, 1991), thereby explaining why

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the damaging physiological changes associated with senescence are tolerated by the evolutionary process. The unity of germ line and soma that occurs in plants and clonal animals is a necessary, although not a sufficient, condition to prevent the evolution of senescence. For senescence to be avoided in plants and clonal species, the force of natural selection on the genetic individual (genet) should not decline with age (Gardner and Mangel, 1997). Plants are a particularly interesting case because the unity of germ line and soma predisposes them to immortality, but the group includes significant numbers of semelparous species that senesce quite dramatically after reproduction, as well as clonal species in which genets appear to be immortal (Watkinson, 1992). It is unclear whether most plant species that lie between these extremes senesce or not (Roach, 1993). The main problem in resolving this question for plants is really no different from that in other taxa and hinges on (1) a clear definition of senescence and (2) the availability of good data. Senescence is customarily defined as a decline in physiological state with age, which can be expected to increase age-specific mortality rate (μ_x). Partridge and Barton (1996) have argued that a decline in Fisher's (1958) reproductive value (v_x) with age is a better test of senescence than μ_x because it measures the combined effect of age-specific changes in fecundity and survival.

Here we use demographic data for 65 species of perennial plants studied in natural populations to test for the signature of senescence in age-specific patterns of mortality rate and reproductive value. Traditionally, to investigate the presumed exponential increase in mortality at advanced ages, the Gompertz function has been fit to data on age-specific mortality (see Finch, 1990). Recently, however, Ricklefs (1998) suggested the use of the Weibull function as a convenient model to separate mortality due to environmental causes from mortality due to physiological deterioration late in life. We therefore use the Weibull function as a mechanistic model to test for an increase in mortality rate independent of early-life mortality. Finally, an indirect test is based upon the hypothesis that senescence arises from a trade-off between early reproduction and later survival (Partridge, 1987). A corollary of this evolutionary trade-off is that, other things being equal, senescence in iteroparous organisms will occur at an earlier age if they reproduce earlier in life (Williams, 1957; Kirkwood and Rose, 1991; Stearns, 1992). If this occurs, there should be a positive relationship between the age at first reproduction (a) and mean lifespan (L). This has been demonstrated for mammals by Harvey and Zammuto (1985); data collated by Harper and White (1974) suggest that it also occurs in plants. Sutherland *et al.* (1986) have pointed out that these two life-history variables are not independent of each other because age at first reproduction is a component of lifespan. We therefore test for a correlation between a and mean reproductive lifespan ($L_a = L - a$).

METHODS

Demographic data

Few life tables are available for perennial plants because, at least for the purposes of studying plant population dynamics, stage-based models are thought to be more appropriate (Caswell, 1989). However, life tables and other age-based life-history parameters can be calculated from stage projection matrices (Cochran and Ellner, 1992). We used the program STAGECOACH (Cochran and Ellner, 1992) for this purpose (see next section). Projection matrices used in this study were taken from the data set of 66 + 11 matrices for perennial

plants compiled by Silvertown *et al.* (1993) and Silvertown and Franco (1993), respectively, augmented by matrices for seven new species. Since we are interested in the age-specific distribution of fecundity (m_x), species in the data set were omitted where m_x values were available for only one stage class (all semelparous species were therefore omitted), or where it had been assumed in compiling the original matrix that all reproductive stages had the same fecundity. A small number of other matrices used by Silvertown *et al.* (1993) and Silvertown and Franco (1993) were not convergent and were omitted because STAGECOACH could not produce a life table (e.g. retrogression to previous stages of the life cycle made individuals 'immortal'). Although one could argue that species comprising 'immortal' individuals provide evidence against senescence in plants, the fact that some individuals retrogress to earlier stages does not mean they can do so indefinitely. By averaging over the whole population, the matrix method cannot separate individuals that retrogress but eventually die from individuals that could potentially progress–retrogress indefinitely. In the end, the data set contained 65 species (44 herbs and 21 woody plants), two of which failed to produce estimates of age at first reproduction (Table 1).

Estimates of survival in the terminal size class were usually based on very small sample sizes and small errors here can have large effects on the estimates of average longevity calculated by Cochran and Ellner's (1992) algorithm. For this reason, survival probabilities in the terminal stage classes of the two tree species *Astrocaryum mexicanum* (Piñero *et al.*, 1984) and *Avicennia marina* (Burns and Ogden, 1985) were reduced from the respective values of 0.999 and 1.0 given by the authors in the original matrices to the value 0.9. This gave average lifespans for these species that were in closer accordance with what is known about their respective longevities. The natural history of species did not require this correction in any of the other 63 species in the data set.

A number of species in the data set were clonal, but the projection matrices for these species described the dynamics of either ramets or genets, because no field study has yet reported both. For the purposes of this study, we therefore followed convention and treated (usually aclonal) genet demography and clonal ramet demography equivalently. The projection matrices for genets of clonal species were for eight of the nine grasses analysed (Table 1).

Computation and analysis of variables

STAGECOACH was used to compute vectors of age-specific survival (l_x) and fecundity (m_x) for each projection matrix (A). Demographic data are input to STAGECOACH as three separate component matrices: $A = B + P + F$, where B corresponds to the birth or fecundity (m_x) elements of the full matrix A, P contains the survival and growth coefficients and F the fission elements (Cochran and Ellner, 1992). Ramet production, where it occurred, was treated as a birth process and so there was no fission in our data set (i.e. $F = 0$). Following Cochran and Ellner (1992), P^{x-1} contains the survival probabilities over an interval of $x - 1$ time units, and the probability of being alive and in stage i at age x for a type-j newborn (e.g. seedling or clonal recruit) is $P^{x-1}(i, j)$. Age-specific survival of a type-j newborn is, therefore:

$$l_x(j) = \sum_{i=1}^{n} P^{x-1}(i, j) \qquad x = 1, 2, \ldots \qquad \text{(equation 2 in Cochran and Ellner, 1992)}$$

Table 1. Life-history attributes and parameters of the Weibull function calculated for 65 species of perennial herbs and woody plants

Species	Family	λ (year⁻¹)	L (years)	a (years)	μ_x trend	v_x trend	n	μ_a (year⁻¹)	$a \pm$ S.E. (year$^{-(b+1)}$)		$b \pm$ S.E. (dimensionless)		ω (year⁻¹)
Herbs													
Agropyron repens*	POAC	2.963	6	1	3	1	6	1.0580	4.4234	0.0394	1.0224	0.0179	2.0860
Andropogon semiberberis	POAC	1.252	8	2	3	4	4	0.2439	1.9361	0.0345	1.1406	0.0243	1.3616
Anthyllis vulneraria	FABA	1.416	5	3	3	2	4	1.2738	0.0596	0.0192	1.0000	0.6947	0.2441
Arisaema triphyllum*	ARAC	1.073	24	8	1	2	7	0.1057	−0.0935	0.0081	1.2752	0.0484	
Aristida bipartita	POAC	1.188	25	2	2	2	4	0.1286	0.0368		1.0001		0.1919
Armeria maritima	PLUM	1.458	28	5	2	2	11	0.1358	3.8651	0.0669	1.1309	0.0205	1.8860
Bothriochloa insculpta	POAC	1.094	14	2	2	2	5	0.0514	0.1133		1.0000		0.3365
Calathea ovandensis	MARA	1.551	15	2	2	2	4	0.2744	1.1126	0.0778	1.0001	0.1007	1.0548
Calochortus albus*	CALO	1.542	16	3	3	2	4	0.1797	0.0483	0.0030	1.0935	0.0631	0.2351
Calochortus obispoensis*	CALO	1.023	71	21	2	4	3	0.0202	1.2291	0.0000	1.0001	0.0000	1.1087
Calochortus pulchellus*	CALO	1.115	16	3	3	2	4	0.3803	0.6563	0.0761	1.3115	0.1770	0.8335
Calochortus tiburonensis*	CALO	1.156	58	5	2	2	3	0.0389	−0.0023		2.7247		
Chamaelirium luteum	MELA	1.004	58	13	2	2	24	0.0622	0.4663	0.0441	1.2350	0.0475	0.7108
Cleome droserifolia	CAPP	1.118	76	8	2	1	15	0.7303	0.5582	0.0003	2.0021	0.0011	0.8235
Clintonia borealis*	CONV	1.128	13	4	1	2	3	0.1381	−0.2170	0.0304	1.0605	0.1240	
Cynoglossum virginianum[a]	BORA	1.103	11	2	2	2	7	0.4883	1.2986	0.0987	1.1711	0.1440	1.1279
Cypripedium acaule	ORCH	1.081	25	4	2	4	8	0.4938	4.6514	0.0153	2.0526	0.0094	1.6546
Danthonia sericea	POAC	1.196	41	2	2	2	6	0.2873	1.9054	0.1625	1.0001	0.1233	1.3804
Digitaria eriantha	POAC	1.203	10	4	1	2	3	0.2006	−0.4441	0.0406	1.2534	0.0856	
Disporum sessile*	CONV	0.936	8	3	3	4	13	0.4396	0.2064	0.0233	1.0001	0.2118	0.4544
Disporum smilacinum*	CONV	1.427	12	3	1	2	8	0.1536	−0.5054	0.0469	1.0302	0.0907	
Erythronium japonicum*	LILI	1.001	14	2	3	2	13	0.4418	−0.0133	0.0039	3.3006	0.1321	
Fritillaria meleagris*	LILI	1.018	19	3	2	2	8	0.2071	−0.0024	0.0043	3.5431	0.4285	

Gentiana pneumonanthe	GENT	1.335	11	2	2	2	4	1.6954	0.0446	1.6984	1.8429	0.0749	1.2048
Heteropogon contortus	POAC	0.974	21	2	2	2	5	0.2240	0.0536	0.1585	1.0000	0.2957	0.3981
*Hieracium floribundum**	ASTE	1.012	19	2	2	2	4	0.5122	0.1756	0.9186	1.3195	0.3488	0.9640
Limonium delicatulum	PLUM	1.264	19	6	3	2	5	0.1042	0.0724	3.0519	1.1410	0.0228	1.6840
*Narcissus pseudonarcissus**	AMAR	0.976	12	1	2	2	3	0.2499		−0.0051	3.4850		
Ophrys sphegodes	ORCH	1.038	4	2	3	4	7	0.5526	0.1047	0.7474	2.1372	0.2716	0.9114
Panax quinquefolium	ARAL	0.996	17	5	3	2	6	0.1097	0.2236	6.0631	1.4230	0.0990	2.1039
*Pedicularis furbishiae**	SCRO	1.035	12	3	3	4	6	0.3592	0.0353	0.0409	1.0000	0.0145	2.0102
Pinguicula alpina[b]	LENT	1.033	41	10	2	2	11	0.0678	0.0110	3.7966	1.0141	0.0020	1.9394
Pinguicula villosa[b]	LENT	0.997	13	5	3	2	7	0.2734	0.0072	2.2510	1.0000	0.0045	1.5003
Pinguicula vulgaris[b]	LENT	1.086	35	10	2	2	11	0.0656	0.0461	4.1184	1.0661	0.0088	1.9839
*Plantago coronopus**	PLAN	1.142	4	2	2	2	3	1.1239	0.0000	0.0267	1.0041	0.0004	0.1640
*Podophyllum peltatum**	BERB	1.158	13	3	2	2	4	0.2136	0.0226	0.2433	1.1009	0.1040	0.5103
*Potentilla anserina**	ROSA	0.883	7		3	4	6	0.3327	0.0341	1.2327	1.1602	0.0474	1.1017
*Ranunculus acris**	RANU	1.206	6	3	2	2	4	0.5238	0.1126	1.7907	2.0272	0.1716	1.2122
*Ranunculus repens**	RANU	0.498	6	4	3	4	4	0.7745	0.0133	2.0651	1.0000	0.0132	1.4370
Scabiosa columbaria	DIPS	1.030	12	7	3	2	3	0.2051	0.0026	0.0360	1.0001	0.0889	0.1898
Setaria incrassata	POAC	0.936	18	4	1	2	5	0.3272	0.0087	−0.3032	1.2852	0.0358	
Themeda triandra	POAC	0.997	52	2	2	2	6	0.1565	0.0041	−0.0158	2.7867	0.0536	
Tolumnia variegata	ORCH	0.847	15	2	2	2	4	0.2831	0.0296	0.3793	1.3884	0.0891	0.6664
*Viola fimbriatula**	VIOL	1.484	16	4	1	2	14	0.0798		0.0079	3.2426		0.3196

Woody plants

*Alnus incana**	BETU	0.971	20	4	3	3	5	0.1303	0.0291	0.2872	1.0939	0.0834	0.5511
Araucaria cunninghamii	ARAU	1.009	245	102	3	3	10	0.0200	0.0486	6.9824	1.2254	0.0126	2.3947
Araucaria hunsteinii	ARAU	1.020	182	63	3	1	7	0.0360	0.0807	4.0163	1.2178	0.0183	1.8719
Astrocaryum mexicanum	AREC	1.007	123	42	3	3	14	0.0112	0.0430	6.8855	1.1395	0.0052	2.4641
Avicennia marina	VERB	1.237	40	3	3	2	6	0.2152	0.1314	1.3238	1.0482	0.1214	1.1468
Banksia ericifolia	PROT	1.609	45	12	1	2	9	0.0559	0.0318	−0.3721	1.2015	0.0356	
*Betula nana**	BETU	0.992	11	2	3	4	4	0.2026	0.0016	0.6740	1.0428	0.0030	0.8244

Table 1.—cont.

Species	Family	λ (year⁻¹)	L (years)	a (years)	μx trend	vx trend	n	μa (year⁻¹)	a ± S.E. (year⁻(b+1))		b ± S.E. (dimensionless)		ω (year⁻¹)
*Calluna vulgaris**	ERIC	2.995	20	5	2	1	6	0.4500	0.0256	0.0012	1.6770	0.0538	0.2542
Cassia nemophila	FABA	1.207	44	3	3	2	12	1.0425	0.4040	0.0075	1.9619	0.0461	0.7364
Cecropia obtusifolia[c]	CECR	1.012	28	5	3	2	8	0.2551	9.2412		2.0837		2.0567
Fumana procumbens[d]	CIST	1.018	17	5	3	2	6	0.1165	0.3026	0.0220	1.0000	0.0662	0.5501
Iriartea deltoidea	AREC	1.081	67	29	2	2	6	0.0778	0.0228		2.2024		0.3070
Lindera benzoin[e]	LAUR	1.017	59	2	2	2	7	0.7827	−0.0146		1.0000		
Nothofagus fusca	NOTH	1.006	247	43	2	2	4	0.0201	0.4096	0.0125	1.9261	0.0163	0.7371
Pentaclethra macroloba	FABA	1.002	138	79	3	2	14	0.0235	2.0945	0.0138	1.8724	0.0117	1.2936
Petrophile pulchella	PROT	1.643	62	6	2	2	9	0.0318	1.9815	0.0638	1.0969	0.0158	1.3856
Pinus palustris	PINA	0.998	226	38	3	3	8	0.0164	0.4193	0.0373	1.2035	0.0296	0.6741
*Podococcus barteri**	AREC	1.013	34	10	3	3	6	0.0513	0.5966	0.0241	1.2332	0.0205	0.7935
Psidium guajava	MYRT	0.994	176	9	2	2	12	0.0408	6.1677		5.4377		1.3266
Rhopalostylis sapida	AREC	1.007	222	62	3	3	8	0.0129	3.2233	0.0016	1.9883	0.0012	1.4794
Vatica hainanensis	DIPT	1.000	63	22	3	2	12	0.0454	4.9543	0.0187	1.4491	0.0069	1.9220

Note: n is the dimension of the projection matrix. All other parameters are explained in the text. Missing values mean these parameters could not be obtained using the methods employed (see text). s.e. = the standard error.

*Demographic information is for ramets; all other plants = genets.

Species added to those in Silvertown *et al.* (1993) and Silvertown and Franco (1993) are as follows: [a]Cipollini *et al.* (1993), [b]Svensson *et al.* (1993), [c]Alvarez-Buylla (1994), [d]Bengtsson (1993), [e]Cipollini *et al.* (1994),

Family abbreviation: AMAR = Amaryllidaceae, ARA = Araceae, AREC = Arecaceae, ARAL = Araliaceae, ARAU = Araucariaceae, ASTE = Asteraceae, BERB = Berberidaceae, BETU = Betulaceae, BORA = Boraginaceae, CALO = Calochortaceae, CAPP = Capparidaceae, CECR = Cecropiaceae, CIST = Cistaceae, CONV = Convallariaceae, DIPS = Dipsacaceae, DIPT = Dipterocarpaceae, ERIC = Ericaceae, FABA = Fabaceae, GENT = Gentianaceae, LAUR = Lauraceae, LENT = Lentibulariaceae, LILI = Liliaceae, MARA = Marantaceae, MELA = Melanthiaceae, MYRT = Myrtaceae, NOTH = Nothofagaceae, ORCH = Orchidaceae, PINA = Pinaceae, PLAN = Plantaginaceae, PLUM = Plumbaginaceae, POAC = Poaceae, PROT = Proteaceae, RANU = Ranunculaceae, ROSA = Rosaceae, SCRO = Scrophulariaceae, VERB = Verbenaceae, VIOL = Violaceae.

If more than one type of newborn exists, an overall measure of survival is calculated by weighting each newborn type according to the formula:

$$l_x = \sum_{j=1}^{n} l_x(j)m_j \qquad x = 1, 2, \ldots \qquad \text{(in Table 2 of Cochran and Ellner, 1992)}$$

where m_j is the distribution of type-j newborns (i.e. j-type fecundity) at stable stage distribution.

STAGECOACH also yielded the mean age of first reproduction a (Cochran and Ellner, 1992, eq. 15) and mean lifespan L (in reality the number of time units until death for an individual currently in stage 1; Cochran and Ellner, 1992, eq. 3). The Malthusian parameter r for each population was calculated as $\ln(\lambda)$, where λ was the dominant eigenvalue of A.

Mortality rate (the instantaneous force of mortality; Tatar *et al.*, 1993) was calculated as $\mu_x = -\ln(l_{x+1}/l_x)$ and v_x was calculated according to the discrete version of Fisher's formula (Caswell, 1989; Cochran and Ellner, 1992, eq. 33). Age-specific trends in μ_x and v_x were each classified by inspection into one of three and four patterns, respectively (see Results). Because the life tables obtained for this study are projections from matrix data (and STAGECOACH assumes the matrix to be literally true) and because many papers do not give sample sizes from which the matrix coefficients were derived, it was not possible to calculate confidence intervals for the resulting life tables. Taken at face value, however, the numerical output of these projections clearly indicates whether μ_x increases monotonically, decreases monotonically or remains constant.

To separate extrinsic mortality at young stages of the life cycle from that associated with senescent decline at later ages, the resulting survivorship curves were fitted to Weibull functions using unweighted non-linear regression (Hooke-Jeeves pattern moves) of Statistica (StatSoft, 2000). The Weibull function has the form:

$$l_x = \exp(-\mu_0 x - [(ax^{b+1})/(b+1)])$$

where μ_0 is the initial mortality rate, a measures the magnitude of additional mortality and b is a shape parameter (for a discussion of the mathematical advantages of the Weibull function over the Gompertz function in separating initial, extrinsic mortality from age-related, intrinsic mortality, see Ricklefs, 1998). Letting Statistica fit all three parameters resulted in the estimation of negative initial mortality rates for many species. Therefore, following Promislow (1991), initial mortality rate was assumed to be equal to that occurring at the age of sexual maturity (i.e. $\mu_0 = \mu_a$). Unlike Ricklefs (1998), however, we did not deem it appropriate to use average mortality at other ages because seed, seedling and even juvenile mortality are usually very high in plant populations, only decreasing after the plant has reached a certain size-position in the canopy (see Fig. 1b,c) and because it is impossible to restrict objectively the age range of adults that measures this baseline mortality. We therefore assumed μ_a to represent a standard baseline adult mortality over which senescent mortality accrues. Once a and b had been estimated, the rate of senescence (ω) was calculated as (Ricklefs, 1998):

$$\omega = a^{1/(b+1)}$$

The method of phylogenetically independent contrasts (Felsenstein, 1985), as implemented by the CAIC program (Purvis and Rambaut, 1995), was used to test for correlations between life-history parameters, using log-transformed data and branch lengths set equal.

A supertree (Appendix) was constructed, based on molecular phylogenies supplemented by taxonomic classification where necessary.

RESULTS

Age-specific mortality rate

Three distinct patterns of variation in μ_x with x were found in the sample of 65 species (Fig. 1). These patterns are easily distinguished by eye: Type 1 (Fig. 1a) showed an asymptotic increase in μ_x with age, Type 2 (Fig. 1b) showed an asymptotic decrease in μ_x with age, and Type 3 (Fig. 1c) showed a minimum μ_x value between the youngest and oldest ages. The pattern shown by each species is indicated in the column 'μ_x trend' of Table 1. Few species displayed Type 1 curves (6/44 herbs and 1/21 woody species), one-half and one-third (23/44 and 6/21) of herbaceous and woody plants, respectively, showed curves of Type 2, and one-third of herbs and two-thirds of woody plants (15/44 and 14/21, respectively) had Type 3 curves. Of those species with an increase in μ_x towards the end of the life cycle
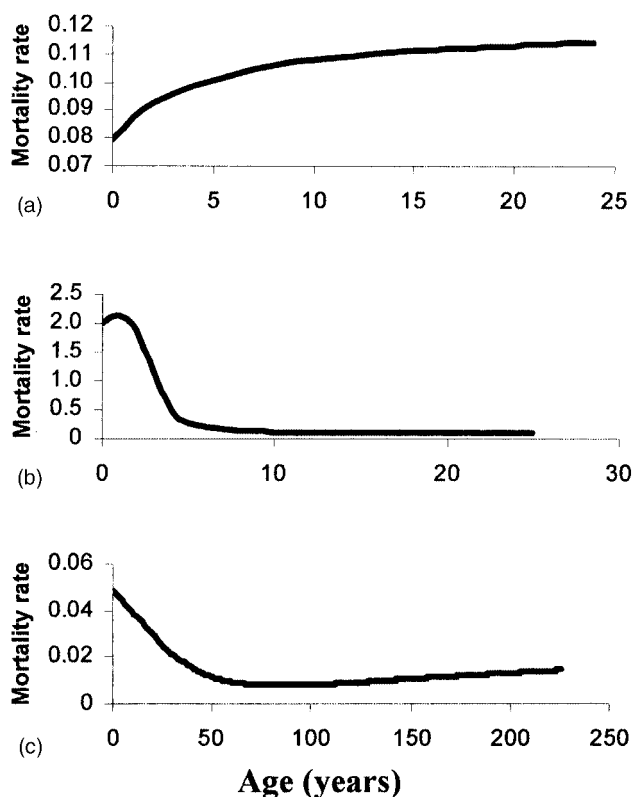
Fig. 1. Patterns of variation in age-specific mortality (μ_x) with age x. (a) Type 1 illustrated by *Arisaema triphyllum*, (b) Type 2 illustrated by *Cypripedium acaule* and (c) Type 3 illustrated by *Pinus palustris*.

(Types 1 and 3), the information for 12 herbs and three woody species corresponded to ramets, not genets.

Rate of senescence

The rate of senescence (ω) varied from 0.16 in *Plantago coronopus* to 2.46 in *Astrocaryum mexicanum*. Considering that survival in the last matrix category for the latter was reduced from the reported value, the next highest value was that of *Araucaria cunninghamii* (2.39). There was no correlation between rate of senescence and initial mortality rate (contrasts of log(ω) *vs* contrasts of log(μ_a); $r^2 = 0.057$; $P = 0.096$). Figure 2a shows this relationship employing the absolute species values (as opposed to their contrasts). Although herbs had higher initial mortality rates than woody plants (mean ± standard deviation: 0.358 ± 0.355, $n = 44$ for herbs *vs* 0.173 ± 0.272, $n = 21$ for woody plants; Kruskal-Wallis $H_{1,65} = 12.30$, $P < 0.001$), their rates of senescence covered similar ranges (mean ± standard deviation: 1.053 ± 0.626, $n = 34$ *vs* 1.198 ± 0.684, $n = 19$; Kruskal-Wallis $H_{1,53} = 0.47$, $P = 0.49$). We could not discern any particular pattern of variation in ω (e.g. with lifespan, successional status as reflected by λ, etc.). Six of seven species with Type 1 mortality curves yielded negative values of parameter a of the Weibull function. This meant that ω could not be calculated for these species (Table 1). In contrasts, this only happened with 5 of 29 Type 2 and 1 of 29 Type 3 curves (Table 1). Beyond this, there did not appear to be any correlation between the parameters of the Weibull function and the types of mortality curve (i.e. Types 2 or 3) found in the previous section. A few of the species yielded ill-conditioned correlation matrices (i.e. these could not be inverted) and their standard errors could not be computed (Table 1).

The regression through the origin between the contrasts of the logarithms of ω and L_a indicates that rate of senescence roughly increases as one-tenth of the duration of the reproductive period ($n_{spp} = 51$; $n_{contrasts} = 47$; $r = 0.350$; $P < 0.05$; slope of the relationship = 0.109 ± 0.043, mean ± standard error; Fig. 2b). Finally, L, L_a and a were all negatively correlated with μ_a (regression through the origin of the contrasts of log-transformed data: $n_{spp} = 65, 63, 63$, respectively; $n_{contrasts} = 59, 57, 57$; $r = 0.679, 0.616, 0.781$; $P < 0.001$ in all three cases; slopes = −0.547 ± 0.078, −1.261 ± 0.215, −0.612 ± 0.065, respectively, mean ± standard error). Figure 2c shows the last of these three relationships.

Reproductive value

The shape of the reproductive value versus age curve (v_x) could be classified into four types (Fig. 3): Type 1 increased exponentially with age in two herbs and two woody species, Type 2 increased asymptotically with age in 34 herbs and 12 woody plants, Type 3 had a maximum value at intermediate ages in six woody species, and Type 4 (eight herbs and one woody plant) peaked at an early age, then dropped suddenly and later either increased asymptotically (without reaching the maximum) or remained constant. We differentiate these two types because, unlike Type 3, in Type 4 curves the drop did not proceed monotonically until the end of life. A common feature of Types 2, 3 and 4 is that v_x decelerated at old ages, but only in six long-lived woody species (Type 3) did it actually decline monotonically with age after reaching a maximum some time during their reproductive lifespan. As might be expected, the shape of the v_x function was not independent of the shape of the
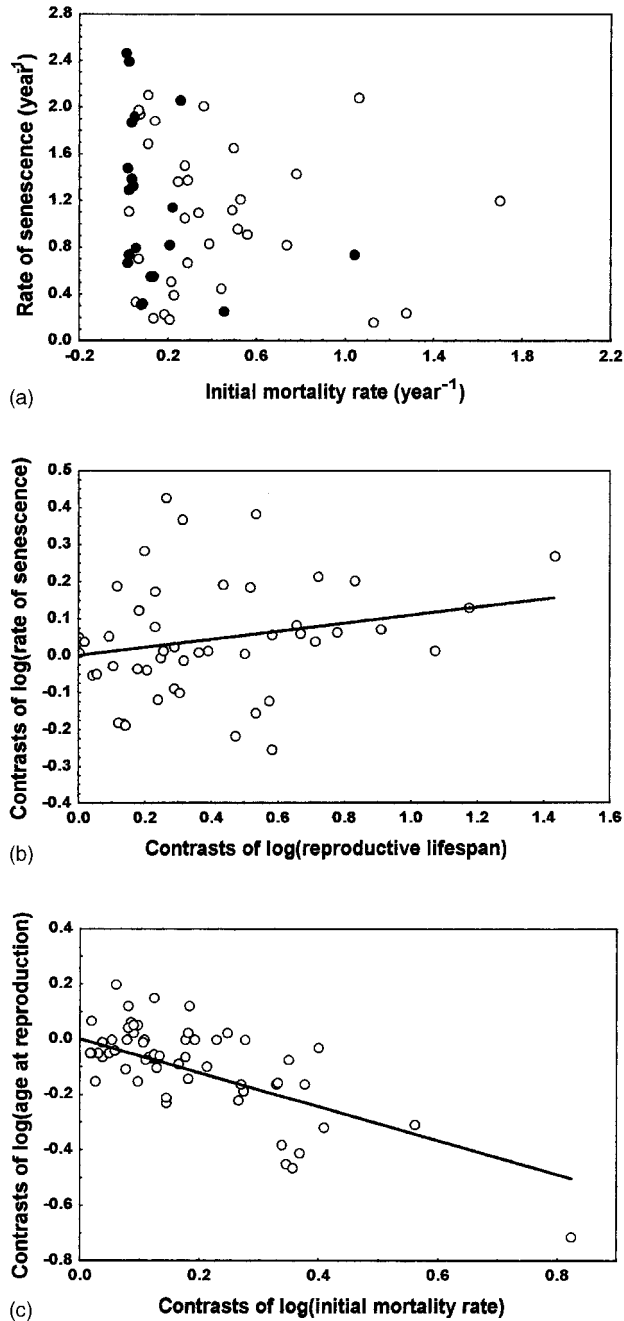
Fig. 2. The relationships between (a) rate of senescence (ω) and initial mortality rate (μ_a), (b) ω and reproductive lifespan (L_a), and (c) age at first reproduction (a) and μ_a. In (a), open symbols represent herbs, filled symbols woody plants. (b) and (c) show the results of the analysis employing phylogenetically independent contrasts on log-transformed variables. Regression statistics are given in the text.

μ_x curve (log-likelihood ratio of the contingency table of μ_x versus v_x types: $\chi^2 = 19.59$; $P < 0.01$). The cell that contributed the most to the total χ^2 was Type 3 coinciding in both functions (i.e. increasing μ_x and decreasing v_x; $\chi^2 = 4.13$; observed frequency higher than expected by chance).

Age of first reproduction and mean reproductive lifespan

Contrasts of age at first reproduction and reproductive lifespan were positively correlated (Fig. 4) (regression through the origin on the respective contrasts of log-transformed data: $n_{spp} = 63$; $n_{contrasts} = 57$; $r = 0.575$; $P < 0.0001$; slope 0.220 ± 0.042, mean $\pm$ standard error). The slope (s) of this relationship indicates that age at first reproduction was between one-fifth and one-quarter of a species reproductive lifespan. Although in cross-species analyses there was evidence of a higher slope–lower intercept for woody plants than herbs in this relationship (analysis of covariance: $F_{1,60} = 32.85$, $P < 0.0001$ for reproductive lifespan; $F_{1,60} = 4.66$, $P < 0.05$ for life form; $F_{1,60} = 9.45$, $P < 0.01$ for the interaction between reproductive lifespan and life form), independent contrasts of the relationship between the residuals of the predicted CAIC (comparative analysis by independent contrasts) relationship and life form (entered as a categorical variable with two possible values: herbaceous or woody) did not show the expected difference ($t = 0.61$, $n_{contrasts} = 8$, $P > 0.5$; Wilcoxon signed-rank test $T_s = 16$, $n = 8$, $P > 0.8$). However, because the number of contrasts in this case was too low, we cannot rule out the possibility of a different a versus L_a relationship between herbs and woody plants unless a larger number of species is studied. Regressions within the two largest herb groups, Liliaceae and Poaceae, showed a contrasts to be correlated with L_a contrasts in the Liliaceae *sensu lato* (*Chamaelirium luteum* to *Cypripedium acaule* in the phylogenetic tree in the Appendix; $n_{spp} = 11$; $n_{contrasts} = 7$; $r = 0.841$; $P < 0.01$; $s = 0.354 \pm 0.093$, mean $\pm$ standard error) but not in the grasses ($n_{spp} = 9$; $n_{contrasts} = 8$; $r = 0.192$; $P > 0.60$).

DISCUSSION

Mortality rate and rate of senescence

In more than half the species in our data set (36/65), mortality rate (μ_x) increased or reached a maximum at the end of life. Such patterns of increasing mortality rate with age in wild populations may reflect senescence or an increase in environmentally induced mortality and it is not usually possible to decide which. In a comparative analysis of senescence in mammals, Promislow (1991) tried to circumvent this problem by fitting the Gompertz equation to life-table data, but this is unsatisfactory because it assumes that senescent mortality is a compound (i.e. multiplicative) effect of the same mortality factors that affect young individuals (Abrams, 1993; Gaillard *et al.*, 1994; Abrams and Ludwig, 1995; Ricklefs, 1998). Thus, Ricklefs has proposed the use of the Weibull function as a model that attempts to separate mortality due to extrinsic causes (approximated by mortality rate at young stages of the life cycle) from mortality due to physiological deterioration late in life. Using this model, Ricklefs found a positive relationship between rate of senescence (ω, calculated from parameters a and b of the Weibull function) and 'baseline mortality rate' (estimated as 'average mortality rate of adults over age classes showing a low and relatively constant mortality rate'). That is, species senesce in proportion to the intensity of extrinsic mortality.
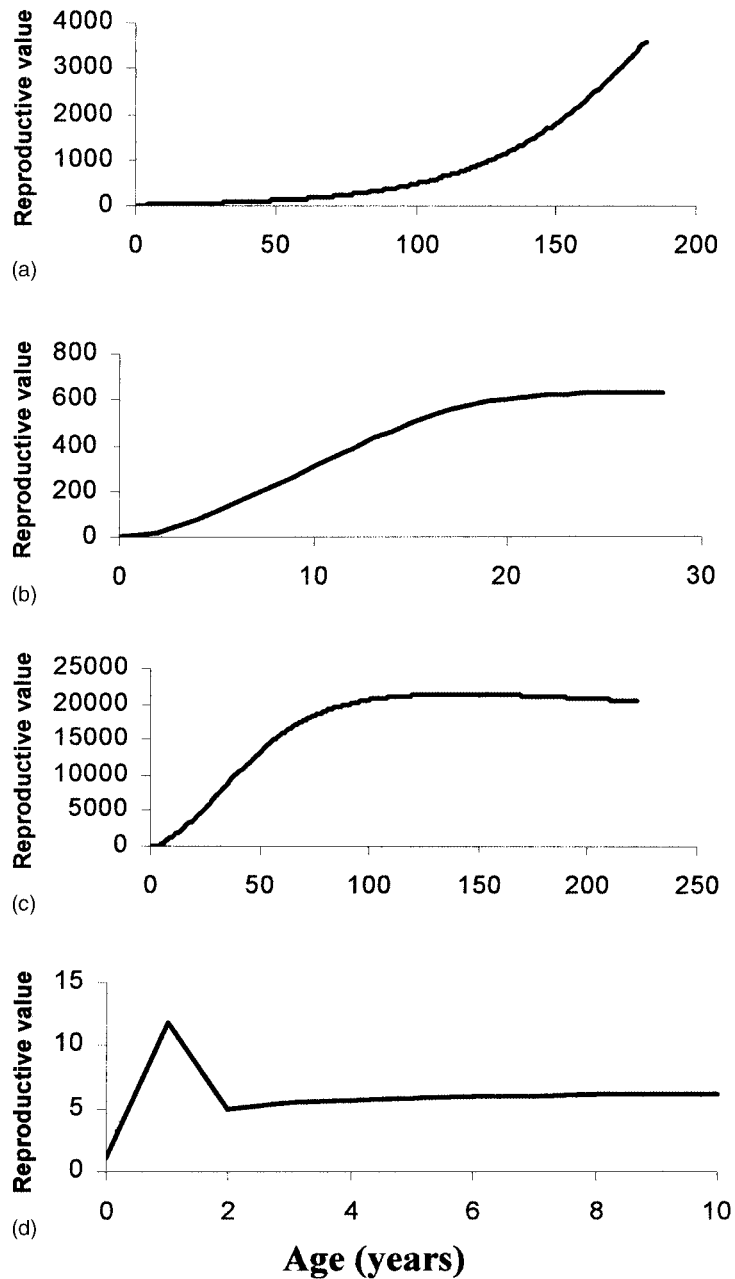
Fig. 3. Patterns of variation in age-specific reproductive value (v_x) with age x. (a) Type 1 illustrated by *Araucaria hunsteinii*, (b) Type 2 illustrated by *Armeria maritima*, (c) Type 3 illustrated by *Rhopalostylis sapida* and (d) Type 4 illustrated by *Andropogon semiberberis*.

We, however, failed to find this positive relationship (regression through the origin on the respective contrasts of log-transformed data: $n_{spp} = 53$; $n_{contrasts} = 49$; $r = 0.238$; $P = 0.096$;
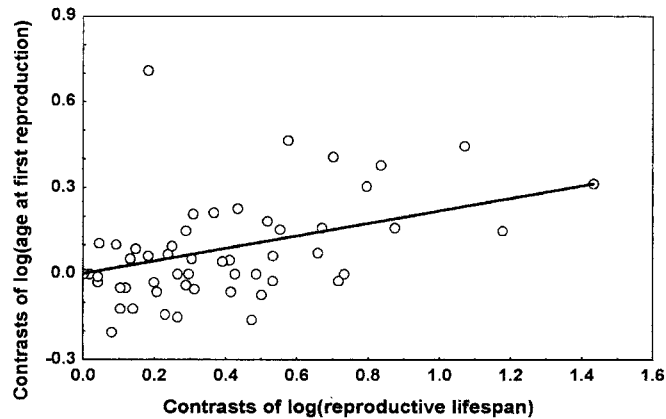
Fig. 4. Relationship between mean age of first reproduction (*a*) and reproductive lifespan (*L_a*) in perennial herbs and woody plants employing phylogenetically independent contrasts. Regression statistics are given in the text.

slope = −0.153 ± 0.090, mean ± standard error). This has two possible interpretations: either plants die due to environmentally induced mortality in the absence of physiological deterioration, or senescence occurs independently of extrinsic mortality. We favour the latter hypothesis because: (1) short-lived herbs have a higher baseline mortality rate (μ_a) than long-lived woody plants (x-axis of Fig. 2a) and (2) there is a positive relationship between rate of senescence (ω) and reproductive lifespan (L_a; Fig. 2b). These relationships suggest that while short-lived plants die of extrinsic causes, long-lived plants die due to physiological deterioration late in life. This is congruent with the finding of increasing mortality rate only in the longest living trees in our data set (μ_x-trend 3 in Table 1; Fig. 1c). Thus, it seems that although higher extrinsic mortality does select for shorter lifespan and earlier age at sexual maturity (Fig. 2c), this does not necessarily imply faster senescence. This interpretation is consistent with the theoretical result of a negative relationship between lifespan (and age at maturity) and extrinsic mortality under optimal resource allocation to body repair (figs 3 and 4 of Cichon, 1997). Unlike semelparous perennials, which senesce dramatically after reproducing, short-lived perennial plants seem to die because of environmental, extrinsic causes, including not only the hazards of disturbance in harsh or periodic environments (Stebbins, 1958), but also the perils of predation and competition. There is, therefore, a clear advantage to reproducing earlier, but this need not be accompanied by physiological deterioration. Indeed, many plants end their lives with reproductive values still increasing rapidly (see below).

Reproductive value

Partridge and Barton (1996) have defended the view that trends in reproductive value (v_x) with age might be a more sensitive indicator of senescence than trends in μ_x. Only a minority (9%) of the species in our data set showed a decline in v_x with age (6/65 with Type 3

v_x curves). This group was formed by the long-lived trees *Araucaria cunninghamii* and *Pinus palustris*, the long-lived palms *Astrocaryum mexicanum* and *Rhopalostylis sapida*, and the ramets of the clonal tree *Alnus incana* and the clonal palm *Podococcus barteri*. Reproductive value actually increased with age in 77% (50/65) of species due to an increase in size-dependent fecundity, although within this group v_x approached a limit in the majority of species (46 with Type 2 curves *vs* 4 with Type 1 curves). If we accept Partridge and Barton's view, it is only long-lived trees that seem to senesce. This is also in line with the results described above about short-lived plants apparently dying from extrinsic causes and not from physiological decline. Thus, the increase in fecundity with plant age/size and the concomitant increase in reproductive value for a large proportion of the plant species analysed here delays the manifestation of senescent physiological decline, which is only shown by the longest-living plants in our data set.

Age of first reproduction and mean reproductive lifespan

The trade-off between reproduction and survival implied by the positive relationship we found between the contrasts of mean age at first reproduction (a) and those of mean reproductive lifespan (L_a) (Fig. 3; data previously logarithmically transformed) provides circumstantial evidence for the existence of senescence across our data set as a whole. When the a/L_a relationship was tested within each of the two largest herb families in our data set, it proved to be present in Liliaceae (*sensu lato*) but not in Poaceae. Although the samples sizes were low, they were similar in the two families (Liliaceae, $n = 7$ contrasts; Poaceae, $n = 8$ contrasts), so we suggest that the difference between them has a biological explanation. Ten of the 11 life tables for lilies pertained to ramets, while eight of nine life tables for grasses pertained to genets (clumps of ramets). Thus, there was apparently a trade-off between reproduction and survival for mortal ramets, but not for genets, which are potentially immortal. On this evidence, grasses thus appear to be the exception to the expected a/L_a relationship that prove the senescence rule. However, the evidence of age-specific trends in μ_x does not suggest the grasses are exceptional in this respect, as all three types of μ_x curve are found in the group (Table 1).

The nature of our data set

The life tables used in this study were derived algorithmically from stage-projection matrices. This is unconventional and therefore merits some discussion. Dynamic life tables are very rare for perennial plants and stage projection matrices are preferred in plant demography because size is the dominant factor in deciding the fate of individuals. Nonetheless, time in the form of the projection interval is explicit in matrix models and the age of individuals is therefore implicit. Life tables and projection matrices are interconvertible and so the primary consideration should be the quality of the underlying data rather than the form in which they are represented. A problem that afflicts all demographic studies including our own is the decline in sample size that inevitably occurs with age. Unfortunately, this cannot be overcome even with extremely large initial cohort sizes. For example, Carey *et al.* (1992) presented a life table for a cohort of 1.2×10^6 medflies; in the last 50% of the lifespan of this cohort, mortality rates fluctuated over a range of zero to 10% on successive days. Stage-projection matrices at least have the merit that size class intervals can be chosen to optimize sample sizes (Moloney, 1986).

Ramet versus genet senescence

Using a modelling approach, Orive (1995), Pedersen (1995) and Gardner and Mangel (1997) have found that, although clonal growth may delay senescence of the genet, unless sexual reproduction increases dramatically with age, genet senescence is an inevitable outcome even in the presence of reduced adult mortality. With the exception of four species whose fecundity (m_x) became constant after a certain age, 61 plants in our data set increased their fecundity with age. Whether this was sufficient to counteract the evolution of senescence in some of them is not clear, but on the whole the evidence would suggest not. In two cases (*Araucaria hunsteinii* and *Calluna vulgaris*), fecundity increased exponentially, but senescence (measured as an increase in μ_x) occurred in the former. In three cases (*Cleome droserifolia*, *Erythronium japonicum* and *Pedicularis furbishiae*), it increased linearly and we have shown senescence to be likely in the latter two (Type 3 μ_x). In the remaining 56 species, fecundity approached an asymptote. Thus, the *disproportionate* increase in fecundity required to avoid senescence is either not present or is sooner or later offset by increasing intrinsic mortality.

If the unity of germ line and soma is not a barrier to the evolution of senescence (Martinez and Levinton, 1992; Pedersen, 1995), we may reasonably ask, why not? We offer the hypothesis that the conditions for senescence to evolve at the genet level depend upon the presence of physiological integration among ramets. The extent to which this occurs varies greatly among clonal species. The argument goes as follows. There is no such thing as a static steady state for a plant – because of its modular construction, it can only live so long as it continues to grow because the maintenance of photosynthetic capacity requires the replacement of leaves and new leaves anatomically require the growth of supporting branches. As growth in size proceeds, a tree increases its growth rate costs (Franco, 1985; Gerrish, 1990). A variety of physiological and anatomical hypotheses based on this idea have been advanced to explain why a tree ultimately reaches a size at which it enters physiological decline (Stevens and Perkins, 1992; Yoder *et al.*, 1994; Gower *et al.*, 1996; Ryan and Yoder, 1997; Ryan *et al.*, 1997). Whatever the precise physiological causes of senescence (which may differ between species; e.g. Pierson and Turner, 1998; Barot and Gignoux, 1999), we argue that three general characteristics determine that they will senesce: (1) the individual plant is a structurally and, in so far as it is single-rooted, integrated physiological unit or IPU (Watson and Casper, 1984); (2) the demands of physiological maintenance cause plants to increase in size; (3) given a set of environmental conditions, any IPU must have an optimum size at which it functions most efficiently.

The inexorable increase in size (2) must ultimately drive an IPU past its physiologically optimum size (3). This must lower the force of selection on older (and larger) single-rooted individuals, thus creating the conditions for further senescence to evolve. This mechanism should apply not only to trees but to any plant or plant part for which conditions 1–3 hold. The mechanism would clearly not operate in plants where the genet is composed of a number of independent physiological units, for example in a clonal herb such as *Trifolium repens*, in which genets fragment into physically separate parts. These separate parts may individually senesce, but so long as new fragments are produced by clonal growth, the force of selection on the genet should be independent of its age and therefore no evolution of senescence should occur. The evolution of senescence by antagonistic pleiotropy demands that genes with benefits to fitness early in life have deleterious effects later on due to physiological trade-offs. Costs of reproduction (e.g. Silvertown and Dodd, 1999) are probably

the most common cause of such trade-offs (Partridge, 1987). Clearly, for such trade-offs to occur, an individual must retain its physiological integrity through life. When a genet fragments, any trade-offs will tend to be confined within each fragment. As a consequence, ramets will senesce but the genet may not.

So far as plants are concerned, the important distinction is not between germ line and soma or even between clonal and aclonal plants, but between plants in which the genet is a single IPU and genets in which it is not. Some clonal plants, for example the arctic herbs *Carex bigelowii* and *Lycopodium antoninum* (Carlsson *et al.*, 1990), are physiologically integrated throughout life. The unity of germ line and soma is a necessary but not a sufficient condition for an organism to escape the evolution of senescence. Our hypothesis, therefore, generates the prediction that physiologically integrated, clonal plants should evolve senescence, whereas the genets of clonal plants lacking physiological integration should not. This could be tested in a group of plants such as the goldenrods (*Solidago* spp.), in which clones of some species fragment and others do not.

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APPENDIX: PHYLOGENY OF SPECIES IN THE DATA SET

The data set (65 species) is taxonomically diverse, comprising 24 families of herbs and 12 families of woody plants. One additional family, the Leguminosae, contains one herb and two tree species, but otherwise there is no taxonomic overlap between the two life forms. The Liliaceae *sensu lato* (11 spp.) was divided into the Convallariaceae (3 spp.), Melanthiaceae (1), Liliaceae *sensu stricto* (2), Amaryllidaceae (1) and Calochortaceae (4). The next most numerous families were the Gramineae (9 spp.), followed by Palmae (4 spp.) and six other families each represented by two or three species of the same life form.

There were three gymnosperm and 62 angiosperm species; these two taxa constituted the basal sister clades. Within the angiosperms, monocots were considered closer to Laurales (Nandi *et al.*, 1998). To resolve the relationships among families, the classification used by Dodd *et al.* (1999) was preferred (after Angiosperm Phylogeny Group, 1998; Stefanovic *et al.*, 1998). Families not included in this classification were incorporated by resorting to classical taxonomy (e.g. Marantaceae next to Zingiberaceae, Dipsacaceae close to Caprifoliaceae and therefore to Araliaceae, and Cecropiaceae related to Moraceae and Euphorbiaceae) and/or more specific molecular studies (Plantaginaceae close to Scrophulariaceae; Olmstead and Reeves, 1995). As mentioned above, the Liliaceae were further divided into five families. Amaryllidaceae was situated next to Orchidaceae and Convalariaceae was assumed to be the sister clade of the other three families (Dodd *et al.*, 1999). These three (Melanthiaceae, Liliaceae and Chalocortaceae) were the only families not resolved in the phylogeny. Finally, to resolve the phylogeny at the species level, we used a combination of classical taxonomy [e.g. in the separation of grasses into tribes (Mabberley, 1997) and of legumes into Caesalpinoideae-Mimosoidea and Papilionoidea (Doyle, 1994, 1995)] and within-family morphological and molecular studies (Kellog and Watson, 1993; Hsiao *et al.*, 1995, 1998, 1999; Catalán *et al.*, 1997). All four species of palms in the data set belong to the subfamily Arecoideae (Mabberley, 1997) and, although each is in a different tribe, the best we could do was to separate *Iriartea deltoidea* from the other three as in the phylogeny for the Arecanae produced by W.J. Hahn for the Tree of Life (http://phylogeny.arizona.edu/tree/eukaryotes/green_plants/embryophytes/angiosperms/monocotyledons/arecanae/arecanae.html) based on Uhl *et al.* (1995) and Hahn (unpublished). The four species of *Calochortus* and the three *Pinguicula* species were left unresolved. Fig. A1 is the resulting tree on which the analyses presented were performed.
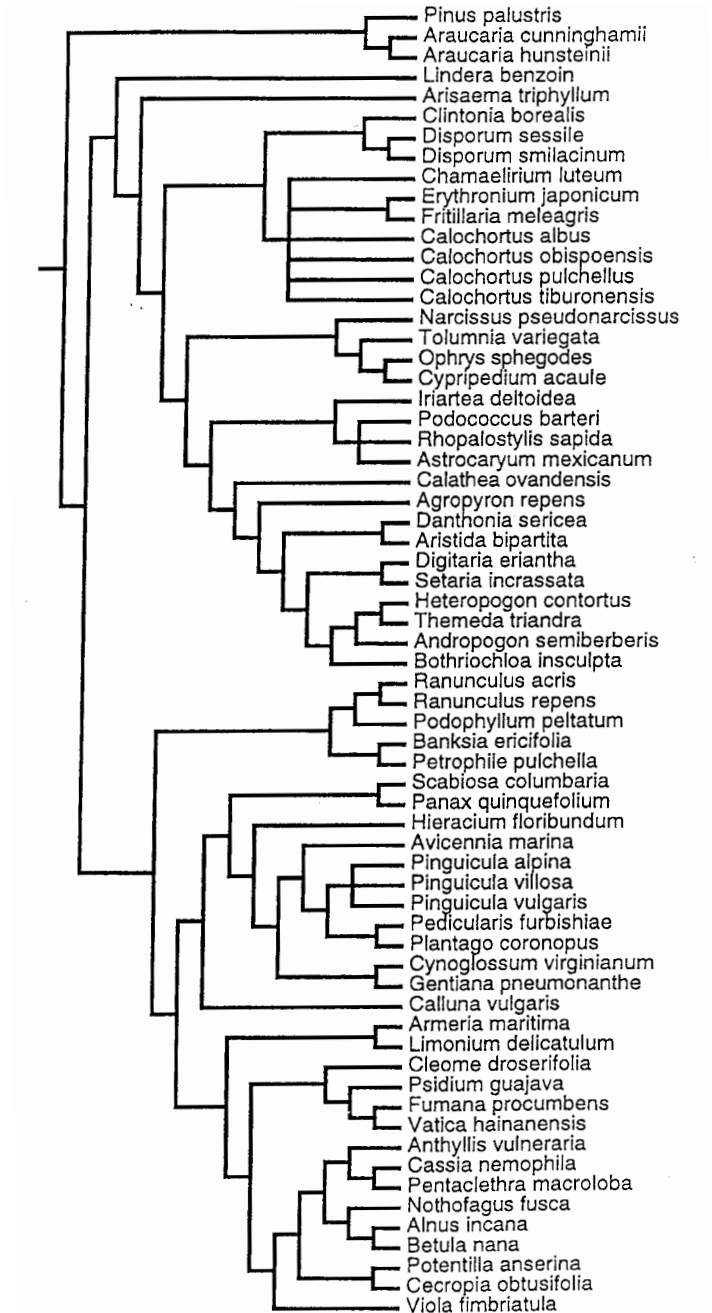
Fig. A1. The tree on which the analyses presented were performed.