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Longevity of seeds stored in a genebank: species characteristics

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Abstract

Seeds of different species are believed to have characteristic shelf lives, although data confirming this are scarce, and a mechanistic understanding of why this should be remains elusive. We have quantified storage performance of *c.* 42,000 seed accessions, representing 276 species, within the USDA National Plant Germplasm System (NPGS) collection, as well as a smaller experiment of 207 cultivars from 42 species. Accessions from the NPGS collection were harvested between 1934 and 1975, and had relatively high initial germination percentages that decreased at a variable rate during storage at both 5 and −18°C. Germination time courses, which represent the average performance of the species, were fitted to Avrami kinetics, to calculate the time at which germination characteristically declined to 50% (P50). These P50 values correlated with other longevity surveys reported in the literature for seeds stored under controlled conditions, but there was no correlation among these studies and seed persistence observed in the classic buried seed experiment by Duvel. Some plant families had characteristically short-lived (e.g. *Apiaceae* and *Brassicaceae*) or long-lived (e.g. *Malvaceae* and *Chenopodiaceae*) seeds. Also, seeds from species that originated from particular localities had characteristically short (e.g. Europe) or long (e.g. South Asia and Australia) shelf lives. However, there appeared to be no correlation between longevity and dry matter reserves, soluble carbohydrates and parameters relating to soil persistence or resource allocation. Although data from this survey support the hypothesis that some species tend to survive longer than others in a genebank environment, there is little information on the attributes of the seed that affect its storage performance.

Keywords: storage, viability, longevity, conservation, genebank, Avrami, composition, evolution, genetic diversity, seed

Introduction

Seed genebanks maintain genetic resources within seeds over decades or centuries. The ageing rate characteristic of seeds of individual species provides essential guidelines for storage conditions, monitoring and regeneration needs of the genebank. Seed longevity is usually reported as studies of survival (e.g. Odum, 1965; Roos and Davidson, 1992; Shen-Miller *et al.*, 1995; Steiner and Ruckenbauer, 1995; Telewski and Zeevaart, 2002), which highlight the remarkable ability of the seeds of some species, or seed lots, to remain viable for many years. In contrast, anecdotal accounts of rapid deterioration have led to the classification of some species as 'bad keepers'. Neither of these types of studies provides a quantitative assessment of the expected behaviour of a species in a genebank situation.

Surveys that compare seed ageing rates among several species stored under similar conditions provide estimates of the inherent longevity of a species relative to others. This information is critical to the understanding of the evolution of seed longevity and will provide a biological basis to help genebank operators prioritize processing procedures. The notable experiments of Beal and Duvel measured germination of seeds in the soil after 120 and 39 years, respectively (Telewski and Zeevaart, 2002; Toole and Brown, 1946, respectively). The bulk of information on relative longevity for seeds in non-field conditions is provided by Priestley and Ellis and their colleagues. Priestley *et al.* (1985) surveyed monitoring records of 92 species in 'open' storage at 13 locations in temperate climates. Presumably, 'open' storage refers to a warehouse environment with little control of temperature or relative humidity (RH). Ellis and colleagues measured deterioration time-courses of species stored at relatively high temperatures or water

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contents, and produced coefficients that could be used to predict deterioration rates under less extreme conditions (Dickie and Bowyer, 1985; Dickie *et al.*, 1985, 1990; Ellis *et al.*, 1986, 1988, 1989, 1990a, b, 1996; Tompsett, 1986; Kraak and Vos, 1987; Belletti *et al.*, 1991; Zewdie and Ellis, 1991). Other survey studies (Went, 1969; Rincker, 1981, 1983; Roos and Davidson, 1992; Hendry *et al.*, 1994) have contributed to the idea that potential life spans of seeds vary among species. Relative longevity data among the various experiments have not been compared, probably because each study focused on different species.

Long-term studies, where seed viability is monitored periodically, provide direct evidence of changes in germination percentage with storage time (Went, 1969; Rincker, 1981, 1983; Priestley *et al.*, 1985; Roos and Davidson, 1992; Specht *et al.*, 1998). Despite the number of established genebanks, these types of data are rare, probably because the early stage of seed ageing is asymptomatic, and it takes years before the cataclysmic decline in germination ability occurs. The long time required to reliably quantify seed life spans presents curatorial problems relating to the stability of infrastructure and funding, the reliability of measurements as methods and personnel change, and the flexibility of experimental design to accommodate the changing interests of future scientific communities that inherit the experiment. When knowledge of the longevity potential of a seed is finally understood, the next obvious experiments become assessments of putative protectants or ageing catalysts; however, by this time the seed is so irrevocably changed as to preclude analysis.

The alternative approach of simulating ageing under adverse conditions (e.g. warm or moist), and extrapolating kinetics to more acceptable conditions (e.g. cold and dry), carries the implicit assumption that the mechanisms of deterioration are similar across a broad range of temperatures and relative humidities. This assumption is not universally supported in the literature (e.g. Walters, 1998) and is difficult to verify because of the dearth of long-term data. Given that there are different mechanisms resulting in seed death, it is also likely that different strategies that protect against deterioration have evolved in seeds. For example, persistence in soil seed banks may relate to the efficacy of dormancy mechanisms for the particular locale (Baskin and Baskin, 1998), the ability for intracellular repair (Villiers, 1974) or anti-microbial agents sequestered in seeds (Hendry *et al.*, 1994). Although a link between seed dormancy or chemical defences and longevity in the genebank has been suggested, the relationship has not been tested formally. Because the mechanisms of deterioration and protection are likely to vary with the environment, one may hypothesize that seeds of different species have characteristic longevities, but relative longevity may vary with the storage condition. A better understanding of the seed ageing process will lead to more reliable predictions of seed performance under genebank conditions.

Although the logistical problems of predicting how long seeds survive will probably not be solved for years to come, the research presented here provides an extensive dataset to document the kinetics of seed deterioration under cold (5 and −18°C), dry (seed water contents maintained between 4 and 8%, depending on species) storage conditions, and to compare those kinetics across diverse species. This dataset, which constitutes monitoring results from the USDA-ARS National Center for Genetic Resources Preservation (formerly National Seed Storage Laboratory) seed collection, continues to grow as storage time increases and additional species are considered. It is believed that such data can provide an important tool for addressing hypotheses about seed ageing, and will ultimately lead to a better understanding of mechanisms of damage and the means to improve predictions of performance under a variety of conditions.

The sigmoidal pattern of seed deterioration makes it difficult to summarize ageing kinetics. Previously developed viability equations (e.g. Ellis, 1991) accommodate this sigmoidal pattern using probits. However, since we wish to test hypotheses implicit to these viability equations, we needed an independent method that has parameters with physical meaning that can be applied to different storage conditions. Avrami kinetics, which describe co-operative reactions based on visco-elastic properties (Avrami, 1941), have been used recently to describe ageing kinetics in seeds (Walters, 1998; Walters *et al.*, 2004). We have used the Johnson–Mehl–Avrami form of the equation to calculate time coefficients (Williams *et al.*, 1993):

$$\ln(N_0/N) = (t/\phi)^n$$

where t is storage time, and N_0/N is the reciprocal of percentage germination. The coefficients ϕ and n describe the shape of the sigmoidal curve, with the abruptness at which germination declines increasing as n increases above 1. When $n = 1$, the Avrami equation assumes the form of a typical first–order equation. The time coefficient, ϕ, can be treated as an Arrhenius function of temperature (Williams *et al.*, 1993; Walters *et al.*, 2004). For this paper, deterioration time courses of seeds of 276 species stored for more than 30 years were fitted to Avrami equations, and the calculated time for seed germination to decrease to 50% was used to summarize the longevity of the species.

Materials and methods

Germination data from 276 species of seed accessions, stored at the USDA National Center for Genetic Resources Preservation (formerly National Seed Storage Laboratory; NSSL), are reported here. Data were retrieved by querying the Genetic Resource Information Network (GRIN) database of the USDA National Plant Germplasm System (NPGS) for accessions from particular genera or species that were harvested between 1934 and 1975, and had initial viability greater than 75% (with the exception of seeds from *Anethum graveolens*, *Rheum* spp., *Zinnia haageana*, *Lesquerella palmeri*, *Elymus drobovii* and *E. hystix*, which had poor initial seed quality) (see Table 1). The number of accessions within a species that fit these criteria ranged from 1 (usually for wild relatives of domesticated species) to 8220 (large numbers of accessions were available for important crop species), with a median of three accessions per species (see Table 1). Accessions are from breeding lines, land races and wild populations collected from around the world, where they presumably represent the genetic diversity of an agronomically important plant species. Most of the stored seeds were from plants grown at government plant introduction sites within the US and harvested between 1963 and 1968. Upon receipt at NSSL, seed water content was adjusted to 4–8%, and seeds were placed in screw–cap metal cans, but transferred years later to foil–laminate bags. Seeds were stored at 5°C until 1978, when the temperature of the NSSL storage vaults was reduced to -18°C. Certified seed analysts monitored viability of seed accessions periodically (AOSA, 2003). To obtain an ageing time course that was characteristic for the species, germination data for all accessions of a species were pooled, and the average germination after various storage times was calculated in 4-year increments (see Fig. 2). In a future paper, time courses for individual accessions will be analysed separately to provide information on intraspecific and harvest year variability.

A second set of seed ageing data was available through an experiment initiated in 1977 by Dr Phillip Stanwood, which compares the longevity of 42 species stored at 5, -18 and -196°C [data for cryogenic storage are reported in Walters *et al.* (2004) and data for -18°C are not presented]. Unlike the NPGS collection described above, seeds used in this experiment were commercially available varieties donated by seed companies or breeders. The experiment included 1–21 accessions per species (median = 3 accessions per species), harvested in 1977 or 1978 (see Table 2). Seeds, with water contents ranging from 3.5 to 9.5% (depending on species), were stored in envelopes, plastic vials or cans at a constant temperature (5°C), and germination was assessed periodically. As with the NPGS dataset, germination data were averaged among accessions within a species for each monitoring time.

Longevity parameters for each species in both datasets were calculated by solving for the coefficients of the Avrami equation using a least squares linear fit of the double logarithmic expression: $\ln[\ln(N_0/N)] = n[\ln(\text{time})] + y_0$, where n is the slope and y_0 is the y-intercept. So that the double ln value of N_0/N could be calculated, the constant N_0 was assigned as 0.5 + the maximum germination percentage of the averaged time course (usually the average initial germination percentage). Values for N were the average germination percentage for the time (t) in years (solid circles in Fig. 2). The coefficient ϕ and the exponential factor n of the Avrami equation were calculated from the coefficients of the regression line ($\phi = e^{(-y_0/n)}$ and $n =$ slope). The time for germination to drop to 50% (P50) was determined by interpolating (if the final average germination percentage was $<50\%$) or extrapolating (if the final average germination percentage was $>50\%$) the Avrami equation, using the coefficients calculated from fitted time courses. For the few species with initial germination percentages $<70\%$, P50 was calculated as the time for germination to decrease to half the initial value.

Values of P50 for species represented in this study were also calculated using the Ellis viability equations if coefficients were reported in the literature. The water content used for this calculation was the average water content for the species in the NPGS collection; the storage temperature was assigned as 5°C; and the initial germination was assigned as the maximum germination percentage of the averaged time course of the NPGS collection (i.e. $N_0 - 0.5$). Longevity in the genebank was also compared to longevity in the soil. Results from Duvel's buried seed experiment (Toole and Brown, 1946) were used as a measure of seed persistence in the soil, expressed as the storage time (in years) in which the greatest proportion of seeds germinated.

Results and discussion

The average initial germination percentage for species within the NPGS collection ranged from 76 to 99% [excluding *A. graveolens* (*Apiaceae*), *Rheum* spp. (*Polygonaceae*), *Z. haageana* (*Asteraceae*), *Lesquerella palmeri* (*Brassicaeae*), *E. drobovii* and *E. hystix* (*Poaceae*), which had low initial germination percentages] (Fig. 1A, Table 1). The average storage time was 38 years, and ranged from 81 [*Lycopersicon esculentum* (*Solanaceae*)] to 16 years [*Senna obtusifolia* (*Fabaceae*) and *Eragrostis tef* (*Poaceae*)] (Fig. 1B). The average final germination was 58%, and ranged from 100% [*Hibiscus micranthus* (*Malvaceae*), stored for 40 years]

Table 1. Storage performance of seeds in the USDA National Plant Germplasm System (NPGS) collection. The study includes accessions that were harvested between 1934 and 1975 and had initial germination percentages greater than 75% (except where indicated). Seeds were initially stored at 5°C, but were transferred to −18°C in 1978. Data for most species reflect storage for 24–26 years at −18°C. Initial and final germination values are averages calculated within 1 year of harvest and after the indicated storage time, respectively. Time courses were drawn for each species as shown in Fig. 2. Coefficients calculated from the Avrami-curve fitting routine (see Methods section) were used to calculate the time for germination to decrease from the initial value to 50%, or to half of the initial germination for species with initial germination <70%. Symbols by family names are used in Figs 5–8. Letters in the family column adjacent to *Gossypium* species indicate the genome type

Family	Genus	Species	No. of accessions	Germination (%)		Years stored	Avrami parameters			
				Initial	Final		Slope	Intercept	ϕ	P50 (years)
*Apiaceae**	*Anethum*	*graveolens*	15	39	15	17.3[2]	1.4	−4.4	23.1	18
	Apium	*graveolens*	111	87	33	37.8	2.8	−9.9	33.8	27
	Carum	*carvi*	1	76	40	42.7	1.10	−4.69	71.1	32
	Daucus	*carota*	100	85	9	45.8[1]	3.0	−10.8	36.9	30
	Pastinaca	*sativa*	11	85	22	26.7[2]	2.30	−8.45	39.4	30
	Petroselinum	*crispum*	22	85	11	34.3[1]	3.2	−10.4	26.0	21
	Pimpinella	*anisum*	1	95	24	43.8	3.80	−13.99	39.7	35
Asteraceae ○	*Carthamus*	*tinctorius*	1049	87	69	40.7	1.1	−5.5	151.7	88
	Cichorium	*endive*	17	91	63	43.2	1.4	−6.1	78.8	55
	Cichorium	*intybus*	4	87	56	42.0	2.4	−9.4	49.3	39
	Cosmos	sp.	1	81	72	35.5	1.8	−7.6	67.5	45
	Guizotia	*abyssinica*	1	76	38	34.8	1.10	−3.69	28.7	13
	Helianthus	*annuus*	36	92	42	49.9	1.7	−7.1	66.7	50
	Lactuca	*altaica*	1	99	9	28.3[1]	5.40	−17.32	24.7	23
	Lactuca	*sativa*	499	97	2	39.1	2.9	−9.4	26.0	23
	Lactuca	*serriola*	5	99	8	31.6	3.4	−10.7	23.3	21
	Lactuca	*virosa*	1	99	78	32.5	4.2	−15.7	42.3	39
	Scorzonera	*hispanica*	1	88	67	40.8	1.40	−5.95	70.0	47
	Tagetes	*erecta*	5	91	83	30.0	1.00	−4.67	107.1	64
	Tagetes	*patula*	11	93	32	25.5[2]	2.6	−8.5	26.1	22
	Tagetes	sp.	38	90	52	42.6	1.7	−6.9	59.1	43
	Tragopogon	*porrifolius*	5	95	47	42.1	2.5	−9.8	50.0	42
	Zinnia	*haageana*	2	74	60	41.8	1.20	−6.04	153.4	70
	Zinnia	sp.	7	89	75	35.1	1.2	−6.3	198.2	124
	Zinnia	*violacea*	12	86	45	41.4	1.3	−5.6	73.8	46
Brassicaceae ▲	*Brassica*	*hirta (Sinapis alba)*	4	94	84	34.5	1.6	−7.4	101.9	76
	Brassica	*juncea*	29	97	55	43.7	1.20	−5.31	83.5	59
	Brassica	*napus*	12	94	26	37.2[1]	2.6	−8.9	30.4	25
	Brassica	*oleracea*	370	91	11	39.0[1]	2.6	−8.7	28.2	23
	Crambe	*abyssinica*	92	86	43	34.5	2.3	−7.6	27.6	21
	Hesperis	*matronalis*	1	82	75	29.8	2.20	−9.17	64.7	47
	Isatis	*tinctoria*	1	86	34	18.7[2]	2.8	−9.8	33.2	27
	Lepidium	*sativum*	3	90	33	28.2[2]	1.7	−6.1	35.7	26
	Lesquerella	*fendleri*	1	98	88	34.8	1.00	−5.00	148.0	100
	Lesquerella	*gordonii*	3	86	21	34.8	2.30	−7.65	27.9	21
	Lesquerella	*grandiflora*	1	87	83	34.8	1.00	−5.69	295.9	164
	Lesquerella	*palmeri*	1	59	10	34.8	2.50	−7.77	22.4	19
	Nasturtium	*officinale*	2	89	44	39.8	2.80	−10.03	35.9	30
	Raphanus	*sativus*	70	97	85	43.9	1.6	−8.1	154.8	120
Chenopodiaceae ◆	*Beta*	*vulgaris*	234	88	2	60.4[1]	3.1	−12.2	50.4	42
	Chenopodium	*quinoa*	3	99	95	29.5	1.0	−5.9	365.9	250
	Spinacia	*oleracea*	51	92	53	64.7	1.8	−8.2	95.4	73
Cucurbitaceae ■	*Citrullus*	*lanatus*	554	92	63	42.9	1.4	−6.4	96.6	68
	Cucumis	*melo*	814	92	53	68.8	1.7	−7.6	89.0	66
	Cucumis	*sativus*	162	94	61	68.7	1.7	−8.1	114.3	87
	Cucurbita	*argyrosperma (mixta)*	14	96	67	43.7	2.10	−9.25	81.8	67
	Cucurbita	*maxima*	209	94	63	43.5	2.20	−9.09	62.2	50
	Cucurbita	*moschata*	70	94	75	43.7	1.40	−6.70	119.6	86

Table 1. *Continued*

				Germination (%)			Avrami parameters			
Family	Genus	Species	No. of accessions	Initial	Final	Years stored	Slope	Intercept	ϕ	P50 (years)
	Cucurbita	*pepo*	104	94	76	42.8	1.70	−7.83	100.1	76
	Lagenaria	*siceraria*	21	93	59	38.5	1.60	−6.91	74.9	56
Cyperaceae +	*Carex*	sp.	1	96	92	29.7	1.30	−7.11	237.0	171
Euphorbiaceae +	*Ricinus*	*communis*	174	86	24	37.3	2.5	−8.7	33.1	26
Fabaceae □	*Arachis*	*hypogaea*	780	89	6	34.0[1]	4.4	−14.8	28.8	25
	Cicer	*arietinum*	2	96	91	36.3	1.5	−6.8	93.1	70
	Glycine	*max*	3635	92	21	35.9[1]	3.0	−10.9	38.0	32
	Lathyrus	*odoratus*	23	91	58	41.9	1.70	−6.79	54.2	40
	Lens	*culinaris*	1727	95	91	34.8	1.00	−6.34	568.0	365
	Lespedeza	*bicolor*	3	81	47	41.3	1.0	−4.5	86.9	42
	Lespedeza	*cuneata (sericea)*	4	95	61	39.6	1.3	−5.3	59.7	43
	Lespedeza	*daurica*	1	96	93	41.3	1.1	−6.6	394.3	267
	Lespedeza	*juncea*	1	88	68	41.4	1.7	−7.2	68.2	49
	Lotus	*corniculatus*	224	92	69	42.3	1.7	−7.7	91.1	68
	Lupinus	*angustifolius*	6	88	6	51.2	2.1	−8.4	53.8	41
	Medicago	*sativa*	423	92	80	49.8	1.20	−5.93	140.1	93
	Melilotus	*alba*	13	89	65	42.5	1.0	−4.7	109.1	63
	Onobrychis	*viciifolia*	41	92	40	42.1	1.6	−6.1	46.5	34
	Phaseolus	*vulgaris*	2471	91	13	43.9[2]	4.5	−16.0	35.1	31
	Pisum	*sativum*	1068	95	70	63.9	2.0	−9.6	121.4	97
	Senna	*corymbosa*	2	85	78	34.8	1.00	−5.82	338.6	180
	Senna	*covesii*	1	98	96	34.8	1.00	−6.25	520.2	350
	Senna	*marilandica*	2	97	98	35.8	1.00	−6.04	419.7	276
	Senna	*obtusifolia*	1	78	66	15.5[2]	1.10	−4.98	92.7	44
	Senna	*occidentalis*	9	91	75	34.8	1.00	−4.53	92.9	56
	Trifolium	*alexandrinum*	10	90	74	43.3	1.60	−7.32	97.1	70
	Trifolium	*ambiguum*	9	92	82	43.7	1.20	−5.84	130.2	86
	Trifolium	*campestre*	1	96	96	43.7	1.20	−8.17	903.7	633
	Trifolium	*caudatum*	1	99	2	37.8	2.80	−8.15	18.3	16
	Trifolium	*dubium*	1	95	84	43.7	1.40	−6.16	81.6	59
	Trifolium	*fragiferum*	59	93	90	43.7	1.20	−6.82	293.1	196
	Trifolium	*hirtum*	3	87	76	43.7	1.00	−5.30	200.0	110
	Trifolium	hybrid	1	93	28	38.7	3.20	−12.09	43.8	38
	Trifolium	*hybridum*	45	96	41	37.6	2.40	−8.53	35.0	29
	Trifolium	*incarnatum*	9	91	54	43.1	1.20	−5.41	91.0	59
	Trifolium	*lappaceum*	1	80	66	43.7	2.50	−10.53	67.6	50
	Trifolium	*medium*	5	87	72	36.8	2.70	−11.14	61.8	50
	Trifolium	*montanum*	1	98	82	37.8	1.90	−8.30	79.0	64
	Trifolium	*nigrescens*	3	97	90	43.2	1.10	−6.21	284.1	196
	Trifolium	*pannonicum*	1	96	96	37.8	1.00	−6.52	680.3	444
	Trifolium	*pratense*	558	88	47	40.5	1.6	−6.6	60.9	43
	Trifolium	*purpureum*	1	98	90	29.8	1.10	−6.64	417.3	291
	Trifolium	*repens*	261	91	71	43.5	2.00	−9.19	99.0	77
	Trifolium	*resupinatum*	2	91	88	42.7	1.00	−5.82	335.6	199
	Trifolium	*tubens*	2	96	90	32.8	1.00	−6.51	675.0	440
	Trifolium	*striatum*	1	95	88	41.7	1.00	−5.86	349.9	225
	Trifolium	*subterraneum*	7	87	72	43.7	1.00	−4.87	130.7	73
	Trifolium	*variegatum*	1	89	80	31.3	1.30	−7.03	222.6	146
	Trifolium	*vesiculosum*	3	96	50	42.2	1.10	−4.63	67.0	46
	Vicia	sp.	74	96	77	41.7	1.6	−7.2	92.6	71
	Vigna	*radiata*	181	93	92	40.5	1.00	−6.60	735.6	457
Lamiaceae ×	*Ocimum*	*basilicum*	2	96	82	43.2	1.40	−6.93	141.0	104
	Salvia	*azurea*	1	78	68	29.8	2.50	−10.96	80.1	58
	Salvia	*officinalis*	1	94	74	43.8	3.00	−12.58	66.2	57
	Salvia	*splendens*	1	87	70	35.8	1.00	−4.70	110.5	61
	Salvia	*sylvestris*	1	91	28	29.8	1.30	−4.00	21.7	15
	Salvia	*virgata*	1	98	16	29.8	4.20	−12.53	19.7	18

Table 1. *Continued*

Family	Genus	Species	No. of accessions	Germination (%)		Years stored	Avrami parameters			
				Initial	Final		Slope	Intercept	ϕ	P50 (years)
Liliaceae –	*Allium*	*ampeloprasum*	10	95	55	43.2	1.5	−5.6	42.9	32
	Allium	*cepa*	223	91	8	40.4^1	2.0	−6.8	29.6	23
	Allium	*dictyoprasum*	1	96	72	29.5	2.4	−9.5	51.5	43
	Allium	*fistulosum*	10	95	13	43	1.5	−5.0	28.3	21
	Allium	*galanthum*	1	92	50	31.5	1.10	−4.20	45.5	29
	Allium	hybrid	1	93	36	41.5	2.0	−6.8	29.3	23
	Allium	*pskemense*	1	98	75	31.5	1.4	−6.6	115.5	87
	Allium	*ramosum*	1	85	70	31.5	1.8	−8.3	99.7	70
	Allium	*schoenoprasum*	1	93	58	29.5	2.8	−9.3	28.1	24
	Allium	*senescens*	1	87	72	29.5^1	1.00	−4.73	112.9	63
	Allium	*tuberosum*	1	80	48	29.5	1.1	−5.0	91.3	46
Linaceae +	*Linum*	*usitatissimum*	2038	93	64	45.3	1.9	−8.0	68.5	53
Malvaceae ◇	*Abelmoschus*	*esculentus*	95	87	71	42.0	1.9	−9.1	118.6	87
B	*Gossypium*	*anomalum*	3	92	73	37.5	1.3	−6.3	125.9	86
A	*Gossypium*	*arboreum*	4	88	74	44.4	1.5	−7.1	117.2	80
D	*Gossypium*	*aridum*	2	94	91	29.9^1	1.0	−5.5	240.3	152
D	*Gossypium*	*armourianum*	2	79	79	37.5	1.0	−5.9	381.9	175
C	*Gossypium*	*australe*	1	89	62	37.5	1.3	−5.6	72.7	48
AD	*Gossypium*	*barbadense*	197	97	87	41.6	1.4	−7.3	188.5	141
G	*Gossypium*	*bickii*	1	92	92	30.0^1	1.0	−6.6	763.5	466
AD	*Gossypium*	*darwinii*	1	86	62	39.5	2.0	−8.2	59.6	44
D	*Gossypium*	*davidsonii*	1	92	92	30.0^1	1.0	−6.4	578.8	353
D	*Gossypium*	*gossypioides*	1	92	90	37.5	1.0	−5.9	365.6	223
D	*Gossypium*	*harknessii*	1	85	36	37.5	2.2	−7.5	29.8	22
A	*Gossypium*	*herbaceum*	1	96	96	30.0^1	1.0	−6.0	423.9	277
AD	*Gossypium*	*hirsutum*	1395	95	60	60.6	1.2	−6.1	166.8	115
	Gossypium	hybrid	18	96	41	32.5	2.0	−7.1	34.4	28
D	*Gossypium*	*klotzschianum*	2	94	94	30.0^1	1.0	−6.0	421.9	266
D	*Gossypium*	*lobatum*	1	86	0	37.5	1.7	−4.8	16.6	12
F	*Gossypium*	*longicalyx*	3	95	95	30.0^1	1.0	−6.2	485.8	310
C	*Gossypium*	*nandewarense*	1	96	96	30.0^1	1.0	−6.4	625.8	408
D	*Gossypium*	*raimondii*	1	92	88	30.0^1	1.0	−5.2	185.4	113
E	*Gossypium*	*somalense*	1	98	98	30.0^1	1.0	−6.0	385.1	259
E	*Gossypium*	*stocksii*	2	83	47	37.5	1.1	−4.3	51.7	28
C	*Gossypium*	*sturtianum*	1	97	97	30.0^1	1.0	−5.9	357.8	237
A	*Gossypium*	*thurberi*	1	88	52	19.4^2	1.3	−5.5	67.0	43
AD	*Gossypium*	*tomentosum*	1	98	94	37.5	1.4	−7.5	211.7	160
D	*Gossypium*	*trilobum*	1	88	88	35.5	1.0	−6.4	604.3	342
	Hibiscus	*acetosella*	2	92	76	39.5	1.0	−5.2	179.2	109
	Hibiscus	*cannabinus*	94	89	66	39.5	1.4	−6.3	88.2	59
	Hibiscus	*costatus*	1	86	66	39.5	1.7	−7.2	67.5	47
	Hibiscus	*diversifolius*	1	91	70	39.5	1.0	−5.5	244.2	146
	Hibiscus	*furcellatus*	3	90	83	39.5	1.7	−8.1	115.7	85
	Hibiscus	*micranthus*	1	92	100	39.5	1.0	−5.6	264.5	161
	Hibiscus	*radiatus*	3	78	67	39.5	1.0	−5.2	176.7	79
	Hibiscus	*sabdariffa*	46	83	78	39.5	1.0	−6.6	766.7	385
	Hibiscus	sp.	3	76	69	39.5	1.0	−6.3	560.4	235
	Malva	*alcea*	1	92	92	28.8	1.00	−5.75	312.8	191
	Malva	*parviflora*	1	75	72	34.8	1.00	−5.63	277.9	113
*Papaveraceae**	*Papaver*	*somniferum*	48	95	75	39.0	1.4	−6.2	85.9	62
Pedaliaceae ×	*Sesamum*	*indicum*	250	93	49	42.8^1	2.4	−9.3	48.0	39
Poaceae ●	*Agropyron*	*cristatum*	75	92	77	38.8	1.40	−6.34	92.4	65
	Agropyron	*desertorum*	20	90	63	40.3	1.20	−5.11	70.9	45
	Agropyron	*fragile*	14	89	55	41.8	2.00	−7.77	48.8	37
	Agropyron	hybrid	4	99	26	37.8	3.20	−10.64	27.8	25
	Agropyron	sp.	1	99	74	41.8	1.00	−4.65	104.8	72
	Agrostis	*canina*	1	98	65	40.8	1.90	−8.00	67.5	55

Table 1. *Continued*

Family	Genus	Species	No. of accessions	Germination (%)		Years stored	Avrami parameters			
				Initial	Final		Slope	Intercept	ϕ	P50 (years)
	Agrostis	*capillaris*	3	96	82	42.8	2.60	−11.15	73.0	62
	Agrostis	*stolonifera*	3	98	90	43.8	1.10	−6.39	332.0	232
	Avena	*sativa*	785	97	83	44.4	1.40	−7.09	158.1	117
	Bromus	*arvensis*	2	94	60	41.8	2.40	−9.25	47.1	39
	Bromus	*biebersteinii*	3	89	62	39.8	1.40	−6.31	90.8	61
	Bromus	*carinatus*	1	98	86	40.8	1.00	−5.19	179.9	121
	Bromus	*catharticus*	35	97	20	41.8	1.10	−3.83	32.5	23
	Bromus	*erectus*	1	89	62	35.8	1.00	−4.25	69.8	40
	Bromus	*hordeaceus*	1	92	72	23.8[2]	2.90	−11.47	52.2	44
	Bromus	hybrid	1	97	6	31.8	4.00	−12.97	25.6	23
	Bromus	*inermis*	12	91	5	28.3[2]	2.7	−8.1	19.8	16
	Bromus	*japonicus*	1	98	98	35.8	1.40	−8.38	397.0	299
	Bromus	*lanceolatus*	1	99	6	34.8	1.90	−5.86	21.8	18
	Bromus	*riparius*	3	96	78	35.8	1.00	−4.87	130.8	85
	Bromus	*sitchensis*	1	77	0	18.5[2]	1.90	−4.64	11.5	7
	Bromus	*tomentellus*	1	75	50	35.8	1.10	−4.18	44.7	20
	Dactylis	*glomerata*	317	88	61	43.8	2.00	−8.90	85.5	65
	Echinochloa	*crus-galli*	1	99	96	27.7	1.00	−5.23	186.6	128
	Echinochloa	*frumentacea*	1	84	80	36.7	2.40	−11.04	99.5	76
	Eleusine	*coracana*	658	87	87	29.8	1.00	−6.67	789.1	437
	Elymus	*agropyroides*	2	98	34	36.9	1.80	−5.74	24.2	19
	Elymus	*antarcticus*	1	97	64	36.8	1.30	−5.82	87.6	64
	Elymus	*batalinii*	1	92	66	29.8	2.50	−8.67	32.0	26
	Elymus	*canadensis*	5	88	36	36.8	1.40	−5.09	37.8	25
	Elymus	*caninus*	6	92	21	36.5	3.40	−10.39	21.3	18
	Elymus	*ciliaris*	1	85	18	35.8	1.60	−4.82	20.3	14
	Elymus	*dahuricus*	5	92	42	36.9	1.10	−3.92	35.1	22
	Elymus	*drobovii*	1	63	0	36.8	1.90	−5.58	18.8	16
	Elymus	*fibrosus*	3	93	26	36.8	2.10	−6.85	26.1	21
	Elymus	*hystrix*	1	64	58	29.8	1.00	−4.70	110.3	76
	Elymus	*lanceolatus*	3	93	20	39.8	2.70	−9.29	31.2	26
	Elymus	*mutabilis*	1	99	26	36.8	1.60	−5.20	25.8	20
	Elymus	*nutans*	1	99	52	37.8	3.10	−11.36	39.0	35
	Elymus	*patagonicus*	1	99	80	34.8	2.20	−9.81	86.3	73
	Elymus	*semicostatus*	2	91	2	36.3	3.70	−11.34	21.4	19
	Elymus	*sibiricus*	9	98	75	36.8	1.30	−6.09	108.2	80
	Elymus	sp.	1	98	0	37.8	2.10	−6.39	21.0	17
	Elymus	*trachycaulus*	33	94	2	22.0[2]	3.10	−8.67	16.4	14
	Elymus	*transhyrcanus*	24	89	86	30.4	1.00	−5.73	306.9	178
	Elymus	*tsukushiensis*	3	94	54	37.8	2.70	−10.29	45.2	38
	Elymus	*villosus*	1	99	86	34.8	1.70	−7.23	70.4	56
	Elymus	*virginicus*	2	92	86	33.8	1.30	−6.59	158.7	109
	Eragrostis	*curvula*	62	97	65	28.7[2]	2.1	−8.3	53.2	44
	Eragrostis	*lehmanniana*	4	93	64	28.1[2]	1.4	−6.1	75.7	54
	Eragrostis	*tef (abyssinica)*	22	96	91	16.7[2]	1.8	−8.0	83.6	66
	Eragrostis	*trichodes*	4	85	83	28.1[2]	1.0	−5.3	203.4	108
	Festuca	*arundinacea (elatior)*	61	92	36	29.2[2]	4.2	−14.0	28.0	25
	Festuca	*rubra*	112	92	33	29.0[2]	2.4	−8.2	31.0	25
	Hordeum	*vulgare*	941	97	86	44.4	1.9	−8.8	103.8	84
	Lolium	hybrid	5	98	89	35.1	1.90	−8.44	84.9	69
	Lolium	*multiflorum*	28	91	56	41.5	1.60	−6.55	59.9	43
	Lolium	*perenne*	114	95	46	40.8	1.80	−7.14	52.8	41
	Lolium	*persicum*	4	90	75	34.5	1.30	−5.77	84.6	56
	Lolium	*rigidum*	13	87	75	36.9	1.30	−6.31	128.1	82
	Lolium	sp.	1	99	96	34.5	1.00	−6.19	487.7	333
	Lolium	*temulentum*	6	88	85	34.1	1.50	−8.94	387.7	263
	Oryza	*sativa*	84	90	54	28.2[2]	1.7	−6.5	46.8	34

Table 1. *Continued*

Family	Genus	Species	No. of accessions	Germination (%)		Years stored	Avrami parameters			
				Initial	Final		Slope	Intercept	ϕ	P50 (years)
	Panicum	*miliaceum*	5	92	84	36.7	1.6	−7.7	120.2	88
	Pennisetum	*glaucum*	13	83	56	26.3[2]	1.3	−5.3	59.3	35
	Phleum	*alpinum*	1	99	94	35.5	2.10	−9.20	80.1	67
	Phleum	*arenarium*	3	90	50	37.5	1.50	−6.02	55.3	39
	Phleum	*bertolonii*	3	94	72	37.5	1.20	−5.80	126.0	86
	Phleum	*boissieri*	1	83	58	37.5	1.30	−5.86	90.6	54
	Phleum	*hirsutum*	1	85	5	37.5	1.90	−5.75	20.6	15
	Phleum	*montanum*	6	94	62	37.5	1.40	−6.03	74.2	54
	Phleum	*paniculatum*	2	94	52	37.5	1.40	−6.02	73.5	53
	Phleum	*phleoides*	6	92	79	36.1	1.50	−7.14	116.5	84
	Phleum	*pratense*	126	95	43	39.1	3.10	−11.16	36.5	32
	Phleum	sp.	1	99	97	30.5	1.00	−6.52	677.6	463
	Phleum	*subulatum*	2	94	28	37.5	3.90	−12.88	27.2	24
	Poa	*pratensis*	84	86	63	42.3	1.90	−8.18	74.2	54
	Secale	*cereale*	28	93	46	43.7	1.3	−5.1	52.4	36
	Setaria	*italica*	5	93	25	29.6[2]	1.7	−5.5	25.0	19
	Sorghum	*bicolor*	8220	89	36	44.4	2.0	−8.5	70.6	53
	Sporobolus	*airoides*	1	96	84	41.8	2.90	−12.49	74.3	64
	Sporobolus	*indicus*	1	98	62	37.8	1.40	−5.41	47.7	36
	Triticum	*aestivum*	427	94	73	43.6	2.0	−8.4	67.9	54
	Zea	*mays*	2272	96	28	60.7	2.40	−9.76	58.4	49
Polygonaceae ∘	*Fagopyrum*	*esculentum*	106	91	52	40.5	3.20	−12.29	46.6	40
	Polygonum	*persicaria*	1	86	85	31.8	1.00	−5.59	266.5	145
	Rheum	× *hybridum*	1	70	67	43.5	1.00	−5.24	188.7	64
Solanaceae △	*Capsicum*	*annuum*	535	90	18	43.9	3.3	−11.6	34.0	29
	Capsicum	*baccatum*	18	93	0	32.8[1]	5.0	−16.4	26.7	24
	Capsicum	*chinense*	51	93	72	37.2	2.10	−8.59	59.7	48
	Capsicum	*frutescens*	9	94	2	31.5[1]	4.00	−12.74	24.2	22
	Capsicum	sp.	3	91	51	37.5	2.40	−9.03	43.1	35
	Datura	*ferox*	7	97	0	36.8	1.50	−4.89	26.1	20
	Datura	*inoxia*	7	89	87	36.8	1.00	−5.30	199.9	115
	Datura	*leichhardtii*	2	96	0	36.8	1.10	−3.66	27.9	19
	Datura	*metel*	15	91	26	36.9	1.20	−3.66	21.2	14
	Datura	*quercifolia*	2	82	44	36.8	2.30	−7.99	32.3	24
	Datura	*stramonium*	142	94	82	36.8	1.00	−5.10	163.8	104
	Lycopersicon	*esculentum*	3749	92	28	80.6	1.7	−7.8	98.0	73
	Nicotiana	*tabacum*	829	91	13	45.7	4.10	−14.57	34.9	31
	Physalis	*alkekengi*	1	90	52	37.8	3.80	−14.63	47.0	41
	Physalis	*nicandroides*	1	89	68	37.8	1.80	−7.84	77.9	57
	Physalis	*peruviana*	3	96	64	37.8	1.50	−6.85	96.5	73
	Physalis	*philadelphica*	3	88	74	37.8	2.30	−10.32	88.8	69
	Physalis	*pubescens*	4	94	34	39.3	1.50	−6.24	63.9	47
	Physalis	sp.	1	98	86	37.8	2.80	−12.84	98.2	85
	Solanum	*aculeatissimum*	1	77	34	37.6	1.20	−4.68	49.3	25
	Solanum	*aethiopicum*	2	84	68	36.6	1.10	−4.60	65.6	36
	Solanum	*americanum*	3	92	14	34.6	1.50	−5.15	31.1	22
	Solanum	*anguivi*	3	87	62	38	1.10	−4.83	80.8	47
	Solanum	*atropurpureum*	1	87	76	35.6	1.70	−7.70	92.8	66
	Solanum	*aviculare*	1	79	38	35.6	1.10	−4.61	66.2	33
	Solanum	*capsicoides*	2	93	83	39.0	2.10	−9.43	89.0	71
	Solanum	*mammosum*	2	84	67	36.5	1.10	−4.72	73.1	40
	Solanum	*melongena*	255	88	43	51.4[2]	2.0	−8.3	61.9	46
	Solanum	*retroflexum*	2	94	26	50.8[2]	4.3	−17.0	51.7	47
	Solanum	*scabrum (nigrum)*	1	98	96	43.5	1.0	−6.5	673.5	453
	Solanum	sp.	3	94	84	35.5	1.60	−7.09	83.8	63
	Solanum	*tuberosum*	159	96	39	24.0[1]	2.3	−7.5	26.2	22

Table 1. *Continued*

Family	Genus	Species	No. of accessions	Germination (%)		Years stored	Avrami parameters			
				Initial	Final		Slope	Intercept	ϕ	P50 (years)
Valerianaceae +	*Valerianella*	*locusta*	1	84	22	43.8	1.70	−6.15	37.3	25
		Average	151	91	58	38	1.8	−7.4	134	88
		Median	3	92	64	38	1.5	−6.7	74	54
		Maximum	8220	99	100	81	5.4	−3.7	904	633
		Minimum	1	39	0	16	1.0	−17.3	12	7
		Total Number	41,847	276	276	276	276	276	276	276

[1] Time of storage at −18°C was 15–19 years (last germination test in the mid-1990s).

[2] Time of storage at −18°C was 7–11 years (last germination test was before 1990).

to 0% [*Datura ferox* (*Solanaceae*), *Datura leichhardtii*, *E. drobovii* (*Poaceae*), *Gossypium lobatum* (*Malvaceae*), 37 years; *Capsicum baccatum* (*Solanaceae*), 33 years; *Bromus sitchensis* (*Poaceae*), 18 years] (Table 1). The rate at which seeds of the various species lost viability in storage was calculated from germination time courses pooled among accessions and harvest dates. Representative datasets for six species (Fig. 2) show individual storage time versus germination percentage data points (small open circles), a pooled time course calculated by averaging data in 4-year intervals (larger solid circles), and the fitted Avrami curve calculated from the pooled time course (solid curve). The large range of germination percentages among accessions with storage time underscores the variability of ageing rates of seeds with similar growth provenances. None the less, the hypothesis that species have characteristic ageing rates is supported by the time period during which percent germination remains clustered at high levels [e.g. in seeds of *Pisum sativum* (*Fabaceae*) germination remained high for about 30 years], and by the time in which most of the accessions show very low germination [e.g. most *Arachis hypogaea* (*Fabaceae*) accessions gave <5% germination after 35 years of storage] (Fig. 2).

The time required to reduce germination to 50% (P50) ranged among species from <13 years [*Gossypium lobatum* (*Malvaceae*), *Guizotia abyssinica* (*Asteraceae*) and *Bromus sitchensis* (*Poaceae*)] to an extrapolated estimate of >450 years [*Trifolium campestre* (*Fabaceae*), *Gossypium bickii* (*Malvaceae*), *Phleum* sp. (*Poaceae*), *Solanum scabrum* (*nigrum*) (*Solanaceae*) and *Vigna radiata* (*Fabaceae*)], and the median P50 was 54 years (Table 1), with a mode between 15 and 30 years (Fig. 1C) There was no significant relationship between initial germination percentage and calculated P50 ($r^2 = 0.03$). Obviously, P50 values that are greater than the experimental storage duration are less certain because they were derived through extrapolation. However, after a 12–15% reduction in germination occurs, calculated Avrami parameters are fairly consistent when additional time course data are added to the curve-fitting routine (analyses not shown), suggesting a relatively reliable prediction of P50 with only partial deterioration. Values of P50 calculated from time courses with less than 30 years of storage, and less than 5–6% reduction of germination, are particularly suspect and are likely to be overestimates. Significant reductions in germination were only apparent after 30 years of storage in many species [e.g. *Raphanus sativus* (*Brassicaceae*), *Pisum sativum* (*Fabaceae*), *Melilotus alba* (*Fabaceae*) and *B. vulgaris* (*Chenopodiaceae*), Fig. 2], which explains the paucity of reliable estimates of seed longevity under refrigeration, since these conditions were rarely used before the 1960s.

Avrami parameters describe the shape of the calculated time course and the rapidity with which germination is reduced. For example, the exponential factor for *Melilotus alba* is 1 (Table 1), resulting in a typical exponential decay curve (Fig. 2). As exponential factors increase to 1.6 (*R. sativus*), 1.7 [*C. melo* (*Cucurbitaceae*)], 2.0 (*P. sativum*), 3.1 (*B. vulgaris*) and 4.4 (*A. hypogaea*), there is a sharper downturn of germination in the cataclysmic decay phase of the time course. Generally, P50 decreases as the exponential factor (slope in the regression analyses) increases and as ϕ decreases ($\phi = e^{(-y_0/n)}$). The average value for the exponential factor among species stored at NCGRP was 1.8. Values reported in another study for different accessions of lettuce (*Lactuca sativa*) seeds stored between −1 and 10°C ranged from 2 to 3 (Walters *et al.*, 2004), which is consistent with the current findings, considering that lettuce seeds tend to age more rapidly than those of most other species (Tables 1–3). Values for ϕ were directly related to the calculated P50 values, and ranged from 11.5 for *Bromus sitchensis* (*Poaceae*) to 904 for *Trifolium campestre* (*Fabaceae*), with a median of 74 (Table 1).

Longevity parameters calculated from deterioration time courses in the Stanwood (unpublished) experiments (Table 2) follow similar patterns as the NPGS data, with the exponential factor ranging from 1 to 3.1 (median = 1.2), ϕ ranging from 10 to 730

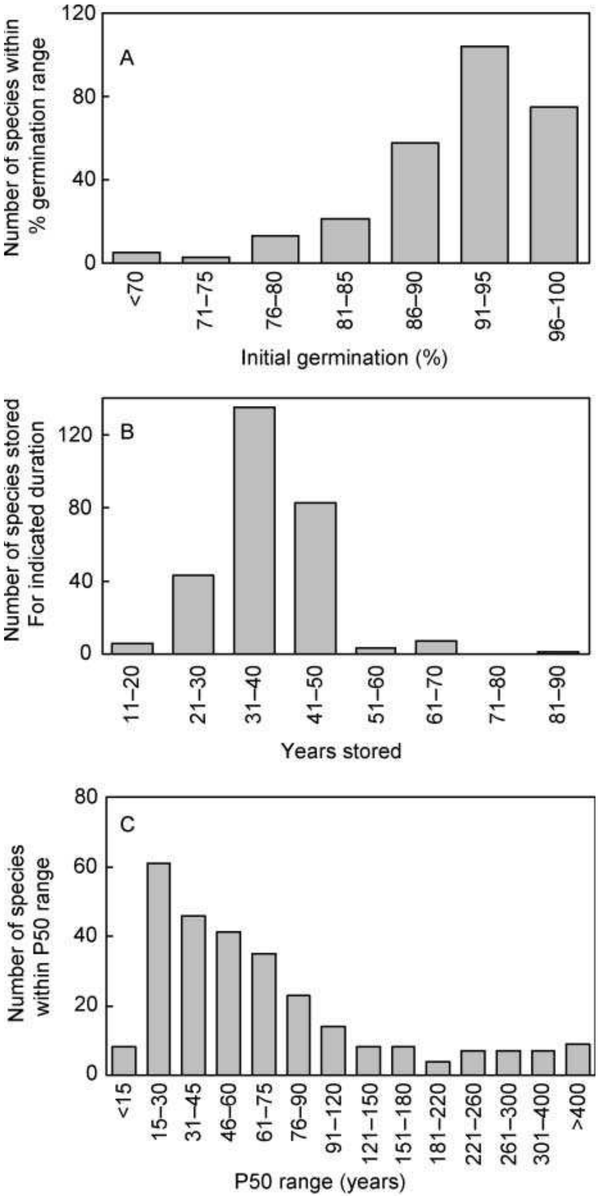

Figure 1. Summary statistics of the initial germination (A), total storage time (B) and calculated P50 (C) of the 276 species in the USDA National Plant Germplasm System (NPGS) collection used in this study. Data are summarized from Table 1.

(median = 94), and P50 ranging from 8 to 497 years, with a median of 56 years (compared with a median of 54 years in the NPGS dataset). For several species common to both the NPGS collection and the Stanwood experiments, P50 estimates are nearly identical [e.g. *Brassica oleracea* (*Brassicaceae*), *Helianthus annuus* (*Asteraceae*), *Lactuca sativa* (*Asteraceae*), *Glycine max* (*Fabaceae*), *Festuca* spp. (*Poaceae*)] (Table 3). However, the slightly lower exponential factors and higher median ϕ in the Stanwood data set led to higher calculated P50s for many species. Lower exponential factors are typical when storage times are too short (between 20 and 25 years in the Stanwood experiment) for seeds to enter into the cataclysmic decay phase. Hence, insufficiently long storage times led to an overestimate of P50 when Avrami parameters were calculated from a double-ln plot, suggesting that large discrepancies between P50s calculated for the NPGS collection and the Stanwood experiments [e.g. *Apium graveolens* (*Apiaceae*), *Cucumis* spp. (*Cucurbitaceae*), *Spinacia oleracea* (*Chenopodiaceae*), *Vicia* spp. (*Fabaceae*)] can be attributed to the insufficient duration of the Stanwood experiment. The low P50s observed in the Stanwood experiment for species such as *Lespedeza cuneata* (*Fabaceae*), *Medicago sativa* (*Fabaceae*) and *Pennisetum glaucum* (*Poaceae*) may not be representative, as the behaviour has been assessed from just one accession.

The large number of species included in the NPGS collection allows comparison with P50 values determined in other survey studies reported in the literature (Table 3). For the 62 species common to both studies, P50 values reported by Priestley *et al.* (1985) were consistently less (median P50 = 7 years) than values reported for the NPGS collection; but this is expected since seeds in the Priestley *et al.* (1985) study were stored under fluctuating temperature and moisture conditions. P50 values calculated using coefficients of the viability equations of Ellis *et al.* (1986, 1988, 1989, 1990a,b) were similar (median = 48 years) to the P50 values determined from the NPGS and Stanwood storage experiments (see Table 3 for species in common, compare also with Tables 1 and 2 for all species). Estimated longevities for vegetable species in the Roos and Davidson (1992) study were also comparable, with a median P50 = 46, despite a higher storage temperature, smaller number of species and smaller range of P50s. Maximum germination in the Duvel buried seed experiment occurred in years 1 to 39, with a median of 6 years (Toole and Brown, 1946). Although the surveys of Duvel and Priestley *et al.* (1985) reported similar average life spans, species that persisted in the soil were not the same ones that survived in storage bins (Table 3). These results demonstrate that expected longevities among widely varying experiments are comparable when seeds are stored under controlled, relatively dry, conditions. However, there was no significant trend observed between seed persistence in a temperate-mesic soil seed bank (Table 4, last column) and seed longevity under controlled storage conditions, suggesting, perhaps, that the mechanisms of deterioration and protection are different in these contrasting environments.

Significant correlation of P50 values ($P < 0.03$ or $P < 0.10$) among different surveys (Table 4) demonstrates that the relative tendency for species to age is

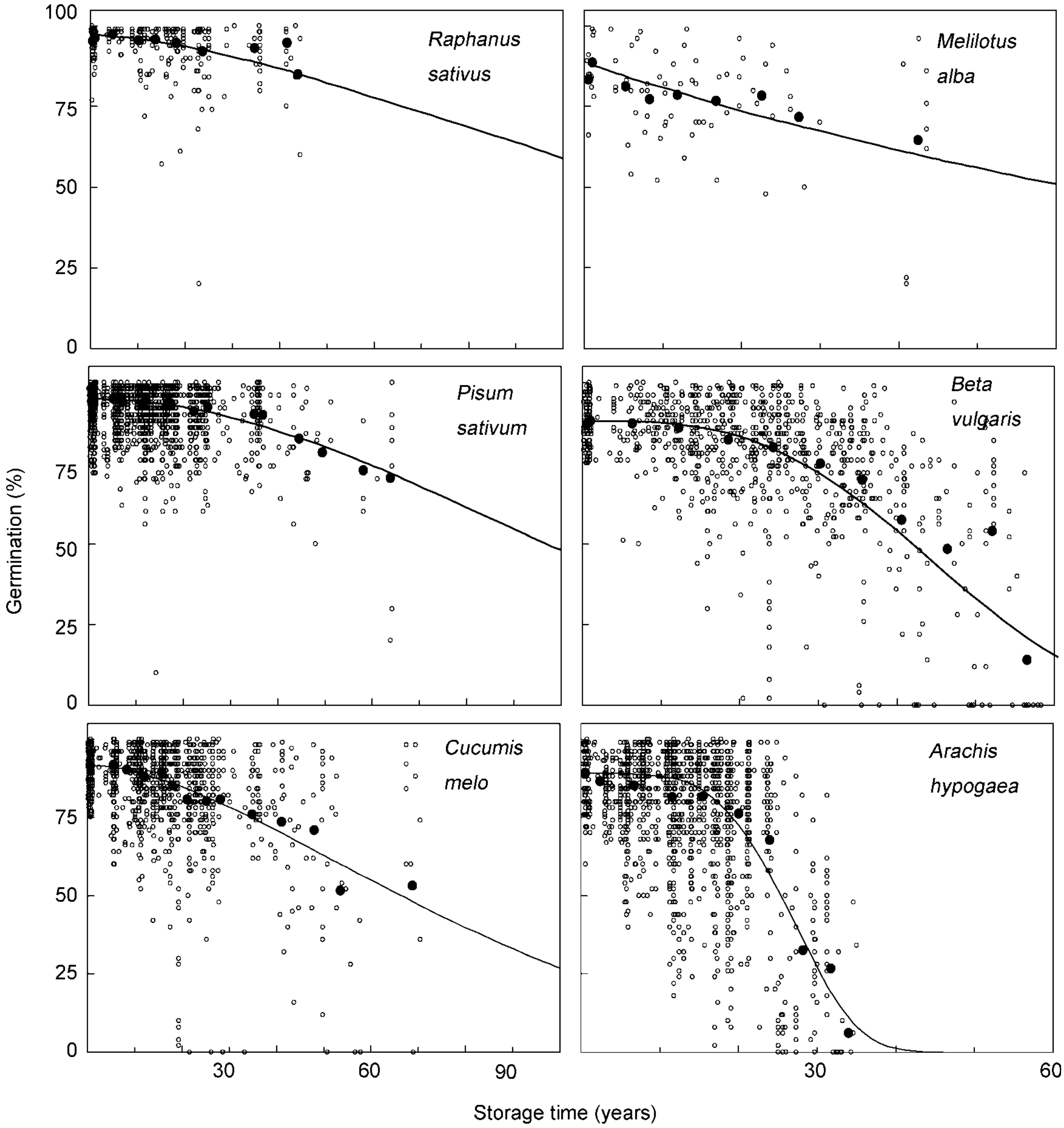

Figure 2. Germination time courses for six species in the USDA National Plant Germplasm System (NPGS) collection constructed from viability monitoring data. Storage time versus percent germination for individual accessions (open circles) were averaged in 4-year increments (solid circles) and the ageing characteristic was calculated by fitting the averaged time course to the Avrami equation (see Methods section) (curve). The time courses and fitted curves described in this figure are typical of the interpolation (*B. vulgaris*, *A. hypogaea* and *C. melo*) or extrapolation (*R. sativus*, *M. alba* and *P. sativum*) required to calculate the time for seed germination to decrease to 50%. Avrami parameters and calculated P50 values for each species are listed in Table 1 (NPGS collection) and Table 2 (Stanwood, unpublished).

consistent among experiments, and supports the hypothesis that species have characteristic ageing behaviours. For the surveys considered in this paper, species were divided into three categories, based on whether the P50 was in the lowest, middle or highest third in the experiment (analysis not shown). Species that were placed in the same category in two or more experiments were considered to have short, medium or long life spans respectively, relative to other species (Table 3, right-hand column). For example, *Allium cepa* (*Liliaceae*), *Bromus inermis* (*Poaceae*) and *Festuca rubra* (*Poaceae*) had consistently low P50s and were placed in the short shelf-life category, while *Abelmoschus esculentus* (*Malvaceae*), *Lycopersicon esculentum* (*Solanaceae*), *Pisum sativum* (*Fabaceae*) and *Raphanus sativus* (*Brassicaceae*) had consistently high P50s and were placed in

Table 2. Storage performance of seeds in an experiment initiated by Stanwood in 1977 to compare longevities of species at different storage temperatures (results of liquid nitrogen study published in Walters *et al.*, 2004). Seeds were stored at 5°C and at the indicated water content throughout the experiment. Initial and final germination values are averages calculated within 1 year of harvest and after the indicated storage time, respectively. Coefficients calculated from the Avrami-curve fitting routine (see Methods section) were used to calculate the time for germination to decrease from the initial value to 50% (except for *Abies procera* where time to half the initial germination is calculated)

Family	Genus	Species	No. of cultivars	H_2O content (%)	Germination (%)		Years stored	Avrami parameters			
					Initial	Final		Slope	Intercept	ϕ	P50 (years)
Apiaceae	*Apium*	*graveolens*	2	7.73	90	76	26	1.1	−5.3	123	75
	Daucus	*carota*	19	7.26	86	79	26	1.0	−5.0	145	79
	Petroselinum	*crispum*	2	7.44	89	73	26	1.0	−4.6	100	58
Asteraceae	*Helianthus*	*annuus*	3	3.67	92	82	27	1.0	−4.5	91	56
	Lactuca	*sativa*	9	5.24	98	13	26	1.7	−5.7	28	23
	Zinnia	*violacea*	4	7.08	88	42	24	1.3	−4.5	31	20
Brassicaceae	*Brassica*	*oleracea*	18	5.40	95	40	26	2.2	−7.5	30	25
	Crambe	*abyssinica*	4	7.18	74	48	27	3.1	−10.2	28	21
	Raphanus	*sativus*	8	5.35	99	97	27	1.0	−6.6	730	497
Chenopodiaceae	*Beta*	*vulgaris*	10	7.52	91	87	26	1.0	−5.0	147	88
	Spinacia	*oleracea*	5	7.96	97	86	27	1.6	−7.7	133	102
Cucurbitaceae	*Citrullus*	*lanatus*	5	5.99	98	95	27	1.0	−6.2	475	318
	Cucumis	*melo*	7	5.67	95	91	27	1.0	−5.9	351	224
	Cucumis	*sativa*	7	6.32	97	93	27	1.0	−5.7	299	199
Fabaceae	*Astragalus*	sp.	3	5.67	93	88	27	2.5	−11.6	98	81
	Glycine	*max*	1	6.78	95	16	27	1.7	−6.3	40	31
	Lespedeza	*cuneata*	1	7.70	92	7	30	1.9	−4.8	13	10
	Lotus	*corniculatus*	3	7.17	84	70	26	1.1	−5.1	93	52
	Medicago	*sativa*	4	6.85	89	70	26	1.0	−4.6	95	55
	Onobrychis	*viciifolia*	3	8.00	84	27	27	2.0	−6.0	20	15
	Phaseolus	*vulgaris*	3	7.56	93	96	26	1.0	−6.2	492	307
	Trifolium	*pratense*	3	6.16	87	57	25	1.0	−5.4	227	127
	Trifolium	*repens*	3	7.66	87	84	25	1.1	−5.0	97	57
	Vicia	sp.	3	9.37	94	91	26	1.0	−5.4	211	133
Liliaceae	*Allium*	*cepa*	21	6.91	94	31	26	1.3	−4.0	22	15
Papaveraceae	*Papaver*	*somniferum*	3	5.40	99	51	44	1.9	−7.54	52	43
Pinaceae	*Abies*	*procera*	4	9.65	49	1	27	1.7	−3.9	10	8
Poaceae	*Eragrostis*	*curvula*	3	8.53	94	82	26	1.0	−4.9	135	85
	Festuca	*arundinacea*	3	8.65	91	33	26	1.3	−4.1	23	15
	Festuca	*rubra*	3	8.11	92	41	26	1.3	−5.2	54	37
	Hordeum	*vulgare*	3	8.49	97	73	26	1.2	−5.3	82	58
	Oryza	*sativa*	2	8.41	98	13	32	3.1	−9.8	25	22
	Pennisetum	*glaucum*	1	8.56	87	63	27	1.2	−4.4	42	25
	Poa	*pratensis*	3	7.32	90	87	26	1.0	−5.6	260	154
	Sorghum	*bicolor*	7	9.17	97	90	26	1.4	−7.2	168	125
	Triticum	*aestivum*	3	8.32	95	26	40	2.4	−9.3	48	40
	Zea	*mays*	1	8.38	99	98	26	1.0	−6.0	385	263
Solanaceae	*Capsicum*	*annuum*	3	5.92	98	76	27	1.4	−5.7	58	44
	Lycopersicon	*esculentum*	6	6.52	92	89	26	1.0	−5.4	215	130
	Nicotiana	*tabacum*	4	5.66	95	89	25	1.0	−4.8	126	81
	Petunia	sp.	6	5.62	93	58	25	1.3	−4.7	37	26
Ulmaceae	*Ulmus*	*americana*	1	6.79	90	1	28	2.0	−5.2	14	10
		Average	5	7.12	91	62	27	1.4	−5.9	139	91
		Median	3	7.22	93	73	26	1.2	−5.4	94	56
		Maximum	21	9.65	99	98	44	3.1	−3.9	730	497
		Minimum	1	3.67	49	1	24	1.0	−11.6	10	8
		Total number	207	42	42	42	42	42	42	42	42

the long shelf-life category. Species with P50s that clustered around the median in two or more experiments exhibited medium shelf-life, and include *Helianthus annuus* (*Asteraceae*), *Linum usitatissimum* (*Linaceae*), *Papaver somniferum* (*Papaveraceae*) and *Trifolium pratense* (*Fabaceae*). Species with P50s that

Table 3. Seed longevity values for species in different surveys. Values represent the calculated time (in years) for germination to decline to 50% for all studies except Duvel's experiment, which gives the years when maximum germination in the soil was measured (Toole and Brown, 1946). A rating of relative longevity is suggested in the right-hand column, based on comparisons of the species P50 with the median P50 for the indicated experiment. If the species $\text{P50} < (\text{median P50} - \text{median P50} \div 3)$ in two or more experiments, the species was considered relatively short-lived. If the species $\text{P50} > (\text{median P50} + \text{median P50} \div 3)$ in two or more experiments, the species was considered relatively long-lived. If $(\text{median P50} - \text{median P50} \div 3) \leq \text{species P50} \leq (\text{median P50} + \text{median P50} \div 3)$ consistently among storage experiments, the species was considered to have medium longevity. An assignment of 'variable longevity' indicates that the species P50 was in the lower third in one survey and the upper third in another survey. Longevities from Duvel's experiment were not considered in the classification scheme

Genus	Species	NPGS	Stanwood (unpubl.)	Ellis Viability Equations	Priestley *et al.*	Roos and Davidson	Toole and Brown	Relative longevity
Brassica	*napus*	25		37	13.94		6	Variable
Daucus	*carota*	30	79	42	6.63	35		Variable
Isatis	*tinctoria*	27			9.82			Variable
Nicotiana	*tabacum*	31	81		10.3		10	Variable
Phaseolus	*vulgaris*	31	307	434	15.97	46		Variable
Ricinus	*communis*	26			13.31			Variable
Setaria	*italica*	19		66			26	Variable
Allium	*cepa*	23	15	27	5.43	29		Short
Apium	*graveolens*	27	74		4.11		1	Short
Arachis	*hypogaea*	25		7				Short
Brassica	*oleracea*	23	25		7.15			Short
Bromus	*inermis*	16			3.38			Short
Capsicum	*annuum*	29	44			27		Short
Carum	*carvi*	32			4.19			Short
Crambe	*abyssinica*	21	21					Short
Festuca	*arundinacea (elatior)*	25	15		4.98			Short
Festuca	*rubra*	25	26		4.7			Short
Glycine	*max*	32	31	37	3.43			Short
Guizotia	*abyssinica*	13		24				Short
Lactuca	*sativa*	23	23	23	6.42			Short
Onobrychis	*viciifolia*	34	15		6.43			Short
Oryza	*sativa*	34	22	46				Short
Pastinaca	*sativa*	30			4.04		1	Short
Pennisetum	*glaucum*	35	25	46				Short
Petroselinum	*crispum*	21	58		3.41			Short
Ulmus	sp.		10	9				Short
Allium	*ampeloprasum*	32			5.30			Medium short
Lepidium	*sativum*	26			5.09			Medium short
Lespedeza	*cuneata (sericea)*	43	10					Medium short
Lupinus	*angustifolius*	41			3.81			Medium short
Secale	*cereale*	36			4.51			Medium short
Solanum	*tuberosum*	22			9.00			Medium short
Tragopogon	*porrifolius*	42			2.58			Medium short
Trifolium	*hybridum*	29			6.16		21	Medium short
Valerianella	*locusta*	25			6.74			Medium short
Zinnia	*violacea*	46	20					Medium short
Cichorium	*intybus*	39			5.42			Medium
Dactylis	*glomerata*	65			6.61			Medium
Fagopyrum	*esculentum*	40			7.46			Medium
Helianthus	*annuus*	50	56	40	5.42		1	Medium
Linum	*usitatissimum*	53		46	8.75			Medium
Lolium	*multiflorum*	43			9.36			Medium
Lolium	*perenne*	41			7.19			Medium
Lotus	*corniculatus*	68	52		6.72			Medium
Papaver	*somniferum*	62	43		7.28			Medium
Phleum	*pratense*	32		33	5.73		6	Medium
Poa	*pratensis*	54	154		6.63		2	Medium
Rheum	× *hybridum*	64			8.68			Medium
Scorzonera	*hispanica*	47			6.74			Medium
Sesamum	*indicum*	39		48				Medium

Table 3. *Continued*

Genus	Species	NPGS	Stanwood (unpubl.)	Ellis Viability Equations	Priestley *et al.*	Roos and Davidson	Toole and Brown	Relative longevity
Solanum	*melongena*	46				54		Medium
Trifolium	*incarnatum*	59			5.25			Medium
Trifolium	*pratense*	43	57		5.36		21	Medium
Triticum	*aestivum*	54	40	69	7.59	65		Medium
Chenopodium	*quinoa*	250		63				Medium long
Citrullus	*lanatus*	68	318			43		Medium long
Cucumis	*sativus*	87	199		4.92	45	1	Medium long
Eragrostis	*curvula*	44	85					Medium long
Eragrostis	*tef (abyssinica)*	66		315				Medium long
Hordeum	*vulgare*	84	58	164	7.19			Medium long
Lathyrus	*odoratus*	40			13.63			Medium long
Lupinus	*polyphyllus*			89	6.2			Medium long
Melilotus	*alba*	63			33.4			Medium long
Sorghum	*bicolor*	53	125					Medium long
Abelmoschus	*esculentus*	87				125		Long
Avena	*sativa*	117			12.96			Long
Beta	*vulgaris*	42	88	152	16.51	43	6	Long
Brassica	*hirta*	76			13.71			Long
Cicer	*arietinum*	70		250	15.29			Long
Cucumis	*melo*	66	224			61		Long
Eleusine	*coracana*	437		168				Long
Lens	*culinaris*	365			10.65			Long
Lycopersicon	*esculentum*	73	130		24.52	124		Long
Medicago	*sativa*	93	55		10.56		1	Long
Panicum	*miliaceum*	88			11.9			Long
Pisum	*sativum*	97		487	15.86	130		Long
Raphanus	*sativus*	120	497		13.82			Long
Spinacia	*oleracea*	73	102		12.76	37		Long
Trifolium	*repens*	77	127		8.21		8	Long
Vicia	sp.	71	133		11.4			Long
Vigna	*radiata*	457		335	19.54			Long
Zea	*mays*	49	263		9.6			Long
Datura	*stramonium*	104					39	Unranked
Elymus	*canadensis*	25					1	Unranked
Elymus	*virginicus*	109					1	Unranked
Lactuca	*serriola*	21					1	Unranked
Polygonum	*persicaria*	145					15.5	Unranked
Solanum	*scabrum (nigrum)*	453					16	Unranked
Sporobolus	*airoides*	64					10	Unranked
	Average	68	95	117	9	62	10	
	Median	42	57	48	7	46	6	
	Maximum	456	497	487	33	130	39	
	Minimum	13	10	7	3	27	1	
	Total number	87	39	27	62	14	22	

were in either the lower or upper third in one experiment and the middle third in another were assigned intermediate categories. Species that stored well in one experiment, but poorly in another, were considered to have variable performance and provide an opportunity to study growth and processing conditions that affect storability. For example, the low P50s for *Phaseolus vulgaris* (*Fabaceae*) from the NPGS collection and *Cucumis sativus* (*Cucurbitaceae*) from Priestley *et al.* (1985) suggest some type of mishandling.

The data presented in this survey confirm some widely held ideas about relative longevities among species. For example, P50s calculated for the small cereal grains (*Poaceae*) in the NPGS collection suggest a relative longevity ranking of *Avena sativa* > *Hordeum vulgare* > *Triticum aestivum* > *Secale cereale* ≥ *Oryza sativa* [Table 1, which is consistent with the ranking of P50s by Priestley *et al.* (1985) in Table 3]. Rankings are also consistent with preliminary findings by Rincker (1981) that classified *Bromus inermis* (*Poaceae*) as having poor keeping quality, while *Medicago sativa*

Table 4. Correlations among seed longevity values measured in different survey studies. Longevity values for each survey are given in Table 3. Correlation coefficients (r^2) are given for each linear regression, with the number of species in the analysis given in parentheses

Survey	Stanwood (unpub.)	Priestley *et al.* (1985)	Ellis Viability Equations	Roos and Davidson (1992)	Toole and Brown (1946)
NPGS	0.33[1] (38)	0.12[1] (61)	0.12[2] (25)	0.49[1] (14)	0.03 (22)
Stanwood (unpub.)		0.21[1] (28)	0.91[1] (12)	0.01 (11)	0.09 (9)
Priestley *et al.* (1985)			0.59[1] (16)	0.44[2] (9)	<0.01 (13)
Ellis Viability Equations				0.47 (6)	0.04 (6)
Roos and Davidson (1992)					Not applicable (2)

NPGS, USDA National Plant Germplasm System.

[1] Indicates a significant trend at $P < 0.03$.

[2] Indicates a significant trend at $P < 0.10$.

(*Fabaceae*) and *Trifolium repens* (*Fabaceae*) had relatively good keeping quality. The reason for differences in relative longevity are unclear, although there is likely to be a genetic basis. The case with *Gossypium* species (*Malvaceae*) may be particularly interesting, in that species within genome D have wide-ranging longevities, while those with other genome types appear to store consistently well (Table 1). In addition to *Gossypium*, congeners within *Allium*, *Brassica*, *Bromus*, *Datura*, *Elymus*, *Lespedeza*, *Lolium*, *Phleum*, *Solanum* and *Trifolium* showed wide-ranging P50 values. Congeners of *Agropyron*, *Capsicum*, *Cucumis*, *Cucurbita*, *Festuca*, *Hibiscus*, *Lactuca* and *Physalis* all gave comparable longevities.

The distribution of P50s within plant families also followed some patterns (Fig. 3). Species of *Apiaceae* consistently had seeds with P50s less than the median value of 54 years. Species in *Brassicaceae* tended to have either short or long shelf lives, with no species with medium longevities. Most species in *Chenopodiaceae*, *Cucurbitaceae* and *Malvaceae* had P50s greater than the median value. Wild species within the *Chenopodiaceae* and *Malvaceae* also produce seeds with exceptional persistence in the soil (Toole and Brown, 1946; Telewski and Zeevaart, 2002). Large families such as the *Asteraceae*, *Fabaceae*, *Poaceae* and *Solanaceae* contained species with wide-ranging P50 values (Fig. 3), and this was also observed in the soil seed bank (Toole and Brown, 1946; Hendry *et al.*, 1994; Telewski and Zeevaart, 2002).

Differences in geographic origin may contribute to variation among P50s within genera and families. Geographic origins of species in the NPGS collection were assigned according to Vavilov (1992), *Hortus third* (LHB Hortorium, 1976) or the NPGS taxonomic website (http://www.ars-grin.gov/cgi-bin/npgs/html/tax_search.pl). The range and median P50s for each region are given in Fig. 4. Despite the wide range of P50 values for all geographic areas, there appeared to be some areas that supported long-lived species with median P50s ≥80 years (South Asia and Australia), and some where shelf life tended to be

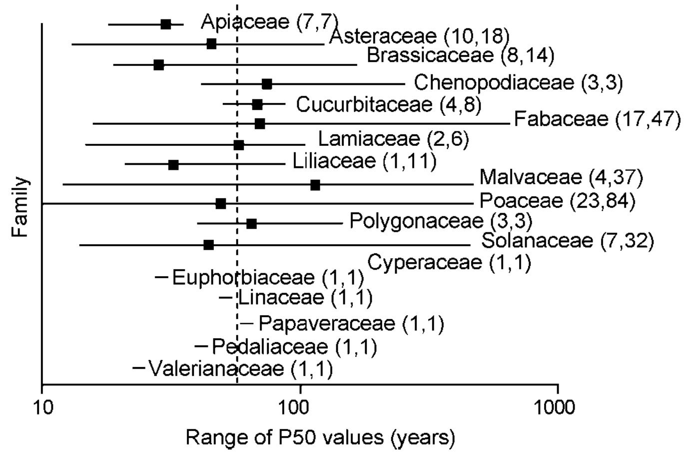

Figure 3. The median (solid squares) and range of P50 values observed among plant families in the USDA National Plant Germplasm System (NPGS) collection. P50 values for each species were calculated from time courses similar to those given in Fig. 2 and are listed in Table 1. Values in parentheses represent the number of genera and species. The dashed vertical line represents the median P50 (= 54) among all species tested.

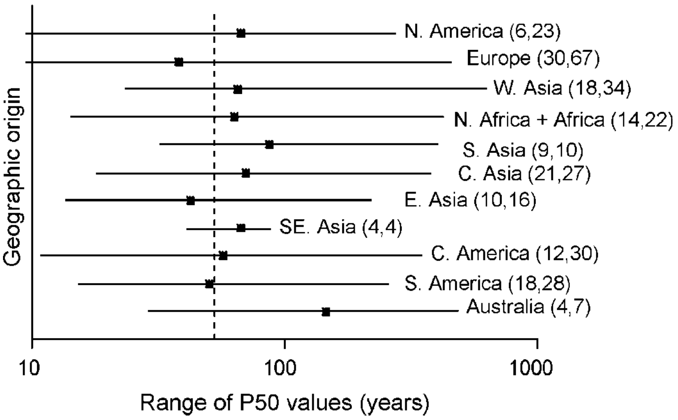

Figure 4. The median (solid squares) and range of P50 values observed for species in the USDA National Plant Germplasm System (NPGS) collection according to their geographic origin. P50 values for each species were calculated from time courses similar to those given in Fig. 2 and are listed in Table 1. Values in parentheses represent the number of genera and species. The dashed vertical line represents the median P50 (= 54) among all species tested.

short, with a median P50 = 38 years (Europe). *Brassica* species (*Brassicaceae*) that are endemic to Europe (*B. napus*, *B. oleracea*) tended to have lower P50s than congeners endemic to Asia (*B. hirta* and *B. juncea*) (Table 1). A similar pattern was indicated by congeners of *Lolium* species (*Poaceae*), but is not apparent for *Allium*, *Bromus*, *Elymus*, *Phleum*, *Salvia*, *Solanum* or *Trifolium* species. Although preliminary, the observation suggests the hypothesis that species originating in warm, arid locations may be more amenable to genebank conditions than species originating from temperate, moister environments. In contrast, species originating from temperate, moist areas may be more adapted for persistence in the soil seed bank. This possibility is supported by the poor correlations between seed longevity under controlled versus field conditions [Table 4, see also results from Hendry *et al.* (1994)], and further suggests that ageing stresses and protective mechanisms vary with moisture and temperature.

Hypotheses relating to chemical constituents of seeds have also been put forward to explain the variation of longevity among species. Anecdotal accounts of poor keeping quality of lettuce or peanut seeds have probably led to the widespread idea that seeds with high oil content store poorly. The shift in soluble carbohydrates during the later stages of seed maturation, and again during germination (Koster and Leopold, 1988; Kuo *et al.*, 1988), led to the hypotheses that raffinose oligosaccharides play some role in seed longevity (e.g. Horbowicz and Obendorf, 1994). These hypotheses are not supported by the data presented in this paper (Figs 5 and 6). Despite the widely ranging protein, lipid and carbohydrate contents of seeds of various species (Earle and Jones, 1962; Jones and Earle, 1966; Sinclair and DeWit, 1975), the present study has indicated that there is no apparent trend between storage reserves and seed longevity. This finding, which surveys 118 species with both longevity and composition data (Fig. 5), is consistent with the analyses by Priestley (1986) and others (Pritchard and Dickie, 2003) that used smaller subsets of species. Perhaps, a slightly significant correlation between seed lipid content and P50 ($r^2 = 0.04$, $P = 0.10$) can be assigned (see also Pritchard and Dickie, 2003), but the relationship does not hold when families with widely varying longevities and compositions, such as the *Asteraceae* (open circles in Fig. 5) or *Fabaceae* (open squares, Fig. 5), are considered separately. Furthermore, species within the *Poaceae* have diverse longevities (Fig. 3), despite fairly similar chemical compositions (solid circles, Fig. 5). Also, soluble carbohydrate contents in seeds (Kuo *et al.*, 1988; Horbowicz and Obendorf, 1994) do not correlate with seed longevity (Fig. 6). Sugar content in seeds ranges from <5 to 140 mg (g dry mass)$^{-1}$; however, there is no apparent relationship between total sugar, oligosaccharides or sucrose content and P50. Species from *Fabaceae* (open squares, Fig. 6) show the widest range of sugar compositions, but do not show a consistent trend with longevity ($P > 0.10$ for the eight species considered). Conversely, species of *Poaceae* (solid circles, Fig. 6) show a wide range of P50 values, but very little difference in sugar composition.

The concentration of soluble protein and ortho-dihydroxyphenol, a fungistatic compound, in the seed (Hendry *et al.*, 1994), also did not correlate with P50s under genebank conditions (Fig. 7), although this was expected since longevity under genebank and soil seed bank conditions also did not correlate (Table 4). Perhaps, the adverse effects of seed-associated fungi (Mycock and Berjak, 1995) are not manifested in genebanks as they are in high humidity conditions of

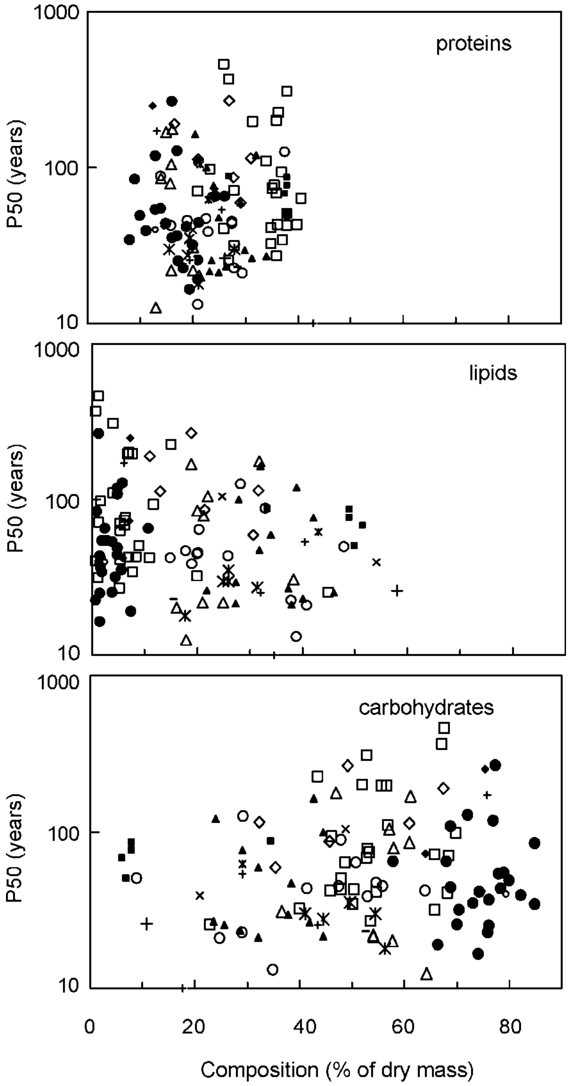

Figure 5. The relationship between species P50 values listed in Table 1 and dry matter reserves accumulated in seeds. Chemical compositions are taken from the literature (Earle and Jones, 1962; Jones and Earle, 1966; Sinclair and DeWit, 1975). Symbols represent different families [e.g. *Poaceae* (solid circle), *Fabaceae* (open square), *Asteraceae* (open circle), *Cucurbitaceae* (closed square), *Brassicaceae* (closed triangle)], with the full key given in Table 1.

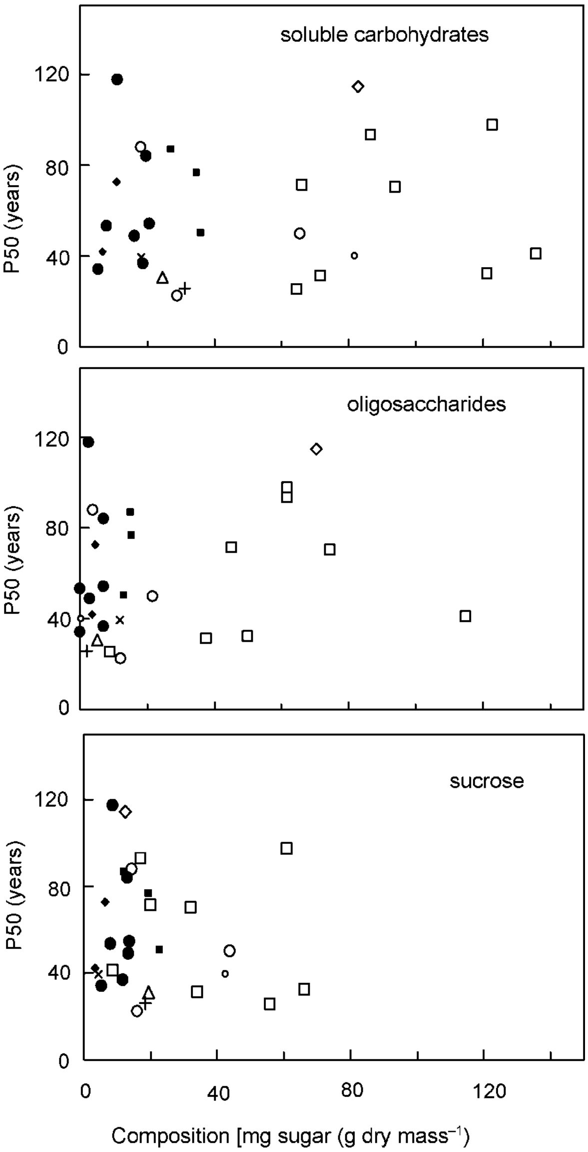

Figure 6. The relationship between species P50 values listed in Table 1 and soluble carbohydrates in mature seeds. Sugar levels are reported in the literature (Kuo *et al.*, 1988; Horbowicz and Obendorf, 1994). Symbols represent different families [e.g. *Poaceae* (solid circle), *Fabaceae* (open square), *Asteraceae* (open circle), *Cucurbitaceae* (closed square)], with the full key given in Table 1.

soil seedbanks or 'open' storage, and so fungistatic agents are not important protectants against ageing under dry conditions.

The NPGS dataset allows us to address some questions about seed longevity and resource allocation during seed development. There is no direct correlation between seed size (AOSA, 2003) and longevity (Fig. 8A), a point that has also been demonstrated using a smaller dataset (Pritchard and Dickie, 2003). The amount of fixed carbon allocated to seed production also does not appear to correlate with seed longevity in a small, but representative, subset of the species from the NPGS collection (Fig. 8B). Similarly, nitrogen requirements do not appear to influence seed longevity (Fig. 8C), although this statistic may be meaningless under cultivation scenarios where nitrogen is not a limiting resource.

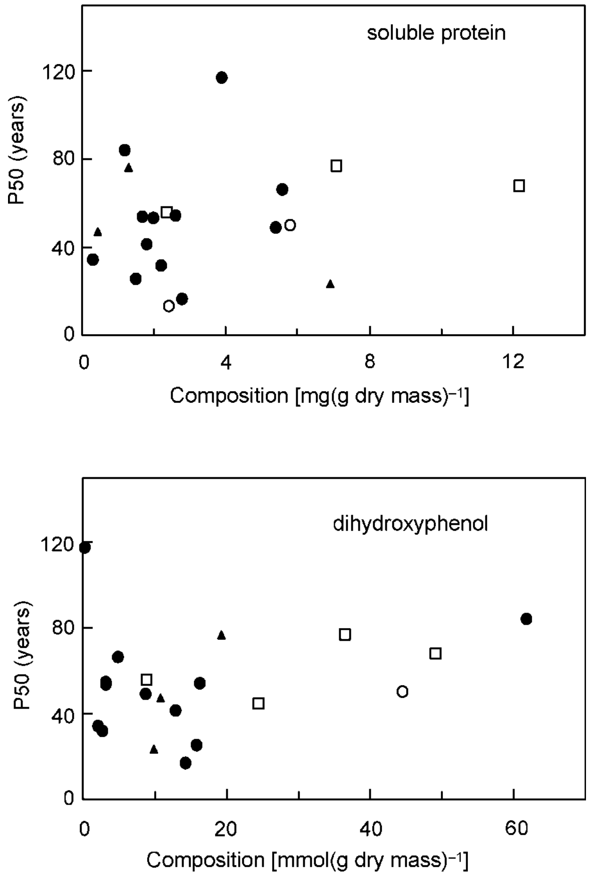

Figure 7. The relationship between species P50 values listed in Table 1 and soluble protein and ortho-dihydroxyphenol content in mature seeds (data from Hendry *et al.*, 1994). Ortho-dihydroxyphenol has fungistatic properties and is associated with persistence of seeds in the soil. Symbols represent different families (e.g. *Poaceae* (solid circle), *Fabaceae* (open square), *Asteraceae* (open circle), *Brassicaceae* (closed triangle)], with the full key given in Table 1.

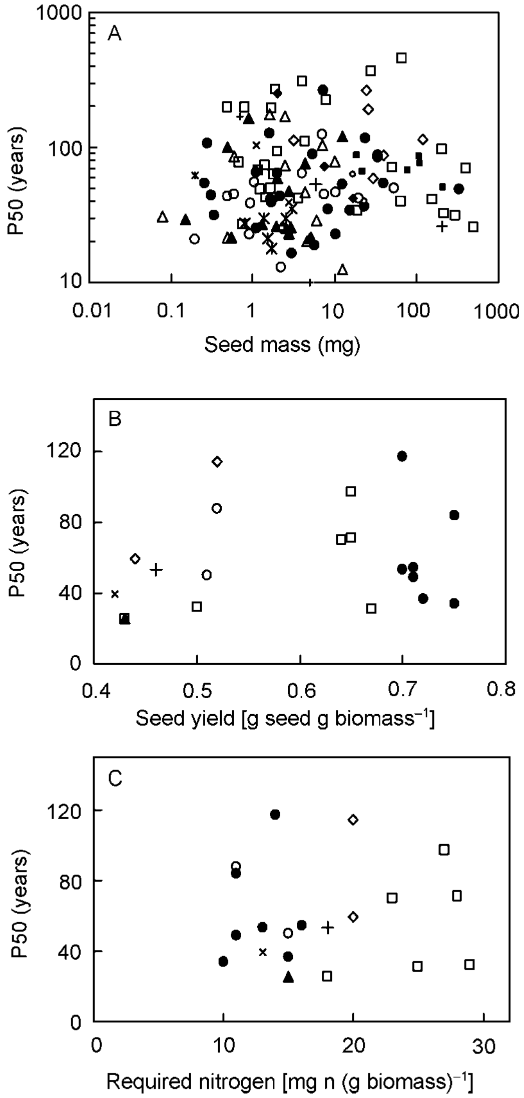

Figure 8. The relationship between species P50 values and parameters relating to resource allocation to seeds: seed mass (A) (data from Jones and Earle, 1966; AOSA, 2003), relative yield (B) and nitrogen uptake by plants (C) (data for B and C from Sinclair and DeWit, 1975). Symbols represent different families [e.g. *Poaceae* (solid circle), *Fabaceae* (open square), *Asteraceae* (open circle), *Cucurbitaceae* (closed square), *Brassicaceae* (closed triangle)], with the full key given in Table 1.

Summary and conclusions

This paper consolidates germination data from over 30 years of storage at 5 and −18°C and near optimal moisture conditions for 276 species in the USDA NPGS collection. Summarized datasets for species are available from the corresponding author. The analyses provide general information on the storage behaviour of species and provide a broader context for the hypothesis that seeds of individual species have characteristic potential life spans. Consistent ranking of relative seed longevity among storage experiments is an important step in verifying that species have particular ageing tendencies. Further studies are required to show that the demonstrated variation of ageing rates among species is greater than the intraspecific variation. Documentation of the general trends and variability of seed longevity provides a foundation for future investigations on the mechanisms of damage and protection during ageing stress.

The idea that species have characteristic seed longevities is important in genebank scenarios, where the frequency of monitoring viability is set by arbitrary standards if biological standards are undefined. Genebank operators must also be able to predict if an accession will have superior or substandard storage, which requires a reference to expected behaviour. The study of species with exceptional (either short or long) shelf lives in an evolutionary context should provide better insights about the genetic factors that contribute to seed storability, and lead to a better understanding of the mechanisms of seed deterioration in storage and the role of seed longevity in the domestication of crops.

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References

AOSA (Association of Official Seed Analysts) (2003) *Rules for testing seeds*. Sacramento, Association of Official Seed Analysts.

Avrami, M. (1941) Kinetics of phase change. III. Granulation, phase change and microstructure. *Journal of Chemical Physics* **9**, 177–184.

Baskin, C.C. and Baskin, J.M. (1998) *Seeds: Ecology, biogeography, and evolution of dormancy and germination*. New York, Academic Press.

Belletti, P., Lanteri, S. and Lotito, S. (1991) The influence of temperature and moisture on seed ageing in Iceland poppy (*Papaver nudicaule L.*). *Scientia Horticulturae* **48**, 153–158.

Dickie, J.B. and Bowyer, J.T. (1985) Estimation of provisional seed viability constants for apple (*Malus domestica* Borkh. Cv. Greensleeves). *Annals of Botany* **56**, 271–275.

Dickie, J.B., McGrath, S. and Linington, S.H. (1985) Estimation of provisional seed viability constants for *Lupinus polyphyllus* Lindley. *Annals of Botany* **55**, 147–151.

Dickie, J.B., Ellis, R.H., Kraak, H.L., Ryder, K. and Tompsett, P.B. (1990) Temperature and seed storage longevity. *Annals of Botany* **65**, 197–204.

Earle, F.R. and Jones, Q. (1962) Analyses of seed samples from 113 plant families. *Economic Botany* **16**, 221–250.

Ellis, R.H. (1991) The longevity of seeds. *HortScience* **26**, 1119–1125.

Ellis, R.H., Hong, T.D. and Roberts, E.H. (1986) Logarithmic relationship between moisture content and longevity in sesame seeds. *Annals of Botany* **57**, 499–503.

Ellis, R.H., Hong, T.D. and Roberts, E.H. (1988) A low-moisture-content-limit to logarithmic relations between seed moisture content and longevity. *Annals of Botany* **61**, 405–408.

Ellis, R.H., Hong, T.D. and Roberts, E.H. (1989) A comparison of the low-moisture-content-limit to the logarithmic relation between seed moisture and longevity in twelve species. *Annals of Botany* **63**, 601–611.

Ellis, R.H., Hong, T.D. and Roberts, E.H. (1990a) Moisture content and the longevity of seeds of *Phaseolus vulgaris*. *Annals of Botany* **66**, 341–348.

Ellis, R.H., Hong, T.D., Roberts, E.H. and Tao, K-L. (1990b) Low moisture content limits to relations between seed longevity and moisture. *Annals of Botany* **65**, 493–504.

Ellis, R.H., Hong, T.D., Astley, D., Pinnegar, A.E. and Kraak, H.L. (1996) Survival of dry and ultra-dry seeds of carrot, groundnut, lettuce, oilseed rape, and onion during five years' hermetic storage at two temperatures. *Seed Science and Technology* **24**, 347–358.

Hendry, G.A.F., Thompson, K., Moss, C.J., Edwards, E. and Thorpe, P.C. (1994) Seed persistence: a correlation between seed longevity in the soil and ortho-dihydroxyphenol concentration. *Functional Ecology* **8**, 658–664.

Horbowicz, M. and Obendorf, R.L. (1994) Seed desiccation tolerance and storability: Dependence on flatulence-producing oligosaccharides and cyclitols – review and survey. *Seed Science Research* **4**, 385–405.

Jones, Q. and Earle, F.R. (1966) Chemical analyses of seeds. II: Oil and protein content of 759 species. *Economic Botany* **20**, 127–155.

Koster, K.L. and Leopold, A.C. (1988) Sugars and desiccation tolerance in seeds. *Plant Physiology* **88**, 829–832.

Kraak, H.L. and Vos, J. (1987) Seed viability constants for lettuce. *Annals of Botany* **59**, 343–349.

Kuo, T.M., Van Middlesworth, J.F. and Wolf, W.J. (1988) Content of raffinose oligosaccharides and sucrose in various plant seeds. *Journal of Agricultural and Food Chemistry* **36**, 32–36.

LHB (Liberty Hyde Bailey) Hortorium (1976) *Hortus third*. New York, Macmillan Publishing.

Mycock, D.J. and Berjak, P. (1995) The implications of seed-associated mycoflora during storage. pp. 747–766 *in* Kigel, J.; Galili, G. (Eds) *Seed development and germination*. New York, Marcel Dekker.

Odum, S. (1965) Germination of ancient seeds: Floristical observations and experiments with archaeologically dated soil samples. *Dansk Botanisk Arkiv* **24**, 1–70.

Priestley, D.A. (1986) *Seed aging*. Ithaca, NY, Comstock Publishing Associates.

Priestley, D.A., Cullinan, V.I. and Wolfe, J. (1985) Differences in seed longevity at the species level. *Plant, Cell and Environment* **8**, 557–562.

Pritchard, H.W. and Dickie, J.B. (2003) Predicting seed longevity: the use and abuse of seed viability equations. pp. 653–722 *in* Smith, R.D.; Dickie, J.B.; Linington, S.L.; Pritchard, H.W.; Probert, R.J. (Eds) *Seed conservation: Turning science into practice*. London, Royal Botanic Gardens.

Rincker, C.M. (1981) Long-term subfreezing storage of forage crop seeds. *Crop Science* **21**, 424–427.

Rincker, C.M. (1983) Germination of forage crop seeds after 20 years of sub-freezing storage. *Crop Science* **23**, 229–231.

Roos, E.E. and Davidson, D.A. (1992) Record longevities of vegetable seeds in storage. *HortScience* **27**, 393–396.

Shen-Miller, J., Mudgett, M.B., Schopf, J.W., Clarke, S. and Berger, R. (1995) Exceptional seed longevity and robust growth: ancient sacred lotus from China. *American Journal of Botany* **82**, 1367–1380.

Sinclair, T.R. and DeWit, C.T. (1975) Photosynthate and nitrogen requirements for seed production by various crops. *Science* **189**, 565–567.

Specht, C.E., Freytag, U., Hammer, K. and Börner, A. (1998) Survey of seed germinability after long-term storage in the Gatersleben genebank (Part 2). *Plant Genetic Resources Newsletter* **115**, 39–43.

Steiner, A.M. and Ruckenbauer, P. (1995) Germination of 110 year-old cereal and weed seeds, the Vienna sample of 1877. Verification of effective ultra-dry storage at ambient temperature. *Seed Science Research* **5**, 195–199.

Telewski, F.W. and Zeevaart, J.A.D. (2002) The 120-yr period for Dr. Beal's seed viability experiment. *American Journal of Botany* **89**, 1285–1288.

Tompsett, P.B. (1986) The effect of temperature and moisture content on the longevity of seed of *Ulmus carpinifolia* and *Terminalia brassii. Annals of Botany* **57**, 875–883.

Toole, E.H. and Brown, E. (1946) Final results of the Duvel buried seed experiment. *Journal of Agricultural Research* **72**, 201–210.

Vavilov, N.I. (1992) *Origin and geography of cultivated plants.* Cambridge, Cambridge University Press.

Villiers, T.A. (1974) Seed aging: Chromosome stability and extended viability of seeds stored fully imbibed. *Plant Physiology* **53**, 875–878.

Walters, C. (1998) Understanding the mechanisms and kinetics of seed aging. *Seed Science Research* **8**, 223–244.

Walters, C., Wheeler, L. and Stanwood, P.C. (2004) Longevity of cryogenically-stored seeds. *Cryobiology* **48**, 229–244.

Went, F.W. (1969) A long term test of seed longevity. II. *Aliso* **7**, 1–12.

Williams, R.J., Hirsh, A.G., Meryman, H.T. and Takahashi, T.A. (1993) The high-order kinetics of cytolysis in stressed red cells. *Journal of Thermal Analysis* **40**, 857–862.

Zewdie, M. and Ellis, R.H. (1991) Response of tef and niger seed longevity to storage temperature and moisture. *Seed Science and Technology* **19**, 319–329.

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