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MINI REVIEW

Differences in seed longevity at the species level

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Abstract. Published seed storage data for 92 species derived from 13 localities were subjected to probit analysis to determine the half-viability period (P_{50}) for each sample. Estimates of half-viability period for each species averaged over all 13 localities were calculated using a least square means procedure applied to known values for the half-viability period for each species at each of its storage stations. The results reported here represent an initial step in the objective organization of seed longevity data.

Key-words: Ageing; deterioration; longevity; seeds; storage.

Introduction

Seeds of most temperate crops deteriorate less rapidly in cool, dry conditions than in hot and humid environments. In consequence, certain geographical localities are more conducive to seed longevity than others. Whatever the environment, however, some species are usually much better than others at maintaining their viability. For example, it is well-established from observations at many different storage localities that rye seed deteriorates faster than wheat, and wheat faster than oats (e.g. Gross, 1917; Bussard, 1935; Robertson, Lute & Kroeger, 1943). In practice, some species are recognized for their inferior storage characteristics, whereas others are far less problematic.

Data on seed longevity occur in a vast range of papers and some attempts have previously been made to summarize at least part of this pool of information. Heydecker (1974) and Justice & Bass (1978), for instance, divided species into three broad groups, depending upon their relative storability, and a rather similar tabulation was provided by Ullman (1949). We have attempted to put such analyses on a more objective footing by ranking species using statistical procedures.

Data were selected from the literature on the basis of the following criteria:

1. The studies described loss of germinability under open storage conditions in a temperate climate.

2. They provided the results of a number of tests of seed lots over several years, so that a well-defined deteriorative trend could be established.

3. The studies considered several different species stored in a similar fashion at the same locality.

Data from 13 storage stations satisfied these criteria: South Australia (Pritchard, 1933), Ottawa, Canada (Sifton, 1920), Děčín, Czechoslovakia (Gross, 1917), Brno, Czechoslovakia (Nádvorník, 1947), Denmark (Dorph-Petersen, 1924), England (Carruthers, 1911), France (Bussard, 1935), Germany (Filter, 1932), Ireland (Lafferty, 1931), Poland (Lityński & Chudoba, 1964), Leningrad, U.S.S.R. (Adamova, 1964; Gvozdeva, 1966, 1970, 1971; Gvozdeva & Yarchuk, 1969; Gvozdeva & Zhukova, 1971), Fort Collins, Colorado, U.S.A. (Robertson *et al.*, 1943) and Yonkers, New York, U.S.A. (Barton, 1935, 1953, 1966a, b).

This extensive pool of data permitted us to rank 92 species in terms of their seed longevity in a more objective manner than has previously been attempted. It must be emphasized, though, that in many cases the data available for individual species are often quite minimal; the present analysis is certainly not definitive, but represents an initial step in the objective organization of seed longevity data.

Methods

Seed longevity data from the 13 storage stations were assessed by probit analysis. Values of P_{50} (the half-viability period) were calculated for all the species represented at each storage location using the FORTRAN IV program developed by Moore, McSay & Roos (1983). Data were rejected if initial germinability (or germinability after 1 year if no initial figure was given) was less than 90%. The mean value of initial germinability for the data used here was 98%. Rarely, when several sets of data were available for a single species at the same locality, a mean germinability for each year of storage was calculated prior to probit analysis. In such cases, no extra weighting was assigned to the observations. Further, since information on sample sizes used in germination assays was frequently lacking, the variance of the P_{50} value for a particular seed lot at a particular

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station could not be calculated. All P_{50} values were therefore considered to be of equal weight in the analysis that follows. For legumes, seeds classed as 'hard' were regarded as viable.

A ranking of species by seed longevity was made using least square means, i.e. unweighted averages of the *estimated* cell means (Searle, 1980). Observed P_{50} values from the 13 storage localities were logarithmically transformed, thereby converting the assumed multiplicative effects of locations and species on P_{50} into additive effects. The model for a two-way crossed classification without interaction on the logarithmic scale was assumed for these calculations (i.e. $y_{ijk} = \mu + \alpha_i + \beta_j + \varepsilon_{ijk}$, where y_{ijk} is the natural log of the P_{50} for the kth replicate for the ith species at the jth location). The parameter μ is the overall mean effect, α_i is the ith species effect, β_j is the jth location effect, and ε_{ijk} is random error. The ε_{ijk}'s are assumed to be independent and identically distributed as normal random variables with a mean of zero and a variance σ^2. The subscript ranges are $i = 1,2,\dots,s$ (no. of species), $j = 1,2,\dots,l$ (no. of locations), and $k = 1,2,\dots,r$ (no. of replicates). For these data, $r = 0$ or 1 for all cells. The estimated cell means are then determined by

$$\hat{\hat{y}}_{ij.} = (1/k)\sum_k \hat{y}_{ijk}$$
$$= \hat{\mu} + \hat{\alpha}_i + \hat{\beta}_j.$$

The least-square means are then

$$\mathrm{LS}(\alpha_i) = (1/l)\sum_j \hat{\hat{y}}_{ij}.$$
$$= \hat{\mu} + \hat{\alpha}_i + (1/l)\sum_j \hat{\beta}_j.$$

For those species for which data were available only from one storage station, an estimated ln P_{50} was calculated using the average location effect $(1/l)\Sigma\hat{\beta}_j$ plus the observed ln P_{50} and minus that storage station's estimated effect. The least j square means were then ranked to give the final ordering of seed longevity for each species.

Results

The curve describing loss of germinability with time of storage is generally held to be of a negatively sigmoidal shape (e.g. Roberts, 1972). Almost ideal deterioration curves of this type were sometimes encountered among the data analysed (e.g. Fig. 1), but most species displayed some degree of skewness. Two extreme examples are shown in Fig. 2. Tailing of the curve was especially evident in hard seeded legumes like *Medicago lupulina*. The use of probit analysis in such cases introduces a slight bias: legumes, for example, are liable to drop below 50% germination rather earlier than the P_{50} value calculated in this way would suggest.

Computed P_{50} values are given in Tables 1 and 2; species for which longevity data were available at more than one storage station are listed in Table 1. The remaining species, recorded at only one station, are given in Table 2. Species are ranked and estimated P_{50} values are summarized graphically in Fig. 3. Nomenclature has been revised as far as possible to conform with *Hortus Third* (Liberty Hyde Bailey Hortorium, 1976).

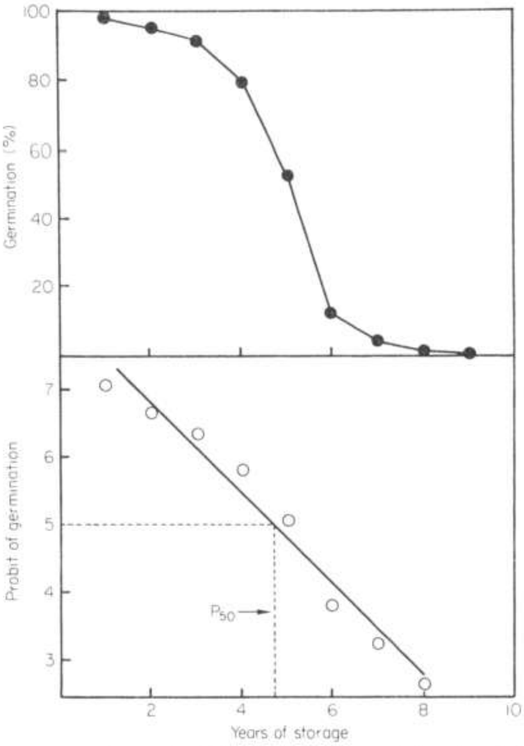

Figure 1. Loss of germinability in a seed lot of timothy (*Phleum pratense*) in open storage in Denmark. A probit value of 5 (equivalent to 50%) determines the half-viability period (P_{50}). Calculated from data of Dorph-Petersen (1924).

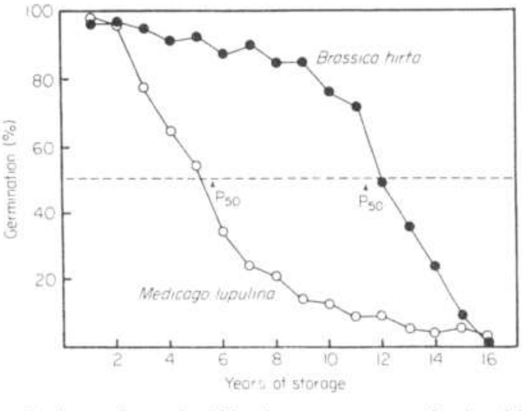

Figure 2. Loss of germinability in open storage. Seeds of black medick (*Medicago lupulina*) and white mustard (*Brassica hirta*, syn. *Sinapis alba*) provide examples of strongly skewed ageing patterns. Despite this deviation from the ideal deterioration curve, the probit analysis program still computes an acceptable P_{50} value (arrows). Data for individual seed lots selected from Dorph-Petersen (1924).

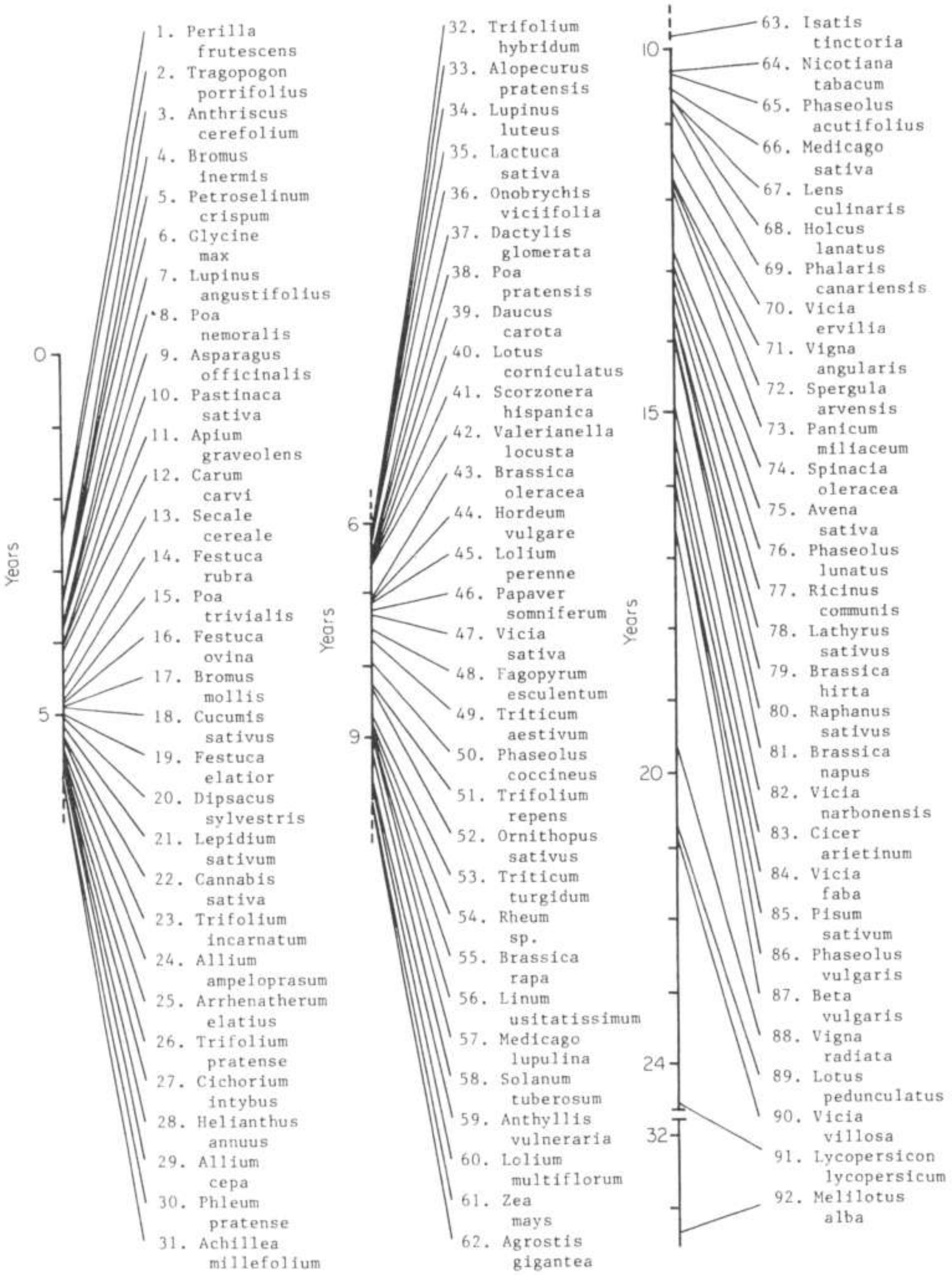

Figure 3. Storability of seeds of cultivated species. The species listed in Tables 1 and 2 have been ranked according to estimated P_{50} values. This provides a measure of what the average P_{50} value of a species would be if it were tested at all 13 locations referred to in the present study.

Discussion

Although differences in seed longevity at the species level have long been recognized in practice, the present analysis is more objectively based than most previous descriptions. Nevertheless, there are obvious limitations, especially for those species for which only minimal data are available (e.g. Table 2). The longevity of a seed lot may be constrained by several factors: genetic effects attributable to particular lines or cultivars, pre-harvest field stresses, immaturity, and mechanical injury, for example. These influences cannot be discounted for data in Table 2, although they are presumably less important for the analysis of species given in Table 1.

The model employed here assumes that a favourable storage location will extend seed longevity (P_{50}) by a constant percentage for all species, compared to a less favourable locality. On this basis, the percentage effects of storage locations were estimated from the P_{50} data available in Table 1. In calculating 'estimated P_{50}' values (Tables 1 & 2), the

Table 1. Half-viability periods (P_{50}) in years computed from seed deterioration data recorded at various storage stations. This table lists species for which deterioration data were available from more than one locality. 'Estimated P_{50}' lists the calculated P_{50} averaged over all 13 storage locations. For this analysis, the square root of the error mean square was 0.2996. Values for percent estimated location effect were obtained by dividing location least-squares mean by the total of location least-squares means. AUST = South Australia; CAN = Ottawa, Canada; COLO = Colorado, USA; CZ1 = Děčín, Czechoslovakia; CZ2 = Brno, Czechoslovakia; DEN = Denmark; ENG = England; FRA = France; GER = Germany; IRE = Ireland; NY = New York, USA; POL = Poland; USSR = Leningrad, USSR.

	Observed P_{50} values at different locations													Estimated
	AUST	CAN	COLO	CZ1	CZ2	DEN	ENG	FRA	GER	IRE	NY	POL	USSR	P_{50}
Allium cepa	4.52	—	—	—	5.08	—	—	—	—	—	2.50	—	—	5.43
Alopecurus pratensis	—	—	—	—	—	—	—	6.50	—	—	—	6.40	—	6.19
Anthyllis vulneraria	—	—	—	—	—	—	—	11.24	10.73	—	—	—	—	9.24
Arrhenatherum elatius	—	—	—	—	—	4.81	—	4.80	7.70	—	—	—	—	5.31
Avena sativa	—	20.71	22.42	15.09	—	—	11.56	8.24	19.01	—	—	11.68	26.00	12.96
Beta vulgaris	—	—	—	—	—	11.13	—	14.72	—	—	—	25.07	—	16.51
Brassica hirta	—	—	—	—	—	11.48	—	14.42	—	—	—	—	—	13.71
B. napus	—	—	—	—	8.41	9.62	8.84	11.88	—	6.41	—	—	—	13.94
B. oleracea	4.03	—	—	—	9.06	6.96	8.47	12.73	—	—	—	—	4.74	7.15
B. rapa	5.35	—	—	—	11.05	9.34	7.83	—	—	—	—	—	—	8.74
Cannabis sativa	—	—	—	—	—	—	—	7.27	5.48	—	—	—	6.24	5.20
Dactylis glomerata	—	—	—	—	—	6.30	5.76	6.58	—	—	—	—	—	6.61
Daucus carota	—	—	—	—	—	—	—	5.08	—	—	—	—	11.36	6.63
Fagopyrum esculentum	—	—	—	—	—	—	—	6.62	—	—	—	9.15	—	7.46
Festuca elatior	—	—	—	—	—	4.27	6.06	4.92	6.55	2.80	—	—	—	4.98
Glycine max	—	—	8.31	—	—	—	—	—	—	—	—	—	3.84	3.43
Helianthus annuus	—	—	—	—	—	—	—	5.07	—	—	—	—	7.63	5.42
Hordeum vulgare	—	—	21.23	4.39	—	4.83	6.77	8.58	10.43	4.71	—	7.89	9.87	7.19
Lactuca sativa	3.39	—	—	—	11.68	—	—	5.19	—	—	3.10	—	—	6.42
Lens culinaris	—	—	—	—	—	—	—	9.52	—	—	—	—	15.65	10.65
Lepidium sativum	3.68	—	—	—	6.60	—	—	—	—	—	—	—	—	5.09
Linum usitatissimum	—	—	—	—	—	—	—	11.88	9.47	7.34	—	—	8.65	8.75
Lolium multiflorum	—	—	—	—	—	6.53	8.14	8.99	—	9.14	—	—	—	9.36
Lolium perenne	—	—	—	—	—	5.88	6.61	—	6.25	—	—	12.16	—	7.19
Lotus corniculatus	—	—	—	—	—	5.40	6.61	—	—	—	—	—	—	6.72
Lycoperiscon lycoperisicum	25.41	—	—	—	—	—	—	—	—	—	7.50	—	29.86	24.52
Medicago lupulina	—	—	—	—	—	5.75	—	—	15.11	—	—	—	—	8.76
M. sativa	6.34	—	—	—	—	9.46	7.14	15.60	17.68	—	—	—	—	10.56
Ornithopus sativus	—	—	—	—	—	7.26	—	—	10.58	—	—	—	—	8.24
Pastinaca sativa	—	—	—	—	4.68	3.41	—	—	—	—	—	—	—	4.04
Phalaris canariensis	—	—	—	—	—	10.57	—	10.01	—	—	—	—	—	10.96
Phaseolus vulgaris	21.15	—	—	—	—	—	—	—	—	—	4.97	—	14.94	15.97
Phleum pratense	—	9.24	—	—	—	5.16	7.80	5.48	7.34	4.93	—	3.12	—	5.73
Pisum sativum	26.80	—	—	—	—	—	—	12.04	—	—	—	12.25	17.60	15.86
Poa trivialis	—	—	—	—	—	4.37	4.18	—	—	—	—	—	—	4.81
Raphanus sativus	13.76	—	—	—	13.03	—	—	—	—	—	—	—	—	13.82
Secale cereale	—	—	10.67	4.39	—	3.16	—	3.86	6.75	—	—	3.66	8.17	4.51
Trifolium hybridum	—	9.68	—	—	—	4.65	5.04	—	10.59	3.83	—	—	—	6.16
T. incarnatum	2.64	—	—	—	—	3.84	—	10.10	—	—	—	—	—	5.25
T. pratense	—	4.71	—	—	—	5.27	5.11	11.70	7.51	2.32	—	—	—	5.36
T. repens	—	—	—	—	—	7.70	6.54	—	11.08	5.96	—	—	—	8.21
Triticum aestivum	—	12.51	16.56	7.50	—	5.85	7.93	6.08	11.16	—	—	6.34	10.93	7.59
Vicia faba	17.35	—	—	—	—	—	—	13.12	—	—	—	16.90	16.84	15.58
V. sativa	5.23	—	—	—	—	—	—	8.68	—	—	—	—	—	7.33
V. villosa	—	—	—	—	—	—	—	—	—	—	—	29.68	19.01	20.82
Zea mays	—	—	15.25	—	—	—	—	9.30	—	—	—	10.91	16.20	9.60
Estimated location effect (%)	5.8	10.2	15.4	6.5	8.3	6.0	6.7	7.5	9.6	.9	2.7	7.4	9.0	

Table 2. Half-viability periods (P_{50}) in years computed from seed deterioration data recorded at various storage stations. This table lists species for which deterioration data were available from only a single locality. For further details, see the legend to Table 1.

	Observed P_{50}	Station	Estimated P_{50}
Achillea millefolium	6.01	FRA	5.75
Agrostis gigantea	10.05	POL	9.69
Allium ampeloprasum	6.17	CZ2	5.30
Anthriscus cerefolium	3.53	FRA	3.37
Apium graveolens	4.31	FRA	4.11
Asparagus officinalis	4.11	FRA	3.92
Bromus inermis	3.54	FRA	3.38
B. mollis	5.13	FRA	4.90
Carum carvi	4.88	CZ2	4.19
Cicer arietinum	16.02	FRA	15.29
Cichorium intybus	6.31	CZ2	5.42
Cucumis sativus	3.97	AUS	4.92
Dipsacus sylvestris	5.23	FRA	4.99
Festuca ovina	5.07	FRA	4.84
F. rubra	4.93	FRA	4.70
olcus lanatus	11.22	FRA	10.71
Isatis tinctoria	10.29	FRA	9.82
Lathyrus sativus	17.10	USSR	13.63
Lotus pedunculatus	27.75	GER	20.59
Lupinus angustifolius	5.13	GER	3.81
L. luteus	8.36	GER	6.20
Melilotus alba	35.00	FRA	33.40
Nicotiana tabacum	10.79	FRA	10.30
Onobrychis viciifolia	6.74	FRA	6.43
Panicum miliaceum	12.34	POL	11.90
Papaver somniferum	7.63	FRA	7.28
Perilla frutescens	2.92	USSR	2.33
Petroselinum crispum	2.75	AUS	3.41
Phaseolus acutifolius	13.04	USSR	10.39
P. coccineus	10.02	USSR	7.99
P. lunatus	16.46	USSR	13.12
Poa nemoralis	4.00	FRA	3.82
P. pratensis	6.95	FRA	6.63
Rheum sp.	10.11	CZ2	8.68
Ricinus communis	16.70	USSR	13.31
Scorzonera hispanica	7.85	CZ2	6.74
Solanum tuberosum	9.35	FRA	8.92
Spergula arvensis	12.40	FRA	11.83
Spinacia oleracea	14.86	CZ2	12.76
Tragopogon porrifolius	2.70	FRA	2.58
Triticum turgidum	18.56	COLO	8.59
Valerianella locusta	7.06	FRA	6.74
Vicia ervilia	14.33	USSR	11.42
V. narbonensis	18.75	USSR	14.95
Vigna angularis	14.75	USSR	11.76
V. radiata	24.51	USSR	19.54

effects of particular storage locations are removed; the estimate obtained provides a measure of what the average P_{50} value would have been for a given species if it had been tested at all 13 locations. Some caution is required before accepting the estimated P_{50} values, however, since these assume that statistical interactions between species and localities do not exist.

In offering a listing of seed longevities it is important to reiterate that this contribution merely represents an initial step. As further data become available, more extensive assessments of increased precision will result.

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