Record Longevities of Vegetable Seeds in Storage

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Agricultural production of food and fiber depends on the ability of seeds to dry and become quiescent for a period before planting for the next season's crop. In many instances seed must be kept for more than one season; plant breeders may hold seed lots for several years before their use, while gene banks may store seed for decades before distribution. For this reason, seed longevity has been of interest to scientists and laypersons alike.

Recent reviews by Ellis (1991), Priestley (1986), Roos (1986), and Toole (1986) have examined the topic of seed longevity. Reports of 'Mummy' wheat seeds surviving 3000 years in Egyptian pyramids are clearly specious (Justice and Bass, 1978; Roos, 1986). Evidence from other archeological sites (Lerman and Cigliano, 1971; Odum, 1965; Sivori et al., 1968), museum herbaria (Becquerel, 1934; Ewart, 1908; Nature, 1942; Youngman, 1951), and buried seed experiments (Kivilaan and Bandurski, 1981) support the thesis that seeds of many species are capable of surviving for more than a century.

Most of the reports of extreme seed longevity have centered on agronomic and weed seeds; while many vegetable seeds are reported to be relatively short lived (Barton, 1961; Boswell et al., 1940; Justice and Bass, 1978; Priestley et al., 1985). Reports of viable vegetable seeds occurring in prehistoric caches in the southwestern United States have appeared in the popular press; however, as pointed out by Nabhan (1977), "The data are unfortunately inadequate to establish with any confidence that Southwestern crop seed from well-defined prehistoric cultural deposits have indeed germinated upon their recent recovery."

Bass (1981) reported that documented evidence for vegetable seed longevity seldom exceeded 30 years. Barton (1953) stored seed of carrot *(Daucus carota* L.), eggplant *(Solanum melongena* L.), lettuce *(Lactuca sativa* L.), onion *(Allium cepa* L.), pepper *(Capsicum annuum* L.), and tomato *(Lycopersicon esculentum* L.) at ambient temperature in the laboratory and at –4C. Only seeds of carrot, eggplant, and tomato, stored at ambient temperature, were still viable after 20 years, while seeds of all species stored at –4C were still viable. For example, seeds of onion germinated 93% when stored dry and sealed at –4C. Unfortunately, these experiments were not continued.

Documented seed longevities for 15 vegetable species are presented in Table 1. James et al. (1964), who reported on the longevity of several vegetable seed lots stored 15 to 30 years at Cheyenne, Wyo., are the source of many of these data. Many of these seed lots are still viable and are the subject of this paper. Interim germination data on some of these seed lots have been presented by Roos (1989).

Table 1. Previously documented longevities of vegetable seeds.

Species and cultivar	Age (years)	Germination (%)	Reference
Bean (*Phaseolus vulgaris* L.)			
Unknown	18	99	Bass, 1981
Alberta Brown	29	26	James et al., 1964
Beet (*Beta vulgaris* L.)			
Unknown (sugar beet)	22	75	Pack and Owen, 1950
Extra Early Bassano	31	31	James et al., 1964
Carrot (*Daucus carota* L.)			
Unknown	20	63	Barton, 1953
Int. Yellow Stump Rooted	31	5	James et al., 1964
Corn (*Zea mays* L.)			
Early Surprise	23	82	James et al., 1964
Dakota Flint	32	79	Haferkamp et al., 1953
Cucumber (*Cucumis sativus* L.)			
Unknown	17	98	Bass, 1981
Butcher's	30	77	James et al., 1964
Eggplant (*Solanum melongena* L.)			
Unknown	20	86	Barton, 1953
Black Pekin	30	30	James et al., 1964
Muskmelon (*Cucumis melo* L.)			
Delicious 51	23.5	81	Bass, 1983
West's	30	96	James et al., 1964
Okra [*Abelmoschus esculentus* (L.) Moench]			
Unknown	17	92	Bass, 1981
Extra Early Dwarf Green Pod	22	60	James et al., 1964
Onion (*Allium cepa* L.)			
Brigham Yellow Globe	22	75	Newhall and Hoff, 1960
Southport White Globe	27	15	James et al., 1964
Pea (*Pisum sativum* L.)			
Alaska	24	86	James et al., 1964
Solo	31	78	Haferkamp et al., 1953
Pepper (*Capsicum annuum* L.)			
Unknown	20	19	Barton, 1953
World Beater	29	34	James et al., 1964
Spinach (*Spinacia oleracea* L.)			
Marco	30	8	James et al., 1964
Unknown	61	1	Buchwald and Jensen, 1974
Swiss chard (*Beta vulgaris* L. var. *Cicla*)			
Unknown	15	94	Bass, 1981
Burpee's Rhubarb	20	88	James et al., 1964
Tomato (*Lycopersicon esculentum* Mill.)			
Marmon	32	87	James et al., 1964
Unknown	43	76	Bass, 1981
Watermelon [*Citrullus lanatus* Thunb. (Matsum. & Makai)]			
Unknown	17	94	Bass, 1981
Arikara	30	92	James et al., 1964

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The objectives of this study were to extend the data base on known vegetable seed longevities and compare longevities among species.

BACKGROUND

In 1962, ≈2000 vegetable seed lots were transferred to the National Seed Storage Laboratory (NSSL). These lots had been stored in metal drawers in an office at the U.S. Dept. of Agriculture Horticultural Field Station in Cheyenne. Old seed lots from 15 vegetable species, represented by three to six cultivars (Table 2), were selected for study. These lots, although not specifically identified, were included in a previous report by James et al. (1964). All seedlots have been in storage at the NSSL in Fort Collins, Colo., since their acquisition in 1962. At the time of acquisition, some of the lots were included in the base collection of the NSSL and thus were stored at low temperature and low seed moisture. From 1962 until ≈1977 the storage conditions were 5C and <40% relative humidity (RH); after 1977 seeds were stored in sealed moisture-proof bags at – 18C (see Roos, 1989, for additional description of storage conditions at NSSL). Other lots were held in paper envelopes in metal trays at room temperature (20C) and ambient RH (≤50%) for several years (exact time period unknown) before being placed in low-temperature storage (either 5 or – 18C).

Remnant seeds from the experiment conducted by James et al. (1964) were reexamined for viability in 1991 under standard germination conditions (Assn. Official Seed Analysts, 1988). Due to the limited quantities of seed available, 25, 50, or 100 seeds were tested, and for a few samples, only 10 seeds were tested. Between 1962 and 1991, all of these lots were retested at irregular intervals, thus providing sequential observations (four to 11) of germination percentage for each seed lot. The oldest tests (on a few samples) were done in 1946 and reported to M.F. Babb at the Cheyenne Horticultural Field Station in a letter from E.H. Toole (U.S. Dept. Agriculture, Beltsville, Md.) dated 28 June 1946. No data are available on the initial germination values when the seeds were originally acquired or produced in Cheyenne.

Seed germination data were examined for each lot, and the half or median viability periods (P_{50}) (Roberts, 1972) were calculated as described by Moore and Roos (1982) and Moore et al. (1983). No adjustment was made for initial mortality. In determining the significance of the χ^2 and regression statistics (Table 2) the degree of freedom for each seed lot was two less than the number of germination tests performed.

FINDINGS

The oldest seed lot tested was a tomato cultivar, Marmon, that still germinated 82% after 60 years in storage (Table 2). Longevities of ≥50 years are reported for beet *(Beta*

Table 2. Germination and estimates of longevity statistics of vegetable seeds following long-term storage.

Species and cultivar	Age^{z} (years)	Germination (%) 1963^{y}	Germination (%) 1991^{x}	P_{50} ± SE (years)	df	χ^2	r
Bean (*Phaseolus vulgaris*)							
Wyoming Pinto	48	72	24^{w}	31 ± 1	7	5^{NS}	0.95^{**}
Idaho Pinto	47	70	8^{w}	20 ± 1	7	35^{**}	0.85^{**}
Dwarf Green Pod	46	64	64^{w}	90 ± 48	6	12^{NS}	0.11^{NS}
Vermont Cranberry	45	78	52	51 ± 4	5	18^{**}	0.76^{*}
Hidatsa	45	78	30^{v}	37 ± 2	6	47^{**}	0.71^{*}
Avg		72	36	46			
Beet (*Beta vulgaris*)							
Extra Early Bassano	59	71	8^{y}	39 ± 1	7	37^{**}	0.89^{**}
Long Smooth Blood Turnip	56	62	18	41 ± 1	6	34^{**}	0.87^{**}
Earlidark	53	63	14	35 ± 1	7	51^{**}	0.80^{**}
Extra Early Red Turnip	49	85	36	43 ± 1	4	3^{NS}	0.99^{**}
Green Top Bunching	48	64	28	34 ± 1	6	59^{**}	0.75^{*}
Early Flat Egyptian	47	94	78	66 ± 6	4	14^{**}	0.80^{NS}
Avg		73	30	43			
Carrot (*Daucus carota*)							
Nantes Touchon Strain	46	63	24	30 ± 1	8	12^{NS}	0.86^{**}
Selected Long Orange Improved	46	70	22	30 ± 1	8	10^{NS}	0.90^{**}
Nancy	45	61	26	28 ± 2	6	25^{**}	0.67^{NS}
New Early Coreless	43	76	72	68 ± 16	6	24^{**}	0.45^{NS}
Wonderkugel	43	61	14	19 ± 1	7	12^{NS}	0.89^{**}
Avg		66	32	35			
Corn (*Zea mays*)							
Early Surprise	50	82	56	52 ± 3	6	12^{NS}	0.85^{**}
Marcross Northern	48	94	64	61 ± 5	4	4^{NS}	0.94^{**}
Lee (Resistant)	47	90	72	65 ± 8	4	5^{NS}	0.87^{*}
Earligold	46	92	84	86 ± 17	4	20^{**}	0.58^{NS}
Golden No. 10	45	90	70	63 ± 8	4	16^{**}	0.72^{NS}
Avg		90	69	65			
Cucumber (*Cucumis sativus*)							
Danish Common	58	69	28^{w}	39 ± 1	4	27^{**}	0.76^{NS}
Snake	58	70	28	32 ± 2	4	20^{**}	0.73^{NS}
Lange Kecskemeter	54	79	48	52 ± 4	6	16^{*}	0.73^{*}
Marketer	46	73	62	48 ± 10	8	97^{**}	0.19^{NS}
National Pickling	45	87	62	53 ± 6	5	10^{NS}	0.77^{*}
Avg		76	46	45			
Eggplant (*Solanum melongena*)							
Ebony King	56	69	4	33 ± 1	6	32^{**}	0.90^{**}
Fort Myers Market	55	67	44	39 ± 2	8	24^{**}	0.83^{**}
Blackee	50	62	12	27 ± 1	5	6^{NS}	0.95^{**}
Minnoval	48	92	80	119 ± 51	2	5^{NS}	0.61^{NS}
Avg		72	35	54			
Muskmelon (*Cucumis melo*)							
Extra Early Sunrise	58	82	42	53 ± 2	6	7^{NS}	0.94^{**}
Perfection	56	75	28	47 ± 1	5	43^{**}	0.77^{*}
Bush Jenny Lind	55	79	52	55 ± 3	7	54^{**}	0.66^{NS}
New Ideal	53	99	76	70 ± 5	4	4^{NS}	0.93^{**}
Early Sunrise	50	92^{u}	74	79 ± 14	4	18^{**}	0.60^{NS}
Avg		85	54	61			
Okra (*Abelmoschus esculentus*)							
Extra Early Dwarf Green Pod	50	60^{x}	34	24 ± 3	4	28^{**}	0.64^{NS}
Wyoming No. 9	48	99^{x}	62	53 ± 2	3	6^{NS}	0.95^{**}
Wyoming No. 10	47	84^{x}	72	130 ± 71	6	14^{*}	0.35^{NS}
Wyoming No. 5	45	96^{x}	90^{v}	161 ± 102	3	24^{**}	0.25^{NS}
Wyoming No. 4	45	82^{x}	70^{v}	258 ± 573	4	31^{**}	0.07^{NS}
Avg		84	66	125			
Onion (*Allium cepa*)							
Valencia Sweet Spanish	52	76	20^{v}	33 ± 1	5	34^{**}	0.88^{**}
Early Yellow Sweet Spanish	49	66	32	32 ± 1	9	51^{**}	0.80^{**}
Yellow Sweet Spanish	48	79	14	32 ± 1	8	25^{**}	0.88^{**}
San Joaquin	47	94	20	38 ± 1	4	61^{**}	0.87^{*}
Espanola	46	61	38	11 ± 6	8	47^{**}	0.45^{NS}
Avg		75	25	29			
Pea (*Pisum sativum*)							
Alaska	51	86^{x}	94	---^{t}	4	14^{**}	0.56^{NS}
Buxbom I	51	76^{x}	82	---^{t}	5	8^{NS}	0.36^{NS}
Randolph Indian Var.13, St.D	51	64^{x}	56	---^{t}	6	27^{**}	0.03^{NS}
Radio	51	76^{x}	45^{y}	46 ± 3	4	16^{**}	0.77^{NS}
Pedigree Extra Early	48	90^{x}	82	232 ± 292	5	14^{*}	0.18^{NS}
Extra Early D.S.C.	45	100^{x}	92	111 ± 42	3	1^{NS}	0.86^{NS}
Avg		82	75	130			
Pepper (*Capsicum annuum*)							

continued

Table 2. *continued.*

Species and cultivar	Age[z] (years)	Germination (%) 1963[y]	1991[x]	P_{50} ± SE (years)	df	χ^2	*r*
Sweet (Thomsen's Own Select.)	51	84	28	37 ± 2	3	49**	0.68[NS]
Early Market	49	70	2	28 ± 1	6	17*	0.92**
Victory	45	76	10	26 ± 1	3	27**	0.86[NS]
World Beater No. 13	45	66	26	17 ± 3	4	58**	0.54[NS]
Avg		74	16	27			
Spinach (*Spinacia oleracea*)							
Blight Resistant Savoy	45	67	60[v]	43 ± 8	7	29**	0.35[NS]
Mt. Evergreen	45	66	14	30 ± 1	7	121**	0.57[NS]
Viking	43	83	40	38 ± 1	4	63**	0.76[NS]
Avg		72	38	37			
Swiss chard (*Beta vulgaris* var. *Cicla*)							
Burpee's Rhubard	48	88[x]	70	68 ± 8	4	24**	0.65[NS]
Special Large White Ribbed	47	76[x]	66	64 ± 11	5	18**	0.58[NS]
Fordhook Giant	45	74[x]	70	65 ± 9	4	25**	0.60[NS]
Dark Green	45	88[x]	60	36 ± 1	4	70**	0.84*
Avg		82	66	58			
Tomato (*Lycopersicon esculentum*)							
Marmon	60	87	82	230 ± 233	3	4[NS]	0.38[NS]
Early Bird	59	96	40	56 ± 1	4	35**	0.87*
Florida Special	58	92	76	103 ± 23	3	6[NS]	0.73[NS]
Morse's Special Early	57	95	82	109 ± 25	3	6[NS]	0.75[NS]
Beauty of Loraine	56	95	98	---[t]	3	32**	0.08[NS]
Avg		93	76	124			
Watermelon (*Citrullus lanatus*)							
Colorado Preserving Citron	58	82	32[w]	41 ± 1	5	62**	0.70[NS]
Arikara	57	76	20	34 ± 1	5	26**	0.79*
Will's Sugar (28140.01)	57	88	24	47 ± 1	4	12**	0.95**
New Winter	56	92	34	46 ± 1	5	65**	0.77*
Will's Sugar (28142.01)	55	76	52[w]	48 ± 2	4	44**	0.74[NS]
Avg		83	32	43			

[z]Calculated from year seed was purchased to 1991.
[y]Germination test of 100 seeds unless noted.
[x]Germination test of 50 seeds unless noted.
[w]Germination test of 25 seeds.
[v]Germination test of 10 seeds.
[u]Germination tested in 1967.
[t]Negative P_{50}
[NS],*,**Nonsignificant or significant at $P = 0.05$ or 0.01, respectively.

vulgaris L.), corn *(Zea mays* L.), cucumber *(Cucumis sativus* L.), eggplant, muskmelon *(Cucumis melo* L.), okra *[Abelmoschus esculentum* L. (Moench.)], onion, pea *(Pisum sutivum* L.), pepper, and watermelon *[Citrullus lanatus* Thunb. (Matsum. & Makai)]. Surprisingly, carrot, onion, and pepper seeds, usually thought to have relatively short viability periods, germinated 72% ('New Early Coreless'), 28% ('Sweet, Thomsen's Own Select'), and 38% ('Espanola') after 43, 46, and 51 years, respectively.

With only a few exceptions, germination declined significantly from 1963 to 1991. On average, most species lost ≥ 30% viability, except for corn, okra, pea, Swiss chard *(Beta vulgaris* var. *Cicla* L.), and tomato (Table 2). Species showing the greatest loss in viability were onion, pepper, and watermelon, which lost, on average, 50%, 58%, and 51% germination, respectively, after 29 years. Pea seeds, in contrast, lost an average of only 7% germination between 1963 and 1991.

Although the data varied considerably from cultivar to cultivar, even within a species, four groups can be identified for P_{50} (Table 2). Species with a P_{50} of > 100 years would include okra, pea, and tomato; species in the 50- to 70-year range would include corn, eggplant, muskmelon, and Swiss chard; species in the 30- to 50-year range would include bean, beet, carrot, cucumber, spinach *(Spinacia oleracea* L.), and watermelon; while those in the <30-year range would be onion and pepper.

Implications

Seed moisture content and storage temperature are well known to be the principal factors in determining seed longevity (Justice and Bass, 1978). However, in this experiment, neither of these factors was precisely known throughout the 60-year storage duration. As discussed by James et al. (1964), the original storage conditions in Cheyenne were cool and dry and most likely resulted in the seeds achieving a low equilibrium moisture content. Storage conditions at NSSL also would have promoted low seed moisture content. Recent studies have shown that equilibrating seeds against RH of ≈25% or lower greatly extends seed longevity, even at ambient temperatures (Ellis et al., 1989, 1990a, 1990b; Vertucci and Roos, 1990). Presumably, the storage conditions for the seeds tested certainly would have contributed to the extreme longevities reported.

Genetic and physiological factors important in seed longevity include the species, seed lot, and/or cultivar, and the original seed quality. These factors are taken into account as constants in the seed viability equation proposed by Roberts (1973) and Ellis and Roberts (1980). Here, cultivars are known from the names written on the original seed packets; however, no data are available on the initial seed viability or quality (vigor). Presumably, the lots used in this study were of high quality and vigor, as most of the other seed lot transferred from Cheyenne either died or were of lower viability after long-term storage. Thus, extreme caution must be taken in interpreting these results, as storage conditions were not constant for all species and seed lots tested, and only data for the best-storing seed lots are presented. However, the data do establish new upper limits to the longevity of all species tested.

The data presented provided a unique opportunity to apply a computer probit analysis program, developed to compute statistics for the evaluation of P_{50} (Moore and Roos, 1982; Moore et al., 1983), to the analysis of vegetable seed deterioration data accumulated under slow-aging conditions, as would be encountered in germplasm banks. Priestley et al. (1985) used this probit analysis program to compare differences in seed longevity at the species level; however, the data used by them were very heterogeneous, being taken from diverse cultivars and storage locations. Of the vegetable species included in their analysis, none had a P_{50} of > 25 years, including tomato, which was just < 25 years.

There are three important statistics generated to test the validity of this approach to analyzing longevities, including the SE of the P_{50}; an estimate of the normality of the distribution (χ^2) of seed deaths in time (an assumption for applying the probit transformation); and a goodness of fit (r^2) for the regression of probit germination on storage time. The data (Table 2) reveal numerous cases where either a significant χ^2 (nonnormal distribution) or a nonsignificant correlation coefficient (lack of relationship between germination and storage time) is encountered. Usually, these data sets are accompanied by large SE of the P_{50}, indicative of low confidence in the value determined (exceptions being when little or no deterioration occurred). Explanations for these poor values are numerous and include one or more of the following: a) nonuniform storage conditions (temperature and RH); b) extreme variability in the germination data, caused by poor sampling and/or the small number of seeds tested; c) variations in seed testing conditions and interpretation; d) lack of seed deterioration; and e) too few data points. In spite of all of these factors, useful information has been generated to evaluate storage longevity at the species level.

The generally accepted belief that some vegetable species (notably carrot, onion, and pepper) have relatively poor seed longevities, even under relatively good storage conditions, is confirmed by these data. Previous studies usually have been based upon storage at ambient conditions or under elevated temperatures and/or RH. Barton (1953) showed that carrot, onion, and pepper stored as well as eggplant and tomato when kept at –4C for 20 years. After 50 to 60 years of storage under conditions described here, carrot, onion, and pepper are clearly less long-lived than okra or tomato.

Many vegetable species had seed longevities and predicted P_{50} of >50 years (Table 2). Okra, pea, and tomato seed in particular appear to have a potential longevity approaching that reported for some agronomic species such as barley *(Hordeum vulgare* L.), oats *(Avena sativa* L.) (123 years, Aufhammer and Simon, 1957), and red clover *(Trifolium pratense* L.) (100 years, Youngman, 1951). Had these seed lots been stored under conditions of subfreezing or cryogenic temperatures for the entire time, it is quite possible that they may have survived 60 years with a minimal loss of viability, such long-term storage being the ultimate objective of seed gene banks.

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