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A LONG TERM TEST OF SEED LONGEVITY. II.

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The problem of longevity of seeds is both of practical and theoretical importance (see for literature review Barton, 1965). There are several types of treatment under which seeds can retain viability for a long time: (1) keeping them in moist soil or peat (examples: *Amaranthus retroflexus:* Barton, 1945, and *Nelumbo nucifera:* Libby, 1955); (2) keeping them dry (see e.g. Barton, 1953); (3) keeping them at low temperatures (see Barton, 1953); and (4) keeping them under anaerobic conditions.

The first of these treatments seems to depend on inhibition of respiration of fully imbibed seeds, the latter three treatments also depend on reduction of respiration.

Theoretically, therefore, absolute drying of seeds should prolong seed viability indefinitely, assuming that it is residual respiration which gradually exhausts the seed reserves. Once seeds are completely dry, respiration should be zero, and then it would be unnecessary to store them at low temperature to prolong their viability. This is now being tried experimentally in a test which was started 20 years ago (Went and Munz, 1949) to determine whether seeds would lose their viability under theoretically optimal storage conditions and whether such loss would occur under conditions of complete anabiosis. Seeds of 98 species and varieties of California plants were used; this should provide a cross-section of the more easily germinating plants from this particular region. An analysis of their viability as a function of length of storage prior to the beginning of the longevity test showed that these seeds are more or less representative. There were three seed lots which were more than 10 years old, of which only one still had reasonable viability (*Encelia actonii,* 12 percent). These 3 lots were selected because they were still viable, whereas most other seed samples more than 10 years old had already lost their viability and, therefore, could not be used. Of the seed samples which were 0–2 years old, 92 percent contained viable seeds, whereas 6–7 year-old samples were only 60 percent viable, for 8 out of 13 samples still germinated. This indicates that under normal seed storage conditions (air-dried seed kept in glass jars in a dry cool room with little fluctuation in temperature) one might expect in the course of 5 years about one-third of the seed samples to lose their viability. The 3–5 year-old seed lots were still 70 percent viable (10 out of 15), but 5 of these 10 had decreased in viability to such an extent that on the average only one-half percent of the seeds germinated.

This shows two criteria by which the aging of seeds can be judged: (1) a drop in the percentage of seeds in each lot which will still germinate, and (2) an increase in the number of species which will not germinate at all any more. A third criterion is the length of time required for germination, which also increases with aging of the seeds.

In August, 1952, one set of sealed seeds (not a complete one) was taken out of storage, the evacuated glass tubes were broken, and 100 seeds were taken from each tube. They were laid out on filter paper wetted with tap water in petri dishes, and these were placed in darkness in a room kept at 17°C. The conditions were almost identical with the germination tests 1 and 2 in 1947. Each day the germinated seeds were counted and removed. After 5 days a few petri dishes were put in 23°C. This speeded up germination for species requiring higher germination temperature (e.g., *Allenrolfea occidentalis* germinated in 17° for the first 10 percent after 10 days, and in 23° after 7 days, two days after the shift to the higher temperature), such as *Lupinus subvexus, Crossosoma californicum, Suaeda torreyana* and *Agrostis longiligula.* Tests were not terminated until no germination had occurred for 40 days or when no further germination occurred a week after the last one for a given species.

Towards the end of April, 1957, another set of tubes was taken out of storage, and germination was again tested under conditions identical with those in 1947 and 1952. In June, 1967, a germination test was carried out in the airconditioned greenhouses of the Desert Research Institute at Reno, Nevada. There the temperature in the testing room was 17°C, but it occasionally increased to 20°. Such a somewhat fluctuating temperature is advantageous for germination which may explain the slightly higher germination percentages in this last test.

In 1947 we forgot to save a set of seeds of the different species under open storage conditions. The seeds from the tubes opened in 1952 which were not needed for the germination test were kept in a laboratory room at about 25°C in the regular seed storage cabinet in the Earhart Laboratory. Each year another sample of 100 seeds of each of these species was laid out in petri dishes on wet filter paper, as in the regular tests, at 17°C. Gradually the seed supply became exhausted for these tests and therefore a smaller and smaller number was tested in successive years. The average germination figures show the normal behavior of seeds in open storage: each year the percentage germination drops, first slowly, later faster, until after 4 years it had dropped to less than 20% of the original rate.

Similarly the tubes opened for the germination test in 1957 were left in open storage, part of the time in the Earhart Laboratory and part of the time elsewhere. These were tested again in 1967.

In the whole experiment thus far 50,000 seeds have been used, 100 for each species at each testing. Since these were checked daily for an average of 20 days, about one million counts have been involved thus far with about 20,000 positive germinations. Duplicate tests always gave closely similar results. No seed was considered germinated until the root had grown several millimeters; mere swelling or breaking of the seed coat was not considered positive germination, nor was the appearance of a coleorhiza counted as germination. Among the persons who have helped in the counting I want to thank specifically Rachel Morgan Behnke (1952–1953), Helene Fox Metzenberg (1954–1955), Dr. Lillian Overland Sheps (1956–1957), and David Johnson (1967). The results of these germination tests are presented in Tables 1, 2, 3, and 4 in which the seeds have been grouped according to their behavior. These tables also include the germination data of 1947 and 1948 (Went & Munz, 1949). Leaving out of consideration seed lots which were tested only once, or which gave consistently a low rate of germination, or which apparently had no or very little viability at the start of the experiment (Table 4), the overall picture is consistent and convincing. In each table the first figure (in roman type) gives the maximal percentage germination of the seed lot after 40–50 days in the germination dishes; the second figure (between brackets) gives the number of days required for germination of the first 17% of the seeds. In Table 1, all seeds with a consistently high germination percentage after storage in vacuum (90% or over) are listed. In Table 3, six of the species which showed a higher germination after 20 years of vacuum storage than upon sealing, are listed. And in Table 2 all species with germinations between 10 and 90% are shown. The seed species and their provenance are all presented in the first paper of this series (Went and Munz, 1949), together with the year of harvesting. For seed numbers 123–126, 128 and 135 no provenance data are available, but they were also sealed in vacuum in 1947.

In the 1957 tests the vacuum-sealed tubes were checked for cracks before opening, and in 1967 the tubes were opened while connected with a manometer, and thus a number of cracked tubes were spotted (less than 10% of the tubes). Viability of the seeds in the cracked tubes (marked with an asterisk) into which outside air had leaked had dropped to a very low value, except for one tube with *Godetia biloba* (tested in 1957), and cracked tubes were not included in the calculation of overall germination percentages. It is likely that some of the low germination values for the 1948 and 1952 tests were also due to cracks in the tubes and an absence of vacuum.

Before sealing, the average germination percentage for all seeds recorded in Tables 1, 2, and 3 was 49.9 before drying. This percentage was seemingly decreased upon drying to 43.7% and even more after 1 year of vacuum storage (to 33.3%) but the germination conditions for 1948 were not strictly comparable, and germination was carried out in an ordinary laboratory room at a slightly higher temperature than in 1947. In 1952 and 1957 germination was the same as before vacuum storage: 47.7% and 48.0%. If we ignore the 1948 data, which are at variance with the others (e.g., germination was both low and slower in numbers 57, 59, 109, and 112), and if we average the germination before and after drying in 1947, we can say that viability has not changed at all during the first 10 years of storage, and probably not in the following 10 years either (see Fig. 1). For the lower germination averages of the 0, 5 and 10 year stored seed compared with the 20 year storage are mainly due to occasional low values, which seem to be out of line with the germinations in other years (e.g. numbers 6, 14, 43, 48, 55, 64, 67 and 69). When we average the two highest values of all except the 1967 germination tests for each species of Tables 1, 2, and

3, we get an average germination of 58.5%. This is essentially the same as the 61.0% for 20-year storage in vacuum.

This lack of change in viability upon vacuum storage contrasts sharply with the loss of viability of these same seeds in open storage. The data in the last column of Tables 1, 2, and 3 show that seeds, which after 10 years in vacuum storage had not changed in viability at all (48.0% against 49.9% for the same seeds before sealing), had almost completely lost the ability to germinate after an additional 10 years of open storage (1.0%). The seeds which germinated were for more than half accounted for by samples of *Phacelia tanacetifolia* and *Encelia actonii* which showed 32% and 8% germination after 10 years' exposure to room air. It is interesting that both of these are desert species, which as seeds in their natural habitat must have a longer life span than seeds from less extreme habitats. Two other plants which retained some viability were both *Lupinus* species, of which seeds are known to be long-lived under natural conditions. The only other species with appreciable germination was another (non-desert) *Phacelia (P. ciliata).*

The data obtained after a year-to-year test of open storage (from 1953–1956) are the same in principle, but show much more detail. In the course of 4 years all but one species had lost more than half its viability (this being *Oenothera deltoides,* a desert species), whereas 5 species had retained one-fifth of their original germinability: *Clarkia elegans, Baeria chrysostoma, Carpenteria californica, Sisyringium bellum,* and *Eschscholtzia californica.*

In the cracked tubes no vacuum was maintained, which caused the same loss of viability as in open storage. This suggests that it is the presence of oxygen which causes the loss of viability, rather than an increase in moisture content of the seeds, which could have taken up only very little water from the air which leaked through the crack and through which presumably little vapor diffused.

The data of Table 3 are plotted separately in Fig. 2. It is clear that in open storage after-ripening occurred, for not only the 1, but also the seeds stored for 2 and 3 years germinated better than the 0, 5 and 10 year vacuum stored seeds, and it is only after 4 and 10 years of open storage that the percentage germination falls well below the vacuum-stored seeds.

In Figures 3–5 the germination behavior of several species is shown in more detail. These behaviors more or less typify those presented in Tables 1-3. Fig. 3 presents the germination rate of seeds of *Oenothera deltoides* var. *cognata,* typical for *Godetia.* In this case the original seeds, and those dried in *vacuo,* germinated rather slowly, and only to about 60%. All subsequent germinations were faster, and reached much higher percentages. Only after 4 years' open storage is there a slight indication that both total germination and rate dropped. In Fig. 4 the germination behavior of *Eschscholtzia caespitosa* var. *hypecoides* is shown. Upon drying the rate of germination decreased even though the total percentage remained high. But after more than 1 year open storage both percentage and rate decreased rapidly. Finally, in Fig. 5, the curious behavior of *Carpenteria californica* is depicted. This is a shrub, and its seeds are the smallest of all tested. Sharp drying drastically reduces the germination rate, which drop in rate continues for 20 years' storage, but is reversed in open storage. One might

TABLE 1.

No.	Name:	Before Drying	After Drying									
	Years in Vacuum:		0	1	5	10	20	5	5	5	5	10
	Years open storage:	0	0	0	0	0	0	1	2	3	4	10
	Year of testing:	1947	1947	1948	1952	1957	1967	1953	1954	1955	1956	1967
23	Clarkia elegans	100(1)	100(2)	71(1)	99(1)	100(2)	95(2)	96(2)	96(2)	69(3)	22(5)	0
61	Godetia whitneyi	94(1)	100(2)	89(2)	98(2)	96(2)	94(2)	92(2)	96(2)	63(5)	16	0
135	Brunella vulgaris				96(3)	100(3)	98(4)	94(3)	77(4)	19(13)	3	0
36	Monardella lanceolata	95(2)	95(2)	95(3)		97(2)	96(2)					0
109	Achillea borealis	98(3)	93(5)	43(7)	89(5)	0*	98(4)	54(6)	0			0
67	Godetia viminalis	92(1)	62(2)	61(7)	98(2)	83(2)	90(2)		77(3)		0	0
62	Godetia lindleyi	85(1)	95(2)	91(2)	82(2)	97(2)	89(2)					0
64	Godetia biloba	87(1)	90(2)	84(5)	55(4)	97*(3)	92(2)		0	0	0	0
65	Godetia biloba var.	85(1)	92(3)	58(3)		78(3)	91(2)					0
112	Godetia bottae		72(1)	26(8)	79(3)	4*	90(2)	73(2)	69(3)	9	0	0
58	Godetia amoena	96(1)	92(1)	78(6)		86(2)	92(2)					0
59	Godetia cylindrica	90(1)	98(1)	59(6)	73(2)	73(3)	80(2)	60(3)	59(2)	12	1	0
60	Godetia dudleyana	90(1)	67(1)	77(2)		75(2)	96(2)		94(3)	45(5)	8	0
55	Gilia staminea	92(1)	93(2)	48(3)		13	93(2)					1
56	Gilia tricolor	96(1)	85(2)	56(2)		43(8)	94(5)					0
6	Baeria uliginosa	49(4)	93(2)	12		69(3)	90(3)					0
48	Linanthus grandiflorus	92(1)	93(2)	1		34(2)	97(2)					0
49	Linanthus montanus	80	80	1		1*	94(6)					0
125	Coreopsis maritima					75(4)	93(13)					0
69	Phacelia parryi	82(1)	47(2)	72(2)	100(2)	56(2)	99(2)		61(3)	2	0	0
51	Eschscholtzia caesp. h.	55(3)	77(6)	54(7)	76(6)	76(9)	92(5)	64(8)	30(10)	0		0
73	Phacelia viscosa	55(1)	46(3)	1	80(3)	45(3)	97(1)	65(3)	28(11)	6		0
54	Gilia chamissonis	72(2)	35(7)	28(6)	56(4)	5	94(3)	9	0	0	0	0
63	Godetia deflexa	100(1)	97(1)	76(5)		97(1)	57*(4)					0
	Average:	85.0	82.0	62.0	83.3	73.5	93.0	67.5	60.5	18.9	5.0	0.0

TABLE 2.

		Before Drying	After Drying									
	Years in Vacuum:		0	1	5	10	20	5	5	5	5	10
	Years open storage:		0	0	0	0	0	1	2	3	4	10
	Year of testing:	1947	1947	1948	1952	1957	1967	1953	1954	1955	1956	1967
No.	Name:											
30	Lupinus subvexus	90(2)	0	41(11)	30(7)	38(7)	36(6)	0				5
32	Cirsium occidentale	77(5)	70(6)	54(6)	96(3)	92(4)	68(4)	83(3)	77(4)			0
50	Eschscholtzia caespitosa K.	44(5)	55(4)	51(7)	55(4)	62(12)	85(5)	31(11)				0
2	Pentstemon heterophyllus					78(6)	74(6)					0
128	Salvia columbariae					56(3)	64(6)					0
53	Eschscholtzia californica	78(1)	72(4)	75(3)		65(4)	75(3)					0
26	Nemophila maculata	30(3)	27(8)	18(5)	36(3)	48(4)	80(3)	34(4)	33(5)	1	0	
47	Platanus racemosa	45(5)	50(6)	34(6)		73(4)	63(8)					0
101	Crossosoma californicum	72(7)		30(10)	37(9)	30(9)	37(6)	53(8)	0			0
13	Pentstemon spectabilis	12	23(10)	32(8)		0	50(8)					0
76	Baeria chrysostoma	32(2)	37(3)	2		0*	70(2)					0
72	Phacelia tanacetifolia	23(1)	5	0		6	76(1)					32(3)
45	Mentzelia lindleyi	4	7	26(21)	24(10)	14	62(3)	26(7)	15	0	0	0
16	Collomia grandiflora	15	3	2		8	57(8)					0
9	Eriogonum arborescens	7		13	8	14	59(5)		6			0
71	Phacelia ciliata	43(1)	28(3)	61(3)	30(3)	22(3)	53(3)	2	1	4		9
57	Gilia achilleaefolia	92(1)	13	20(14)		19(22)	78(4)					1
128	Salvia columbariae					56(3)	64(6)					0
77	Chaenactis orcuttii	47(4)	47(7)	3	56(7)	0*	54(3)	36(8)	25(8)	46(4)	0	0
28	Allenrolfia occidentalis	5	5	27(7)	40(7)	40(7)	40(8)	28(7)	9			0

TABLE 2. (con'td)

No.	Name	Before Drying	After Drying									
	Years in Vacuum:		0	1	5	10	20	5	5	5	5	10
	Years open storage:		0	0	0	0	0	1	2	3	4	10
	Year of testing:	1947	1947	1948	1952	1957	1967	1953	1954	1955	1956	1967
1	Coreopsis bigelovii	58(9)	46(12)	66(17)	60(9)		63(6)	25(9)	0			
29	Lupinus succulentus	13	32(4)	39(6)		42(1)	38(2)					5
39	Oenothera brevipes	10	10	15		11	43(5)					0
40	Malacothrix arachnoidea	25(7)	8	14	38(6)	29(8)	29(7)	10	4	0	0	0
10	Chaenactis glabriuscula	33(6)	20(19)	1	0	17(12)	32(7)		0	0		0
27	Chorizanthe douglasii	3	0	13	0	33(11)	21(11)		0		0	0
9	Eriophyllum nevinii	18(9)	23(8)	7		17(10)	32(5)					0
42	Suaeda torreyana	23(5)	7	16	19(7)	19(7)	24(8)	8	12	2	1	0
76	Chorizanthe staticoides	22(15)	20(18)	3		25(14)	22(13)					0
11	Agrostis longiligula	0	5	10	29(11)	12	9	5	0	0		0
7a	Baeria chrysostoma	3	0	0	7	2	18(3)	8	30(10)		17(49)	0
19	Eremalche parryi	8	12	16	16	13	12	7	2	0	0	0
79	Laya platyglossa	20(4)	17(15)	4	12	11	14	4	0	0		0
17	Lathyrus alefeldii	3	0	0	11	10	8	12				0
38	Tanacetum camphoratum	23(7)	5	8	22(7)		0*	4	0	0	0	
105	Encelia actonii	13	12	1		25(3)	7					8
102	Atriplex hymenelytra	0	0			32(2)	10					0
103	Grayia spinosa	0		15	4	20(30)	10		0			
107	Calycanthus occidentalis	3	0	20(25)		42(31)	20(20)					
110	Salvia spathacea	7	7	3	8	17(31)	28(18)	10				
	Average:	27.2	19.6	20.6	27.2	31.1	43.2	20.3	11.3	4.8	2.0	1.8

TABLE 3.

No.	Name	Before Drying	After Drying									
	Years in Vacuum:		0	1	5	10	20	5	5	5	5	10
	Years open storage:		0	0	0	0	0	1	2	3	4	10
	Year of testing:	1947	1947	1948	1952	1957	1967	1953	1954	1955	1956	1967
No.	Name:											
43	Oenothera deltoides	52(3)	60(3)	54(3)	82(2)	91(2)	91(2)	91(2)	94(2)	93(3)	76(3)	0
123	Eriophyllum lanatum				24(10)	25(14)	22(12)	45(9)	56(10)	9	0	0
111	Carpenteria californica	100(2)	22(12)	0	22(18)	31(22)	35(27)	49(12)	59(7)	45(8)	35(9)	0
14	Lasthenia glabrata	36(3)	69(3)	2	62(2)	34(4)	70(3)	79(3)	50(6)	22(19)	0	0
21	Sisyringium bellum	23(15)	18(22)	1	71(10)		49(12)	87(10)	88(10)	60(14)	17(38)	
82	Cercidium microphyllum	40(8)	30(7)	21(10)	33(8)	24(4)	56(5)	40(5)				
	Average:	50.2	38.8	15.6	49.0	41.0	53.8	65.2	69.4	49.8	25.6	0.0
	Average Tables 1, 2, & 3:	49.9	43.7	33.3	47.7	48.0	61.0	40.8	36.5	19.0	8.2	1.0

TABLE 4.

No.	Name	Before Drying	After Drying									
	Years in Vacuum:		0	1	5	10	20	5	5	5	5	10
	Years open storage:		0	0	0	0	0	1	2	3	4	10
	Year of testing:	1947	1947	1948	1952	1957	1967	1953	1954	1955	1956	1967
3	Artemisia pycnocephala	0	0	10		0	9					0
66	Godetia quadrivulnera	0	0	8	1	1	0*		1	0	0	0
8	Boisduvalia densiflora	0	3	0	3	0	0		0	0	0	0
52	Eschscholtzia glauca	0	0	1	2	3	1		0	2	4	0
104	Chilopsis linearis	3	0	0	0	0	0		0			
15	Haplopappus parishii	0	2	0		1	15					0
37	Monardella undulata	0	0			1	0*					0
68	Phacelia curvipes	0	0	1	0		0		1	0	1	
78	Layia heterotricha	2	0	0		1	0					0
124	Eurotia lanata				0	1						0
44	Mentzelia laevicaulis	0	0	2	0	0	0		0	0	0	0
70	Phacelia brachyloba	2	0	0	0	0	0*		0	0	0	0
74	Phacelia grandiflora	0	0	0	0	1*	0		0	0	0	0
12	Artemisia Suksdorfii	0	0	0		0	0					0
22	Salvia carduacea	0	0			0	0					0
35	Eryngium articulatum	0	0	0	0	0	0		0	0	0	0
46	Baileya pleniradiata	0	0	0	0	0	0		0	0	0	0
108	Adenostoma fasciculatum	0	0	0		0	0					0
113	Trichostema lanatum	0	0	0	0	0	0					0
126	Abronia umbellata					0*	0					
18	Madia elegans	0										
5	Fallugia paradoxa	5		2	3	0	2		0			
24	Lotus scoparius	7	0	20(9)		5	0					0
33	Eriogonum fasciculatum	0	0	17	0	1	0	0				0
34	Pectis papposa	0	4	3		12	2					0
106	Geraea canescens	7	0	2		0	3					0
	Average:	1.1	0.4	3.1	0.6	1.2	1.3		0.2	0.2	0.5	0.0

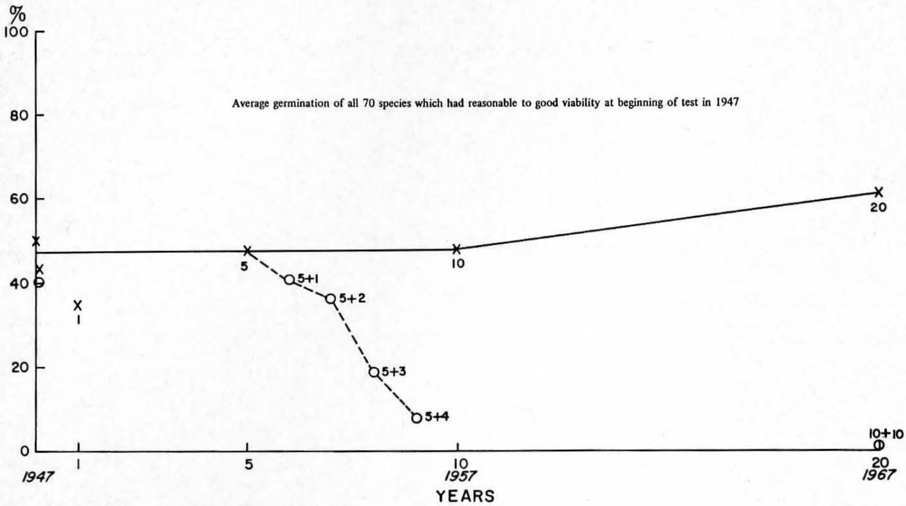

Fig. 1. Average germination percentage (ordinate) of 70 species of California seeds, which had reasonably good viability at beginning of test in 1947. Crosses: Values based on 5–7000 seeds, tested after 0, 1, 5, 10 or 20 years of storage *in vacuo*. Circles: germination of seeds stored for 5 or 10 years *in vacuo*, and then left for 1, 2, 3, 4 or 10 years in open storage, open to laboratory air.

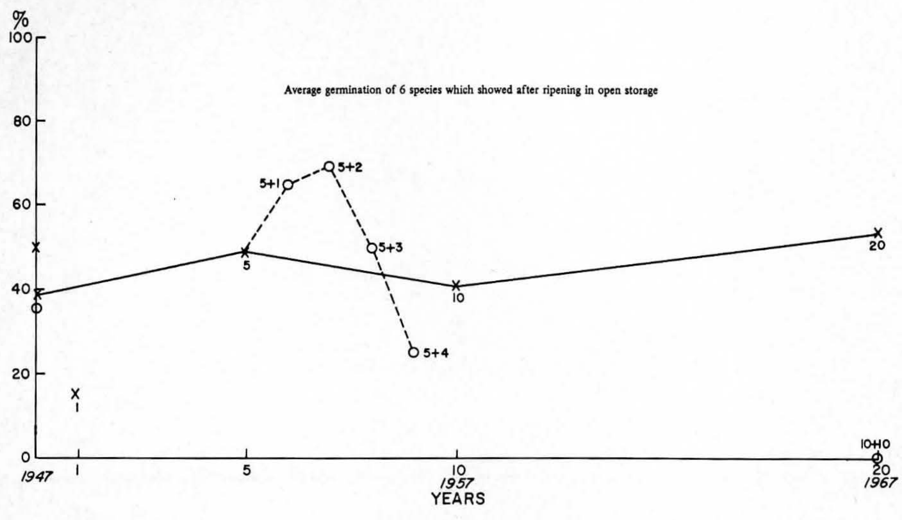

Fig. 2. Same as Figure 1, except that only the averages are taken of 6 seed species which showed after-ripening.

assume that the drying in *vacuo* causes dehydration of the seedcoat, with concomitant slowing of re-hydration during germination. This re-hydration seems to occur slowly during open storage, at least during the first two

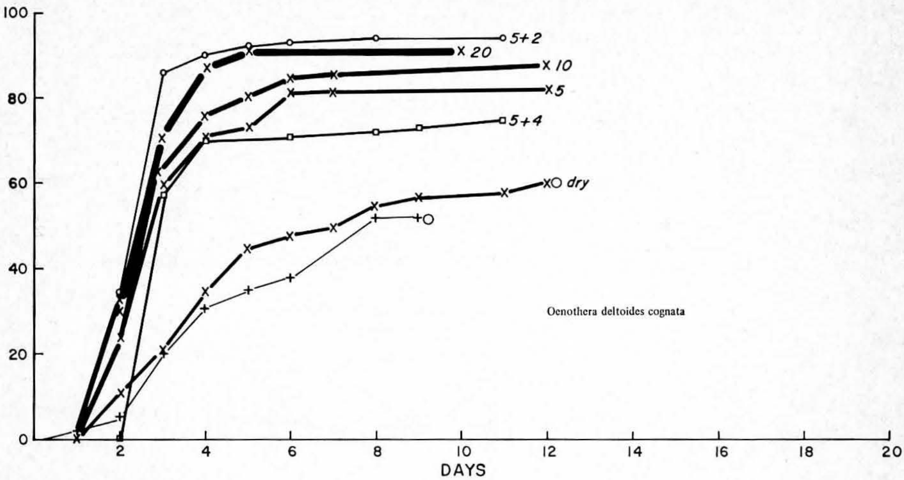

Fig. 3. Rate of germination (ordinate: in percentage, and abscissa: days after moistening of the seeds of *Oenothera deltoides cognata,* after 0, 5, 10 and 20 years of storage *in vacuo,* and after 5 years' dry storage plus 2 or 4 years' open storage.

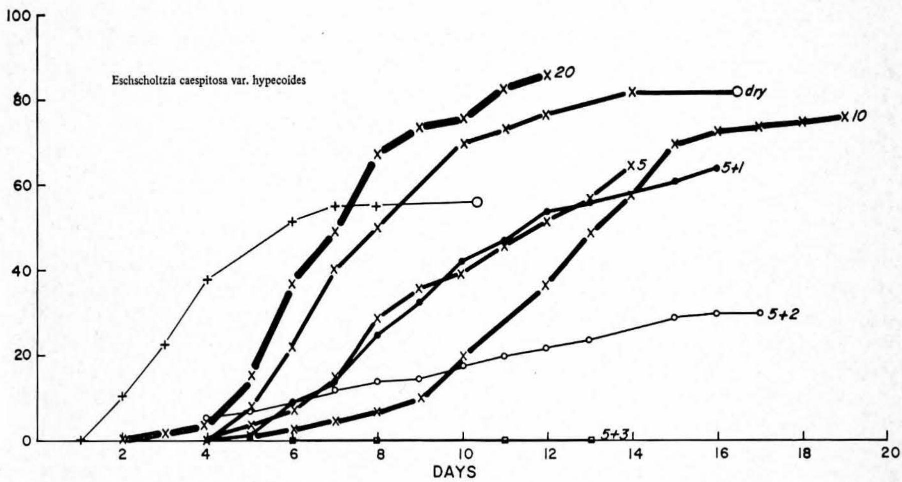

Fig. 4. Same as Figure 3, but data for *Eschscholtzia caespitosa hypecoides.*

years, after which the gradual loss of viability sets in and overtakes the acceleration.

In other cases the after ripening may be due to microbial decomposition of the seed coat (such as one might assume for some composites, notably *Cirsium occidentale* and *Chaenactis orcuttii,* and for *Lupinus subvexus*). But in most cases the attack of seeds by fungi and bacteria indicates that

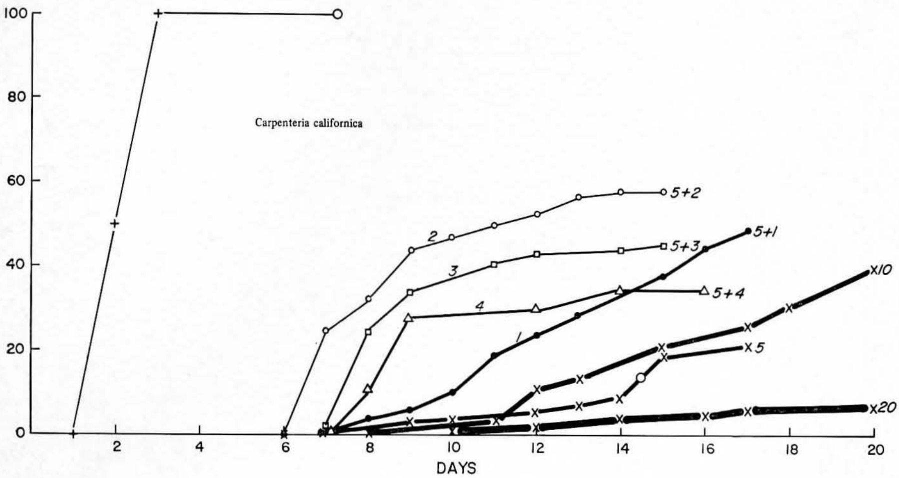

Fig. 5. Same as Figure 3, but data for *Carpenteria californica.*

they have lost their viability, and there *both* seed *and* seedcoat are digested by microbes.

In view of the excellent retention of viability, the next germination test needs not to be performed until 1987 or 1997, and after that (depending upon germination behavior) every 50–100 years. In following germination tests it might be advisable to grow the seedlings to maturity to see whether mutations or other changes occur in the seeds during vacuum storage.

SUMMARY

Almost 100 different kinds of seeds of California plants were tested for germinability, after 5, 10 and 20 years of storage in *vacuo*. For 70 different kinds which had originally a good germination (49.9%) and after several weeks' drying *in vacuo* over P_2O_5 still germinated 43.7%, the percentage germination was 47.7 after 5 years, 48.0 after 10 years, and 61.0 after 20 years. These same seeds, when left exposed for 1, 2, 3, 4, and 10 years to atmospheric air germinated for 40.8%, 36.5%, 19.0%, 8.2% and 1.0%. It was primarily desert species which survived open air storage.

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