Storage Effects on Dormancy and Germination of Native Tickseed Species

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SUMMARY. Fresh seeds of prevaryety germplasms of goldenmane tickseed (*Coreopsis basalis*), florida tickseed (*Coreopsis floridana*), lanceleaf tickseed (*Coreopsis lanceolata*), and leavenworth's tickseed (*Coreopsis leavenworthii*) were harvested from cultivated plants and stored under dry conditions for 1 to 24 weeks at 15 or 32 °C to alleviate dormancy, that is, to promote after-ripening. The relative humidity (RH) was 33% for all species except lanceleaf tickseed (23% RH). Seeds were subsequently stored for 24 weeks in a commercial storage facility at 23% RH/17 to 19 °C to determine whether after-ripened seeds could be stored without loss in quality (viability, germination velocity). The only substantial after-ripening occurred with seeds of lanceleaf tickseed, although most after-ripening of lanceleaf tickseed seeds occurred during the 24 weeks of dry storage in the commercial storage facility regardless of storage conditions for the previous 24 weeks. After the 24 weeks in commercial storage, germination of lanceleaf tickseed seeds was 48% to 80%, but germination was only 2% to 15% after 24 weeks of dry storage at 15 or 32 °C, respectively. Freshly harvested seeds of the other three species were much more nondormant than seeds of lanceleaf tickseed, but after-ripening effects were still evident because there were increases in germination or germination velocity (an indicator of after-ripening). Maintenance of seed quality was species-dependent. Seed quality of the two upland species, goldenmane tickseed and lanceleaf tickseed, was maintained during the initial 24 weeks of dry storage plus the subsequent 24 weeks in the commercial storage facility. In contrast, viability of seeds of the two wetland species, florida tickseed and leavenworth's tickseed, declined to varying degrees either during the initial 24 weeks of after-ripening or during storage in the commercial facility. The greatest decline in quality occurred for florida tickseed seeds that were stored for 24 weeks at 32 °C and then for 24 weeks in the commercial storage facility.

Over the past 10 to 20 years, production of prevaryety germplasm of native wildflower seeds has risen dramatically in response to the demand for site- or regionally specific ecotype seeds for roadside plantings as well as for ecological restoration and revegetation projects (Booth and Jones, 2001; Harper-Lore and Wilson, 1999; Houseal and Smith, 2000). Researchers and practitioners realize that survival, growth, and flowering of native wildflower species can be strongly affected by seed origin (Marois and Norcini, 2003; Norcini et al., 1998, 2001). Demand for prevaryety germplasms is being met by a niche industry that is primarily in the midwestern and

western United States (Booth and Jones, 2001; Houseal and Smith, 2000). Production in the southeastern United States is mainly in Florida with one full-time grower and 18 part-time growers. Native ecotype wildflower seed production began in Florida in the late 1990s. To the best of our knowledge, there is only one commercial native wildflower seed producer each in North Carolina and Alabama.

One challenge facing the industry is seed quality, which can often vary within a species and even by seed origin (Andersson and Milberg,

1998; Baskin and Baskin, 1998) and harvest season (Norcini et al., 2004, 2006). One aspect of seed quality that can vary is the percentage of dormant seeds. Although seed laws in some states allow dormant seeds to be included in minimum germination specifications, those using seeds in nonarid regions typically desire a high percentage of nondormant seeds to facilitate quick stand establishment. As the length of time over which wildflower seedlings emerge increases, there is a greater likelihood that weeds will interfere with stand establishment. Weed interference is one of the major reasons that wildflowers stands fail to establish (Doubrova, 1979).

Seed dormancy of commercially produced, prevaryety germplasm of native wildflower species is more likely to be an issue than for their domesticated varieties as Takahashi (1984) concluded for wild and domesticated rice (*Oryza* spp.). In domesticated flower seed crops, any minimal amount of dormancy that occurs is easily overcome by typical dry storage conditions used by flower seed producers (Geneve, 1998), a process referred to as after-ripening. Flower seed producers must ensure their customers, especially plug producers, that nearly every sown seed will germinate within a short period of time. Although the end users of prevaryety germplasm of native wildflower seeds do not have such strict germination requirements, relatively high germination percentages are very important as noted previously. We are not aware of any published study in which after-ripening has been formally investigated as a means of alleviating dormancy of prevaryety germplasm of native wildflower seeds produced under cultivated conditions.

Moreover, research involving factors that affect seed quality of commercially produced, prevaryety

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Units

To convert U.S. to SI, multiply by	U.S. unit	SI unit	To convert SI to U.S., multiply by
29.5735	fl oz	mL	0.0338
3.7854	gal	L	0.2642
2.5400	inch(es)	cm	0.3937
25.4000	inch(es)	mm	0.0394
0.5933	lb/yd ³	kg·m ⁻³	1.6856
1	ppm	mg·L ⁻¹	1
(°F - 32) ÷ 1.8	°F	°C	(1.8 × °C) + 32
(°F ÷ 1.8) + 255.37	°F	K	(K - 255.37) × 1.8

germplasms is very limited. Nearly all work has centered on ecology of seeds harvested directly from natural stands (Baskin and Baskin, 1998). Germination and dormancy characteristics of seeds harvested from commercial production plots could be substantially different from those of seeds harvested from natural stands. Under commercial production conditions, water and nutrition usually are much less limiting compared with natural conditions, and both factors can influence germination and dormancy (Fenner, 1991; Roach and Wulff, 1987). We have noted that freshly harvested seeds of prevaryety germplasms of two native tickseed species grown under cultivated conditions can possess varying levels of dormancy. Viable seeds of lanceleaf tickseed harvested early in the summer were nearly 80% dormant, but seeds harvested later that year were only $\approx 50\%$ dormant (Norcini et al., 2004). Commercially produced leavenworth's tickseed harvested in early Summer 2001 and 2002 were nearly all dormant (Kabat, 2004). In contrast, seeds of the same prevaryety germplasm harvested from containerized plants exhibited less than 18% dormancy (Norcini et al., 2006).

Seeds of a prevaryety germplasm of native tickseeds (*Coreopsis* spp., Asteraceae)—a genus distributed throughout North and South America (Smith, 1975; Tadesse et al., 1995)—are being produced in the United States. Of the 28 species of tickseeds native to the United States [U.S. Department of Agriculture (USDA), 2006a], ecotype seeds of at least eight species are being commercially produced in the United States based on information in seed catalogs and Internet sites: goldenmane tickseed, lanceleaf tickseed, leavenworth's tickseed, largeflower tickseed (*C. grandiflora*), stiff tickseed (*C. palmata*), star tickseed (*C. pubescens*), tall tickseed (*C. tripteris*), and whorled tickseed (*C. verticillata*). Seeds of three other species, coastal plain tickseed (*C. gladiata*), florida tickseed, and sickle tickseed (*C. falcata*), are being increased with the intention of getting them into large-scale seed production within the next few years (M. Fiely, personal communication). The most common species in production seems to be lanceleaf tickseed. Lanceleaf tickseed

occurs throughout most of the United States, the main exception being the Rocky Mountain states (USDA, 2006b). The range of this upland species extends southward into central Florida (Wunderlin and Hansen, 2004a). In Florida, lanceleaf tickseed is a low-growing, spring-blooming, short-lived perennial. Seed production of goldenmane tickseed, also an upland species, occurs mainly in Texas and Florida, although goldenmane tickseed occurs from Texas to North Carolina and even in Illinois and Connecticut (USDA, 2006c). This spring-blooming annual, like lanceleaf tickseed, ranges into central Florida (Wunderlin and Hansen, 2004b). Leavenworth's tickseed currently is only produced in Florida. It is nearly endemic to Florida (USDA, 2006d) with the only populations documented outside of Florida occurring in two Alabama counties (M. Nishino, personal communication). Leavenworth's tickseed, a facultative wetland species that occurs in most Florida counties (Wunderlin and Hansen, 2004c), tends to be an annual in northern Florida and a short-lived perennial in central and southern Florida (authors' unpublished observations; N. Bissett, personal communication). Flowering occurs mainly in late spring and summer, but it can occur at any time in southern Florida. Florida tickseed is a fall-flowering, short-lived perennial that is endemic (Wunderlin and Hansen, 2004d). This species is classified as a facultative wetland species at the state level but as an obligate wetland species at the federal level (Wunderlin and Hansen, 2004d). However, florida tickseed can be successfully established under landscape conditions (Aldrich et al., 2006). Florida tickseed mainly occurs in peninsular Florida with sporadic occurrences in the Florida panhandle (Smith, 1976). All four of these species are self-incompatible (Smith, 1982).

In this study, we evaluated changes in germination, germination velocity, and viability of seeds of prevaryety germplasms of these four native tickseed species when freshly harvested seeds from cultivated plants were stored under dry conditions that might result in after-ripening. Germination velocity was evaluated because it can increase as seeds after-ripen (El-Keblawy and Al-Rawai, 2006; Finch-

Savage and Leubner-Metzger, 2006). However, after-ripened seeds might not be sold immediately and would have to be stored. Thus, we also assessed germination, germination velocity, and viability for seeds that had been subjected to dry conditions and subsequently stored in a commercial native wildflower seed producer's cool storage facility.

Materials and methods

SEED ORIGIN. Achenes (hereafter referred to as seeds) of goldenmane tickseed and lanceleaf tickseed were obtained from Wildflowers of Florida (Alachua, FL). The grower harvested Generation 0 (G0) seeds of goldenmane tickseed from a naturally occurring population in Suwannee County, FL [American Horticultural Society (AHS) Heat Zone 10, USDA Hardiness Zone 9b]. The origin of lanceleaf tickseed was a composite of seeds collected in 1996 and 1997 from natural upland populations located mainly in Leon and Wakulla Counties, FL (both AHS Heat Zone 9 and USDA Hardiness Zone 8b) with some seeds from populations in Gadsden and Jefferson Counties, FL (both AHS Heat Zone 9 and USDA Hardiness Zone 8b). These G0 seeds were used to establish a seed increase plot in 1998 at the North Florida Research and Education Center (NFREC) in Monticello (Jefferson County, FL; AHS Heat Zone 9, USDA Plant Hardiness Zone 8b). Seeds provided to Wildflowers of Florida, Inc., were harvested in 2002. Because lanceleaf tickseed is a short-lived perennial, the generation of seeds provided to the grower was not known. Seeds of florida tickseed (G1) were harvested from an increase plot at the USDA Plant Materials Center in Brooksville, FL (Hernando County; AHS Heat Zone 10, USDA Hardiness Zone 9a). The origin of florida tickseed was Polk County, FL (ASH Heat Zone 11, USDA Hardiness Zone 9a). Leavenworth's tickseed originated (G0) in Orange County, FL (AHS Heat Zone 10, USDA Hardiness Zone 9b); seeds in this study (G1) were harvested in 2001 from a production population in Pasco County, FL (AHS Heat Zone 10, USDA Hardiness Zone 9a).

PLANT CULTURE. Plants were grown at the NFREC-Quincy (Gadsden County, FL; AHS Heat Zone 9,

USDA Hardiness Zone 8b). All plants were randomly selected from the median 90% of the respective seedling populations to adequately represent the genetic and phenotypic diversity of the source populations. On 18 Dec. 2003, seeds of all species were sown on the surface of flats containing Metro-Mix 200 (The Scotts Co., Marysville, OH). They were covered with 1 to 2 mm of Metro-Mix® 200 and placed in a glasshouse on a propagation mat (ProGrow Supply Corp., Brookfield, WI) that was set at 21 °C. Weekly fertilization of seedlings with 100 mg·L⁻¹ of N delivered as 15N-13.2P-12.4K liquid fertilizer (15-30-15; The Scotts Co.) began on 31 Dec. 2003 and continued through 16 Mar. 2003, except for lanceleaf tickseed and leavenworth's tickseed. Liquid fertilization of these two species was halted on 3 Mar. 2003 because seedlings were large and they could not yet be transplanted to large containers and placed outdoors because of potential frost or freeze damage. On 15 Jan. 2004, single seedlings of all species were transplanted to cell packs (2.5 fl oz volume, product no. 1204; Cassco, Montgomery, AL). Goldenmane tickseed seedlings were transplanted to larger cups (22 fl oz) on 19 Feb. 2004. On 17 Mar. 2004, single seedlings of all species (50 per species, except 46 of goldenmane tickseed) were transplanted into a soilless substrate in 1-gal containers. The substrate was composed of 3/4-inch shaker-screened pine bark (Georgia-Florida Bark & Mulch, Capps, FL), Canadian sphagnum peat (Berger Peat Moss Inc., St. Modeste, Quebec, Canada), and rescreened 6B gravel (Martin Aggregates, Chattahoochee, FL) at a ratio of 3:1:1 (by volume). Incorporated into this soilless substrate were Osmocote 18N-2.6P-10K (18-6-12; 8- to 9-month formulation at 21 °C; The Scotts Co.) at 6.0 lb/yard³ and Micromax (The Scotts Co.) at 1.6 lb/yard³. Pots were placed outdoors on a full sun bed that was covered in black plastic. Daily overhead irrigation (pH 7.8) was 0.35 inch to ensure that substrate moisture was nonlimiting. Containers were hand-weeded as necessary.

SEED HARVEST. Fully mature seeds were hand-harvested directly from mature seed heads over a 2-week

period in late May/early June 2004 or mid-Nov. 2004 (florida tickseed only). Seeds of each harvest were stored separately in a desiccator [$\approx$ 23% relative humidity (RH)] at 72 to 78 °F for up to 2 weeks until enough seeds for each species had been harvested to start the storage experiment. Seeds of each harvest were pooled, by species, because there were no differences in viability among the harvests within a species (data not shown). Viability of these fresh seeds was determined by tetrazolium (TZ) testing [1% TZ at 32 °C for 24 h in the dark (Grabe, 1970)] of four 50-seed samples. Extracted embryos that were white, turgid, and otherwise appeared normal also were deemed viable as were such embryos with only faint pink staining at the radicle end (Dehgan and Norcini, 2006). Four other 50-seed samples were subjected to germination testing under an alternating temperature regime of 15/25 °C [Association of Official Seed Analysts (AOSA), 1988; Dehgan and Norcini, 2006; Kabat, 2004] or 20/30 °C for lanceleaf tickseed (AOSA, 1988; unpublished data). All seeds were germinated under an 8-h photoperiod with the warmer temperature during the lighted period. A seed was deemed germinated if the radicle protruded 1 mm or more. Germination was recorded at 7 and 21 d. All germinated seeds at 7 d were removed. We realize that seeds are often termed nondormant when they germinate at high percentages over a wide range of temperatures (Baskin and Baskin, 1998), but germination tests for each species were conducted under a single temperature regime because germination testing of seeds over a wide variety of temperature regimes was impractical.

The remaining seeds of each species were subdivided into 100-seed subsamples, each of which were placed into small bags (2 × 2 inches) constructed from polypropylene mesh (35% open area, product no. XN-6065; InterNet, Minneapolis, MN). These bags of seeds were placed on top of an elevated fiberglass screen in 5.1-L polyethylene containers (Multipurpose Specimen Storage Container; Fisher Scientific, Pittsburgh) that contained solutions of potassium acetate (23% RH; lanceleaf tickseed only) or magnesium chloride

(33% RH; all other species) (Rockland, 1960). The seed-filled containers were tightly sealed and incubated in the dark at 15 or 32 °C. The relative humidities and temperatures selected were based on previous studies (Carpenter and Ostmark, 1992; J.G. Norcini, unpublished data). At 1, 2, 4, 12, and 24 weeks, eight 100-seed samples were removed. Seeds from four 100-seed samples were subjected to viability and germination testing as previously described. The other four 100-seed samples were transferred to a commercial wildflower seed producer's cool storage unit (17 to 19 °C, 23% RH) to determine whether viability, germination, and germination velocity were affected by 1) 24 weeks of cool, dry storage, and 2) previous dry storage of seeds at 15 or 32 °C for up to 24 weeks. These conditions are hereafter referred to as "commercial cool, dry storage" (CCDS). Germination velocity was assessed based on percent germination at 7 d. We have observed that the rate of radicle emergence greater than 1 mm of relatively nondormant seed lots is logarithmic $\approx$ 6 to 8 d after seeds were incubated (J. G. Norcini, unpublished data). After 24 weeks in CCDS, seeds were subjected to viability and germination testing as previously described.

SEED MOISTURE CONTENT. A follow-up study was conducted to estimate seed equilibrium moisture contents (EMCs). The seeds used in this study were either seeds not used in the original study or seeds harvested from container-grown plants at the NFREC-Quincy. Seeds (four 100-seed replications) were incubated at 15 or 32 °C at 23% RH (lanceleaf tickseed) or 33% RH (all other species) for 2 weeks. Seed moisture content was then determined using the low-temperature oven test method (103 °C for 17 h) (International Seed Testing Association, 1985).

DATA ANALYSIS. Data for all species were analyzed separately. Before statistical analyses, germination data were corrected for the fraction of viable seeds based on results of the pregermination TZ tests. All germination results are expressed as percent germination of viable seeds. Percentage data were tested for homogeneity of variance and arcsine transformed, if required, before

analyses by general linear model methods of SAS (version 8.01; SAS Institute, Cary, NC). Data from the two parts of the study were analyzed separately to determine temperature and week effects on seeds that had been stored under CCDS for 24 weeks and seeds that had not. Data from both parts of the study were pooled to determine main and interactive effects involving 24 weeks of CCDS (R. Littell, personal communication). Significant week effects ($P \leq 0.05$), as well as interactions involving weeks with $P \leq 0.10$ (R. Littell, personal communication), were subjected to sequential, regression analyses. The quadratic, cubic, or quartic terms were included in the final model only if their inclusion was significant at $\alpha = 0.05$ and the adjusted R^2 value improved by at least 0.05. Comparisons of individual viability, germination, and 7-d germination means to those of fresh seeds (0 weeks) were determined using least squares means analyses [LSMEANS with PDIF option (SAS version 8.01)].

Results and discussion

SEED MOISTURE CONTENT. Equilibrium seed moisture contents of all four species under the different storage regimes were 7.3% to 8.6% (data not shown). Our results concurred with EMCs of several native tickseed species incubated at 50% RH/25 °C (D. Rukuni, personal communication). All seeds used by D. Rukuni were harvested from cultivated plants. Equilibrium moisture contents ranged from 7.2% for florida tickseed to 9.2% for a North Carolina ecotype of lanceleaf tickseed with EMCs $\approx 0.5\%$ to 2% lower at 23% RH. The EMCs of the other Florida ecotypes used in our study as determined by D. Rukuni (personal communication) were lanceleaf tickseed, 7.9%; goldenmane tickseed, 8.8%; and leavenworth's tickseed, 7.6%. Schütz et al. (2002) concluded that seed moisture contents of 5% to 12% were appropriate for after-ripening of native Australian Asteraceae species that grow in a Mediterranean environment. A similar range for after-ripening was reported by Leopold and Vertucci (1989). Hence, EMCs in our study likely were in the range at which after-ripening under dry conditions could occur.

GOLDENMANE TICKSEED. Germination at week 0 was 87.7% (Table 1). Despite this relatively high percent germination, seeds appeared to undergo after-ripening during dry storage, but mainly only for seeds stored for 4 weeks or more at 32 °C. Variability in germination data precluded detection of a significant temperature by weeks of storage interaction. However, when data for 32 °C were analyzed, germination increased linearly over time (adjusted $R^2 = 0.187$, $P < 0.001$), peaking at $\approx 99\%$ (Table 1). When percent germination data were pooled by temperature, there was a quartic response of germination to weeks of storage (adjusted $R^2 = 0.208$, $P < 0.001$) with a peak germination rate of 98.1% at week 12. When pooled by week, germination at 32 °C (90.5%) was greater than that at 15 °C (87.4%) ($P \leq 0.05$). After-ripening also was indicated by a cubic response in germination velocity (germination at 7 d) at both temperatures (Table 1). Although this response varied by temperature, percent germination at 7 d at 12 and 24 weeks was much greater than that at week 0 and even more so at 32 °C (Table 1). There was no loss in viability after 24 weeks of storage at either temperature (Table 1). Although there was a significant quartic response for weeks of storage, the relationship was very poor and of no practical significance. This quartic response was an example of a non-practical significant effect resulting from large sample sizes and concomitant high number of degrees of freedom for some pooled effects combined with the fact that seeds of all species were of prevaryety germplasms and presumably were genetically and phenotypically diverse. Because morphological dormancy has not been reported in Asteraceae (Baskin and Baskin, 1998), observed viability means greater than those at week 0, or any observed increases in viability, were of no practical value.

Seeds that had been stored in CCDS for 24 weeks all exhibited similar viability (greater than 90%), total germination (greater than 95%), and 7-d germination (greater than 79%) regardless of previous storage conditions (Table 2). These similarities resulted in some significant interactions involving CCDS seeds because characteristics of seeds not stored

under CCDS were affected by weeks of storage or storage temperature as noted previously (Table 1). Germination at 7 d for CCDS seeds ranged from 79.2% to 95.6% regardless of previous storage conditions (Table 2). However, for non-CCDS seeds, these percentages were only attained after 12 weeks storage at 32 °C (Table 1). Hence, 24 weeks of CCDS increased germination velocity (an indicator of after-ripening) for all seeds stored at 15 °C and for seeds stored for less than 12 weeks at 32 °C. There was also a significant weeks of storage by CCDS interaction. Seeds stored for up to 24 weeks at 15 or 32 °C that did not achieve greater than 98% germination eventually attained greater than 98% germination after 24 weeks of CCDS.

In summary, it was evident that after-ripening was occurring for seeds stored at 33% RH and 15 or 32 °C. In addition, there was no loss in viability for up to 48 weeks after harvest, and there was no evidence that 24 weeks of CCDS caused any loss of vigor. A decline in percent germination at 7 d would have indicated vigor loss. Carpenter and Ostmark (1992) reported that storage at low temperatures (at 5 °C/10% to 20% RH or 15 °C/20% to 35% RH) for 6 months was more effective at breaking dormancy of wild-collected tickseed than storage at a warmer temperature (25 °C/11% to 75% RH), which slightly contrasts with our results. Contrasting results in dormancy and germination studies involving prevaryety germplasm are not surprising because seed quality characteristics can vary by season and germplasm source (Fenner, 1991; Roach and Wulff, 1987); moreover, our results were based on the percentage of viable seeds and those of Carpenter and Ostmark (1992) were not.

FLORIDA TICKSEED. Germination at week 0 was 95.5% (Table 1). Despite this high percent germination, seeds appeared to undergo a very slight after-ripening regardless of storage temperature. This slight after-ripening effect was evident in the significant quartic response when percent germination was pooled by temperature (Table 1). Germination first increased to 100% by week 2, declined to 82.2% at week 4, and then slightly increased to 90.4% by week 24. Although 100% germination at

Table 1. Effect of dry storage at 15 or 32 °C (59.0 or 89.6 °F) on percent viability, germination velocity (percent germination at 7 d), and total percent germination (21 d) of native tickseed species seed.^z

Weeks	Temp (°C)	Goldenmane tickseed			Florida tickseed			Lanceleaf tickseed			Leavenworth's tickseed		
		Germination			Germination			Germination			Germination		
		Viable seeds at 7 d (%)	Viable seeds at 21 d (%)	of viable seeds at 21 d (%)	Viable seeds at 7 d (%)	Viable seeds at 21 d (%)	of viable seeds at 21 d (%)	Viable seeds at 7 d (%)	Viable seeds at 21 d (%)	of viable seeds at 21 d (%)	Viable seeds at 7 d (%)	Viable seeds at 21 d (%)	of viable seeds at 21 d (%)
0	—	92.6 ± 0.6	14.4 ± 4.0	87.7 ± 1.4	85.0 ± 2.1	78.0 ± 1.2	95.5 ± 2.1	95.3 ± 0.4	0.2 ± 0.1	1.8 ± 0.4	92.9 ± 0.8	78.2 ± 2.0	87.3 ± 1.6
1	15	95.5 ± 1.2	4.7 ± 1.1	84.3 ± 3.2	86.0 ± 2.2	79.6 ± 6.2	94.8 ± 3.3	95.7 ± 0.5	0.3 ± 0.3	3.9 ± 1.6	89.8 ± 2.6	85.1 ± 3.0	88.7 ± 1.9
2	15	96.0 ± 0.4	0.8 ± 0.3	72.7 ± 2.6**	86.5 ± 1.0	100.0***	100.0	93.4 ± 2.4	0	2.7 ± 1.3	85.8 ± 2.4**	82.8 ± 5.8	96.1 ± 3.6
4	15	93.8 ± 1.2	3.2 ± 1.1	86.4 ± 3.1	90.5 ± 1.0	75.2 ± 1.0	88.4 ± 1.3	94.5 ± 1.3	0	3.2 ± 1.1	79.2 ± 5.7***	88.1 ± 5.5*	94.9 ± 4.6
12	15	91.5 ± 1.3	28.4 ± 5.7*	97.3 ± 0.9**	86.5 ± 1.3	75.7 ± 6.4	87.9 ± 4.1	94.5 ± 1.3	0	1.9 ± 0.5	88.2 ± 1.2*	85.0 ± 3.2	91.5 ± 3.5
24	15	94.2 ± 1.1	55.4 ± 0.9***	94.0 ± 3.6	87.4 ± 1.2	77.5 ± 3.0	91.1 ± 3.2	93.3 ± 2.2	0.3 ± 0.3	2.4 ± 0.8	91.0 ± 1.3	78.5 ± 3.2	80.6 ± 2.4
1	32	97.0 ± 0.4***	9.0 ± 2.0	90.2 ± 4.2	81.7 ± 1.0	89.4 ± 2.9*	98.3 ± 1.7	96.2 ± 1.3	0	4.9 ± 1.9*	87.9 ± 2.1*	81.3 ± 4.1	84.2 ± 3.8
2	32	94.7 ± 1.2	1.8 ± 0.9	87.6 ± 1.9	90.1 ± 2.2	100.0***	100.0	92.0 ± 2.1*	0.5 ± 0.5	4.4 ± 1.0	93.4 ± 2.2	79.0 ± 0.9	87.3 ± 1.3
4	32	92.5 ± 1.3	23.2 ± 3.3	95.8 ± 1.7*	92.0 ± 1.8*	65.8 ± 5.0	76.1 ± 5.8***	90.7 ± 1.0**	0	1.9 ± 0.8	84.7 ± 3.6***	92.1 ± 3.4**	94.4 ± 2.4
12	32	90.2 ± 2.1	84.5 ± 3.2***	99.0 ± 0.6**	86.4 ± 3.5	57.3 ± 1.1***	88.0 ± 2.5	96.0 ± 1.3	0	11.0 ± 2.4***	80.0 ± 1.8***	97.5 ± 3.6***	98.8 ± 1.0**
24	32	91.0 ± 2.5	85.7 ± 5.1***	98.6 ± 1.0**	88.2 ± 1.8	51.0 ± 5.3***	89.5 ± 2.4	93.9 ± 1.0	0	15.2 ± 3.3***	80.3 ± 2.3***	95.8 ± 1.8***	96.7 ± 1.6**

Significance ($P > F$)

Temp (T) 0.3673 0.0072 0.0002 0.3626 0.0052 0.3626 <0.0001 0.1557 <0.0001 0.4338 0.1417 0.4338

Weeks (W) <0.0054 <0.0001 <0.0001 <0.0001 <0.0001 <0.0001 <0.0001 <0.0001 <0.0001 0.0494 0.0494

Model^w Qt** (0.124) Qt*** (0.208) C** (0.204) C*** (0.374) C*** (0.662) Qt* (0.304) Qt*** (0.854) C* (0.151) C*** (0.375) Q* (0.109)

T × W 0.7762 0.1921 0.3932 0.0004 0.0004 0.3932 0.3626 0.1672 <0.0001 0.0197 0.0197 0.0197

Model^w 0.1921 0.0066 0.0066 0.0066 0.0066 0.0066 0.0066 0.0066 0.0066 0.0066 0.0066 0.0066

15 °C — — — — — — — — — — — —

32 °C — — — — — — — — — — — —

^zResults (mean ± SE) are normalized for the percentage of viable seeds based on results of pregermination tetrazolium tests. Data were transformed before analysis but nontransformed means are presented.

^yLanceleaf tickseed seeds stored at 23% relative humidity; seeds of all other species were stored at 33% relative humidity; fresh seeds at 0 weeks were not subjected to dry storage conditions.

*, **, *** Means, within a column, are significantly different from the 0-week mean at $P < 0.05$, 0.01, or 0.001, respectively, as determined using LSMEANS with the PDIF option of SAS (version 8.01; SAS Institute, Cary, NC).

^wRegression models were fitted sequentially with the model shown having an adjusted R^2 value ≥ 0.05 (shown in parentheses) than the preceding lowest order model. All models contained components with $P < |t|$ of ≤ 0.05 up to and including the highest order shown as well as the intercept. ns = No significant linear (L), quadratic (Q), cubic (C), or quartic (Qt) components. Results of regression analyses for 15 and 32 °C only shown when the P value for T × W ≤ 0.10 .

^xRegression analysis results omitted because all means were <1.

week 2 was not significantly greater than that at week 0, the significant increase in 7-d germination provides evidence that after-ripening was occurring (Table 1). The gradual decline in both germination and germination velocity after week 2 indicated a loss in seed vigor. In addition, vigor loss at 32 °C was greater than that at 15 °C as indicated by the sharper decline in 7-d germination (Table 1). There was no concomitant decline in viability, because seed viability remained constant over the 24 weeks regardless of temperature (Table 1).

Decline in seed quality occurred during CCDS for seeds that previously had been stored at either temperature for 4 weeks or more as evidenced by the substantial drop in 7-d germination (Table 2). Loss in seed quality was even greater for seeds that previously had been stored at 32 °C for 24 weeks. After 24 weeks in CCDS, seeds that previously had been stored for 24 weeks at 32 °C had substantially lower viability, germination, and 7-d germination compared with seeds at week 0.

In summary, seeds of freshly harvested florida tickseed were nearly nondormant but seemed to slightly after-ripen during 2 weeks of dry storage. After 2 weeks of dry storage, germination and germination velocity declined. Loss of vigor below that of freshly harvested seed was clearly evident for florida tickseed seeds in CCDS that previously had been stored for only 4 weeks at 15 °C/33% RH. Hence cool, dry conditions seem to be sufficient for only short-term seed storage, and cold, dry storage seems warranted for maintaining seed quality.

LANCELEAF TICKSEED. Unlike the other three species, seeds of lanceleaf tickseed were nearly dormant at week 0 because germination was less than 2%. A slight after-ripening effect occurred but only for seeds stored at 32 °C (Table 1). Germination increased linearly over time with an after-ripening effect first evident at week 12; after 24 weeks at 32 °C, germination had increased to 15.2%. The lack of a concomitant increase in germination velocity based on germination at 7 d is not surprising given the minor after-ripening effect. Seed viability was the same at week 0 as it was at week 24 at either temperature (Table 1).

Table 2. Effect of 24 weeks of storage at 23% relative humidity at 17 to 19 °C (62.6 to 66.2 °F) on percent viability, germination velocity (percent germination at 7 d), and total percent germination (21 d) of native tickseed species seeds that had been previously stored dry at 15 or 32 °C (59.0 °F or 89.6 °F) for up to 24 weeks.^z

Goldenmane tickseed			Florida tickseed			Lanceleaf tickseed			Leavenworth's tickseed		
Germination			Germination			Germination			Germination		
Weeks	Temp (°C)	Viable seeds (%)	seeds at 7 d (%)	seeds at 21 d (%)	Viable seeds (%)	seeds at 7 d (%)	seeds at 21 d (%)	Viable seeds (%)	seeds at 7 d (%)	seeds at 21 d (%)	Viable seeds (%)
0 ^a	—	92.6 ± 0.6	14.4 ± 4.0	87.7 ± 1.4	85.0 ± 2.1	78.0 ± 1.2	95.5 ± 2.1	95.3 ± 0.4	0.2 ± 0.1	1.8 ± 0.4	92.9 ± 0.8
1	15	91.2 ± 1.8	81.6 ± 3.1***	99.5 ± 0.4***	88.5 ± 1.7	82.5 ± 4.2	89.8 ± 3.4	92.0 ± 1.2*	24.7 ± 2.4***	76.6 ± 3.8***	89.3 ± 1.3
2	15	93.9 ± 0.6	84.4 ± 1.5***	99.8 ± 0.2***	91.0 ± 3.1	67.6 ± 4.6	84.1 ± 3.6*	96.2 ± 0.5	59.0 ± 5.3***	84.7 ± 2.5***	89.0 ± 1.2
4	15	93.0 ± 1.8	87.4 ± 1.6***	99.0 ± 1.0**	86.4 ± 3.3	52.6 ± 1.1***	79.2 ± 2.6	95.2 ± 1.7	0	62.0 ± 5.5***	87.8 ± 0.5
12	15	90.7 ± 0.7	79.2 ± 7.7***	97.1 ± 1.1*	82.8 ± 4.8	—	84.6 ± 4.9	93.5 ± 1.6	10.7 ± 1.6	47.9 ± 4.3***	85.8 ± 2.1
24	15	92.2 ± 2.4	94.7 ± 1.3***	98.2 ± 0.7**	71.6 ± 2.9**	53.1 ± 5.7***	88.6 ± 4.8	94.2 ± 1.2	36.6 ± 4.1***	73.2 ± 3.5***	80.9 ± 4.4***
1	32	93.6 ± 1.3	89.4 ± 2.7***	99.4 ± 0.4***	90.0 ± 3.6	77.8 ± 2.4	86.7 ± 4.9	97.0 ± 0.4	28.3 ± 5.5***	74.0 ± 5.5***	85.4 ± 1.0***
2	32	92.2 ± 2.0	88.0 ± 3.2***	99.9 ± 0.1***	83.9 ± 3.0	73.8 ± 6.4	85.8 ± 5.1*	96.5 ± 0.9	55.3 ± 6.5***	79.8 ± 3.9***	91.0 ± 1.8
4	32	95.0 ± 1.1	84.8 ± 5.1***	95.7 ± 4.2	90.2 ± 2.2	42.1 ± 6.9***	81.0 ± 8.3	94.0 ± 1.4	0	74.2 ± 4.2***	86.5 ± 1.5
12	32	93.7 ± 1.8	92.0 ± 3.4***	98.0 ± 1.9**	82.0 ± 2.9	—	73.8 ± 3.6	96.6 ± 1.3	18.9 ± 3.8	65.2 ± 3.5***	84.5 ± 2.0**
24	32	95.8 ± 2.3** ^w	95.6 ± 2.9***	99.5 ± 0.5**	75.0 ± 3.9*	9.3 ± 1.7***	81.3 ± 5.2**	95.0 ± 2.3	42.2 ± 2.8***	80.4 ± 2.6***	86.3 ± 2.3
Significance ($P > F$) (within stored seed) ^y											
Temp (T)	0.0758	0.0822	0.8411	0.9963	0.0006	0.0006	0.2814	0.0238	0.2128	0.0464	0.9239
Weeks (W)	0.5976	0.0818	0.4483	0.0003	<0.0001	<0.0001	0.3143	0.5464	<0.0001	<0.0001	0.0397
Model	—	—	—	L*** (0.445)	—	—	—	—	Q*** (0.884)	—	L** (0.146)
T × W	0.5906	0.2395	0.7827	0.3496	<0.0001	<0.0001	0.6482	0.2769	0.4882	0.0727	0.2307
Model	—	—	—	—	Q*** (0.673)	—	—	—	—	Q*** (0.711)	—
15 °C	—	—	—	—	Q*** (0.869)	—	—	—	—	NS	—
32 °C	—	—	—	—	—	—	—	—	—	—	—
Significance ($P > F$) (to determine storage effects) ^{u, v}											
Storage (S)	0.4951	<0.0001	<0.0001	0.0168	<0.0001	<0.0001	<0.0001	0.1609	<0.0001	<0.0001	0.8416
T × S	0.0408	0.0289	0.0170	0.7664	0.0760	0.0760	0.7276	0.0531	0.1623	0.3198	0.4879
W × S	0.0418	0.0006	0.0006	<0.0001	<0.0001	<0.0001	0.2620	0.1774	<0.0001	<0.0001	0.3865
Model	—	—	—	—	—	—	—	—	—	—	—
Nonstandard	Qt** (0.124) NS	Q*** (0.208) NS	L*** (0.436) L**	C** (0.204) L***	—	—	—	—	Qt*** (0.881) Qt*** (0.884)	—	—
Stored	—	—	—	—	—	—	—	—	—	—	—
T*W*S	0.6516	0.6516	0.2938	0.1270	0.0819	0.0819	0.3019	0.9560	0.2398	0.0086	0.0078
Model	—	—	—	—	—	—	—	—	—	—	NI
(standard) ^t	—	—	—	—	—	—	—	—	—	—	—
15 °C	—	—	—	—	Q*** (0.304)	—	—	—	—	Q*** (0.702)	—
32 °C	—	—	—	—	Q*** (0.869)	—	—	—	—	NS	—

^aResults (mean ± SE) are normalized for the percentage of viable seeds based on results of pregermination tetrazolium tests. Data were transformed before analysis but nontransformed means are presented.

^bLanceleaf tickseed seeds stored at 23% relative humidity (RH); seeds of all other species were stored at 33% RH.

^c0-week (fresh seeds) data included for companion only and were not included in regression analyses. These seeds were not stored at 15 or 32 °C or at 17 to 19 °C.

^d*** Means, within a column, are significantly different from the 0 week mean at $P < 0.05$, 0.01, or 0.001, respectively, as determined using LSMEANS with the PDIF option of SAS (version 8.01; SAS Institute, Cary, NC).

^eRegression models were fitted sequentially with the model shown having an adjusted R^2 value ≥ 0.05 (shown in parentheses) than the preceding lowest order model. All models contained components with $P < |t|$ of ≤ 0.05 up to and including the highest order shown as well as the intercept. NS = No significant linear (L), quadratic (Q), cubic (C), or quartic (Qt) components. Results of regression analyses only shown when the P values for interactions were ≤ 0.10 .

^fSignificance of main and interactive effects were based on data from the entire study so as to determine the influence of weeks of storage at 15 or 32 °C as well as to determine cool, dry storage effects.

^gRegression model significances for each temperature are those for stored seed; regression model significances for each temperature for nonstored seed are in Table 1. NI = No significant T × W interaction for seeds stored for 24 weeks at 23% RH and 17 to 19 °C.

Dormancy was substantially alleviated during 24 weeks of CCDS regardless of the previous storage conditions (Table 2). Even more noteworthy was that up to 24 weeks at 15 °C/23% RH did not alleviate any dormancy (Table 1), but 1 week at 15 °C plus 24 weeks of CCDS substantially reduced dormancy. Because relative humidities for CCDS and storage conditions before CCDS were the same (23%), and cool temperatures were nearly the same (15 °C versus 17 to 19 °C), 25 to 48 weeks of cool, dry storage was an effective after-ripening treatment, although dormancy was not completely alleviated. A less likely but possible explanation was that seeds were exposed to ethylene at some point during CCDS. Ethylene enhances germination of tickseed (Carpenter and Ostmark, 1992) and can substitute for after-ripening in Asteraceae (Bewley and Black, 1994). However, common sources of ethylene (fruit, combustion engine exhaust) were absent based on information provided by the owner of the CCDS facility.

For seeds subjected to 24 weeks CCDS, the response of germination over previous weeks of storage at 15 or 32 °C varied by temperature (Table 2). At 15 °C, there was a quartic response of germination based on weeks of previous storage mainly attributable to the decline in germination at 4 and 12 weeks. Because the 7-d germination exhibited a quartic response similar to the germination response implies that the length of previous storage at 15 °C affected dormancy under CCDS and might not simply be an artifact. Further research is needed to verify whether these quartic responses represented changes in dormancy. There are no reports of changes in dormancy of lanceleaf tickseed stored under cool, dry conditions. Banovetz and Scheiner (1994a) observed secondary dormancy of imbibed seeds of lanceleaf tickseed at 5 °C. At 32 °C, germination was generally similar regardless of length of previous storage (Table 2). There was no loss in seed viability after 24 weeks of CCDS. We expected the seeds to remain viable after 48 weeks in dry storage. Banovetz and Scheiner (1994b) reported that seeds of a midwestern ecotype of lanceleaf tickseed remained viable in the soil for up to 13 years.

In summary, seed dormancy of lanceleaf tickseed was most effectively alleviated after 25 to 48 weeks at 23% RH under cool conditions without loss of viability. However, dormancy was not completely alleviated so additional cool, dry storage would seem to be required. Carpenter and Ostmark (1992) noted that dormancy of tickseed declined as storage time at 5 °C increased. Dormancy might also be alleviated by storing seeds at 32 °C/23% RH for more than 24 weeks because there was some after-ripening under these conditions after 24 weeks.

LEAVENWORTH'S TICKSEED. Germination at week 0 was 87.3% (Table 1). However, like goldenmane tickseed and florida tickseed, seeds appeared to undergo after-ripening. After-ripening only occurred at 32 °C as evidenced by the linear increases in germination and 7-d germination (germination velocity) (Table 1). Warm stratification can alleviate dormancy (Kabat, 2004), a conclusion that does not necessarily conflict with results of our current study because warm temperatures might be the key to breaking dormancy. Seed moisture content of seeds at 33% RH/32 °C was ≈8% (data not shown), much too low for stratification to occur. Viability of seeds declined slightly as weeks of storage increased at 15 or 32 °C, declines that did not occur in seeds of the other tickseed species (Table 1).

Under CCDS, there was no evidence of additional after-ripening because both germination and 7-d germination rates remained relatively constant (Table 2) nor was there any additional loss of viability.

In summary, germination of leavenworth's tickseed was increased by storing seeds at 33% RH/32 °C, but there was a slight loss in viability. Subsequent storage of this seeds under CCDS conditions preserved seed quality for 24 weeks.

Conclusions

Several similarities among species for storage effects on seed quality were apparent under the conditions of this study, although this study was not designed to compare species. First, there was evidence of dry after-ripening of all four species, although the only substantial after-ripening occurred in lanceleaf tickseed. Second, after-ripening under dry conditions for 24 weeks generally was

greater at 32 °C than at 15 °C, which concurs with the generally accepted view that after-ripening time is inversely related to storage temperature (e.g., see Roberts, 1965). However, after-ripening of lanceleaf tickseed was greatest under long-term cool, dry storage. Third, maintenance of seed quality after seeds had been subjected to dry conditions for the purpose of after-ripening was species-dependent. Interestingly, only seed quality of the two upland species, goldenmane tickseed and lanceleaf tickseed, was maintained regardless of the previous after-ripening temperature to which seeds of these species had been subjected. Hence, we suspect that upland tickseed species might have a shelf life greater than 1 year although tickseed seeds have been classified as having a shelf life of less than 1 year if stored under "satisfactory storage conditions" (McDonald, 2005). Banovetz and Scheiner (1994b) reported that seeds of a midwestern ecotype of lanceleaf tickseed remained viable in the soil for up to 13 years. Based on evidence in our study, McDonald's (2005) conclusion is consistent for the two wetland tickseed species.

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