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Soil-seed bank survival in forests of the Southern United States

James S. Meadows · Frank T. Bonner · James D. Haywood

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Abstract We evaluated the longevity of seeds of 12 common woody species buried in fresh condition in the forest floor at three forest locations in Mississippi and Louisiana. Seed samples of each species were retrieved annually for 5 years from each location. Germination and tetrazolium chloride staining tests were conducted on the samples to determine germinative capacity. When averaged across all species, seeds remained viable longer at the Alexandria, Louisiana site than at the two sites in Mississippi. Seeds of the 12 species varied widely in their response to burial. Some species, such as American beautyberry (*Callicarpa americana* L.), muscadine grape (*Vitis rotundifolia* Michx.), and sugarberry (*Celtis laevigata* Willd.), had relatively high germinative capacities (from 33 to 60 percent, depending on species) even after burial in the forest floor for 5 years, whereas other species, such as flowering dogwood (*Cornus florida* L.) and yaupon (*Ilex vomitoria* Ait.), had very low germinative capacities (less than 6 percent) by the end of the first year after burial. Species were classified into five groups based on their similarity of response.

Keywords Seed viability · Buried seed · Germinative capacity · Southern hardwoods · Woody shrubs

J. S. Meadows (✉)
USDA Forest Service, Southern Research Station, P.O. Box 227, Stoneville, MS 38776, USA
e-mail: smeadows01@fs.fed.us

F. T. Bonner
USDA Forest Service, Southern Research Station, 310 Thompson Hall, Mississippi State, MS 39762, USA

J. D. Haywood
USDA Forest Service, Southern Research Station, Alexandria Forestry Center, 2500 Shreveport Highway, Pineville, LA 71360, USA

Introduction

The seed bank is the collection of viable seeds present on or within the soil and associated litter (Simpson et al. 1989). It is vital to the regeneration of many plant communities. Renewed interest in restoration and management of southern forest ecosystems has identified seed banks as potentially important components of stand dynamics. Knowledge of the seed banks of plant communities can provide an understanding of the factors or processes that drive community dynamics.

Seed bank composition and dynamics have been described in northern hardwood forests (Tierney and Fahey 1998), Allegheny hardwood forests (Hanlon et al. 1998), southern Appalachian hardwood forests (Schiffman and Johnson 1992), and central hardwood forests (Roberts and Vankat 1991). In one of the few studies conducted in southern forests, Titus (1991) described the species composition of the seed bank beneath a floodplain swamp in Florida dominated by Carolina ash (*Fraxinus caroliniana* Mill.). Seeds of most of the dominant tree species in the stand were not found in the seed bank, but the contribution of the seed bank to the species composition and structure of the forest canopy was difficult to assess in this short-term study.

These studies did not assess the longevity of seeds found in the soil or forest litter. However, Haywood (1994) evaluated seed viability after storage under litter and burial in mineral soil over a 5-year period on an upland hardwood site and on a recently clearcut longleaf pine (*Pinus palustris* Mill.) site in central Louisiana. In another study that assessed survival of buried seeds in southern forests, Bonner and Summerville (1999) reported that about 50 percent of buried Atlantic white-cedar (*Chamaecyparis thyoides* (L.) B.S.P.) seeds survived for 1 year in the forest floor and about 6 percent survived for 2 years. It is generally believed that the high temperatures and high moisture conditions found in southern forests are not conducive to retention of viability of seeds found in the forest floor, although Haywood (1994) reported that American beautyberry (*Callicarpa americana* L.), oneflower hawthorn (*Crataegus uniflora* Muenchh.), shining sumac (*Rhus copallina* L.), and summer grape (*Vitis aestivalis* Michx.) seeds still germinated after 5 years of field storage. Our study was conducted to broaden our knowledge of the longevity of seeds of several common woody species buried in fresh condition in the forest floor at three locations in Mississippi and Louisiana.

Methods

Twelve woody species common to southern forests were selected for study (Table 1). Approximately 8,000 fresh seeds of each species were collected in Mississippi and Louisiana and shipped by overnight express delivery service to the USDA Forest Service's Forest Tree Seed Laboratory in Starkville, Mississippi for cleaning and initial testing. Four samples of 25 seeds each were used to perform initial tests for each species. Two samples per species were used to conduct tetrazolium chloride (TZ) staining tests, as described by Bonner et al. (1994), and two samples per species were used to conduct standard germination tests. Because of seed dormancy and the long stratification periods required for most of the species, we were unable to complete germination tests prior to the scheduled time of burial of the remaining seed. Consequently, TZ staining tests were used to estimate initial germinative capacity of all species except green ash (*Fraxinus pennsylvanica* Marsh.) and sweetgum (*Liquidambar styraciflua* L.). Because dormant seeds often do not germinate during standard germination tests, results from the TZ staining tests were generally higher

Table 1 Common and scientific names of species evaluated in this study

Common name	Scientific name	Species code
American beautyberry	*Callicarpa americana* L.	AMB
American hornbeam	*Carpinus caroliniana* Walt.	AMH
Boxelder	*Acer negundo* L.	BXE
Flowering dogwood	*Cornus florida* L.	DWD
Green ash	*Fraxinus pennsylvanica* Marsh.	GRA
Muscadine grape	*Vitis rotundifolia* Michx.	MUS
Sassafras	*Sassafras albidum* (Nutt.) Nees	SAS
Southern bayberry	*Myrica cerifera* L.	SBB
Sugarberry	*Celtis laevigata* Willd.	SUG
Shining sumac	*Rhus copallina* L.	SUM
Sweetgum	*Liquidambar styraciflua* L.	SWG
Yaupon	*Ilex vomitoria* Ait.	YAU

than the results from the germination tests. We believed that TZ values more accurately estimated initial seed viability and therefore used those values to represent initial germinative capacity in 10 of the 12 species. Results from the germination tests were used to estimate initial germinative capacity in green ash and sweetgum.

All seed samples were prepared as described below at the Forest Tree Seed Laboratory and were shipped to each of three locations for study installation: (1) the J. K. Johnson Tract of the Palustris Experimental Forest in Rapides Parish near Alexandria, Louisiana (31°10′ N, 92°40′ W); (2) the Talking Warrior Unit of the Mississippi State University School Forest in Oktibbeha County near Starkville, Mississippi (33°20′ N, 88°51′ W); and (3) the Delta Experimental Forest in Washington County near Stoneville, Mississippi (33°28′ N, 90°55′ W). Ten plots were established at each of the three locations. Plots within each location were not distributed across the entire site, but rather were established within areas generally smaller than 0.1 ha.

The Alexandria site was a 12-year-old loblolly pine (*Pinus taeda* L.) stand that contained about 3,000 trees/ha and 37 m^2/ha of basal area. The understory was nearly devoid of vegetation, but the forest floor was covered with a bed of pine litter about 5 cm thick. The Starkville site was a mature bottomland hardwood stand that consisted primarily of water oak (*Quercus nigra* L.) and sweetgum. The Stoneville site was a 55-year-old bottomland hardwood stand that contained about 500 trees/ha and 30 m^2/ha of basal area. Species composition at the Stoneville site was primarily green ash, sugarberry (*Celtis laevigata* Willd.), and eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.).

Each sample consisted of 50 seeds of a single species sealed in a nylon mesh pouch. At each of the ten plots at each location, five sample pouches of each species were buried in a single layer and covered with a layer of loose soil followed by a layer of litter to a depth of 2.5 cm. The buried samples at each plot were covered with 0.6-cm mesh hardware-cloth frames secured with metal pins to prevent rodent predation. All plots were installed in January 1993.

One sample pouch of each species was retrieved annually for 5 years from each plot at each location beginning in January 1994. On each sampling date, samples were shipped by overnight express delivery service to the Forest Tree Seed Laboratory in Starkville, Mississippi for cleaning and for germination and TZ staining tests. Beginning with the January 1994 samples and continuing through the end of the study with the January 1998 samples, germination tests to determine germinative capacity were conducted on all species except southern bayberry (*Myrica cerifera* L.), American hornbeam (*Carpinus* *caroliniana* Walt.), shining sumac, and yaupon (*Ilex vomitoria* Ait.). Because these four species continued to exhibit seed dormancy, TZ staining tests were used to estimate germinative capacity of the buried seed. We used TZ staining tests to estimate germinative capacity of the 1994 samples of southern bayberry, the 1994 and 1995 samples of American hornbeam, and the 1994, 1995, and 1996 samples of both shining sumac and yaupon. Germination tests were conducted on the 1997 and 1998 samples of all species. All TZ staining tests were conducted according to procedures outlined in Bonner et al. (1994). Germination tests were conducted according to either Association of Official Seed Analysts (1988) or International Seed Testing Association (1985) rules for testing seeds, depending on species.

Germinative capacity values for each species at each plot at each location were subjected to an arc sine of square root transformation (Neter and Wasserman 1974) prior to statistical analyses. Two separate statistical analyses were performed on these transformed data. The first test consisted of an analysis of variance for a randomized block design with multiple observations (plots) per location. This analysis was used in an attempt to detect differences among locations and differences among species in mean germinative capacity within each of the 5 years after study establishment. The second statistical analysis was performed separately on each of the 12 species and consisted of an analysis of variance to detect differences in mean germinative capacity among years since burial. This set of tests allowed us to evaluate the effect of time since burial on the germinative capacity of each species. Significance tests in all statistical analyses were conducted at the $\alpha=0.05$ level of probability. Duncan's New Multiple Range Test was used to separate means within each statistical analysis.

Results and discussion

Initial values for germinative capacity of some species prior to burial were quite low (Table 2). Germinative capacity values of less than 50 percent were observed for seed samples of flowering dogwood (*Cornus florida* L.), muscadine grape (*Vitis rotundifolia* Michx.), shining sumac, and yaupon. Seeds of all four of these species exhibit some form

Table 2 Seed source and initial germinative capacity, in percent, of species prior to seed burial in the forest floor

Species	Seed source	Germinative Capacity	Test
American beautyberry	Starkville	69	TZ
American hornbeam[a]	Starkville	–	–
Boxelder	Stoneville	59	TZ
Flowering dogwood	Starkville	26	TZ
Green ash	Stoneville	74	G
Muscadine grape	Stoneville	27	TZ
Sassafras	Alexandria	54	TZ
Southern bayberry	Alexandria	84	TZ
Sugarberry	Stoneville	77	TZ
Shining sumac	Alexandria	43	TZ
Sweetgum	Stoneville	80	G
Yaupon	Alexandria	33	TZ

Germinative capacity is based on either germination (G) tests or tetrazolium chloride (TZ) staining tests. All percentages are based on filled seeds, not total seeds, in duplicate, 25-seed samples per species

[a]All seeds were inadvertently used in plot installation, leaving none for initial tests

of seed dormancy. For example, seeds of flowering dogwood contain dormant embryos that often reduce germinative capacity (Brinkman 1974a). Seed dormancy in many grape species can only be broken after long periods of stratification (Bonner and Crossley 1974). Dormancy in seeds of shining sumac is due to a hard, impervious seedcoat that inhibits and delays germination (Brinkman 1974b). Yaupon seeds exhibit a deep dormancy caused by both a hard endocarp surrounding the seedcoat and an immature, dormant embryo, which results in extremely retarded germination that is commonly delayed for as much as 16 months but may require up to 3 years for completion (Bonner 1974b). Initial germinative capacity of American hornbeam could not be determined because all seeds were inadvertently used in plot installation, leaving none for initial germination or tetrazolium chloride staining tests.

Mean germinative capacity, averaged across all 12 species, did not differ significantly among the three locations at the end of the first year after seed burial (Table 3). Germinative capacity dropped off slightly during the second year and then declined considerably during the third year at both the Starkville and Stoneville bottomland hardwood sites, but was significantly higher at the Alexandria upland pine site. Germinative capacity of seeds buried at the Starkville and Stoneville sites averaged less than 10 percent at the end of the fourth and fifth years after burial. From the end of the second year after burial to the end of the study, germinative capacity remained significantly higher at the Alexandria site than at the Starkville and Stoneville sites. Perhaps differences in soil moisture regime or soil chemical condition between the two bottomland hardwood sites and the upland pine site influenced the longevity of seed viability in the soil-seed bank. The continuous presence of foliage and the relatively thick layer of pine litter on the forest floor may have also protected the seeds buried at the Alexandria upland pine site and therefore may have led to environmental conditions more conducive to increased longevity of seed viability in the soil.

A significant location-by-species interaction was detected for germinative capacity within each of the 5 years of burial (Table 4). For most of the species tested in this study, the pattern of decreasing germinative capacity over time was similar across the three locations. For example, germinative capacity of shining sumac seeds remained high (greater than 55 percent) during the first 2 years of burial in the forest floor at all three locations, but dropped to less than 3 percent at each of the three locations during subsequent years of burial.

In contrast, four species—American beautyberry, American hornbeam, muscadine grape, and sugarberry—exhibited patterns of decreasing germinative capacity over time that differed from one location to another (Table 4). In some cases, there appeared to be a relationship between the ability of a species to maintain relatively high values for

Table 3 Mean germinative capacity, in percent, of seeds, averaged across all species, after burial in the forest floor for 5 years at three locations in Mississippi (MS) and Louisiana (LA)

Location	Years since burial				
	1	2	3	4	5
Alexandria, LA	32.4 (3.3) a	35.0 (3.8) a	26.6 (3.9) a	9.7 (2.6) a	21.6 (3.6) a
Starkville, MS	35.5 (3.2) a	23.2 (3.3) c	12.4 (2.7) b	5.7 (1.8) b	6.0 (1.9) b
Stoneville, MS	33.5 (3.1) a	29.1 (3.1) b	3.9 (1.3) c	2.1 (0.7) c	5.5 (1.8) b
Mean	33.8	29.0	13.9	5.7	10.8

The standard error of each mean is enclosed in parentheses. Means within years since burial followed by the same letter are not significantly different at the 0.05 level of probability

Table 4 Mean germinative capacity, in percent, of seeds of 12 species after burial in the forest floor for 5 years at each of three locations: Alexandria, Louisiana (AL), Starkville, Mississippi (SK), and Stoneville, Mississippi (SV)

Species	Years since burial														
	1			2			3			4			5		
	AL	SK	SV	AL	SK	SV	AL	SK	SV	AL	SK	SV	AL	SK	SV
AMB	71	90	77	92	82	86	92	75	0	89	37	2	86	39	57
AMH	62	75	76	62	18	60	17	0	6	4	0	0	0	0	0
BXE	22	10	9	0	3	0	0	0	0	0	0	0	0	0	0
DWD	11	4	1	0	0	0	0	0	0	0	0	0	0	0	0
GRA	19	26	18	3	0	0	0	0	0	0	0	0	0	0	0
MUS	75	—	76	84	—	56	94	—	18	0	—	0	83	—	9
SAS	0	5	3	11	10	24	26	0	0	0	0	0	8	0	0
SBB	21	10	9	22	3	1	15	0	0	0	0	0	0	1	0
SUG	28	60	34	73	76	53	75	62	22	22	25	22	79	25	0
SUM	67	64	78	73	62	56	0	1	0	0	0	2	0	1	0
SWG	17	39	20	1	1	12	0	0	0	0	0	0	0	0	0
YAU	0	7	1	0	0	0	0	0	0	0	0	0	0	0	0

Species codes are listed in Table 1

germinative capacity and the site type on which that species is most commonly found. For example, germinative capacity of American beautyberry, a medium-sized shrub most commonly found on upland sites and on minor streambottom sites, remained very high throughout the 5 years of burial at the Alexandria location, an upland pine site, declined somewhat during the fourth and fifth years of burial at the Starkville location, a bottomland site within the floodplain of a small stream, but was erratic at the Stoneville location, a bottomland site within the floodplain of the Mississippi River. In other cases, there appeared to be no relationship between germinative capacity and site suitability. For example, germinative capacity of sugarberry, a very common tree species in the floodplain of the Mississippi River, was consistently lower at the Stoneville location than at the other two locations during most years of the study.

When averaged across all three locations, seeds of the 12 species evaluated in this study varied greatly in their response to burial (Table 5). Some species were able to maintain relatively high levels of germinative capacity even after burial for 5 years, whereas

Table 5 Mean germinative capacity, in percent, of seeds of each of 12 species for each of the 5 years of burial in the forest floor

Year	Species											
	AMB	AMH	BXE	DWD	GRA	MUS	SAS	SBB	SUG	SUM	SWG	YAU
1	80 a	71 a	14 a	5 a	21 a	76 a	3 b	13 a	41 b	70 a	26 a	3 a
2	86 a	46 b	1 b	0 b	1 b	69 a	15 a	8 b	67 a	64 a	5 b	0 b
3	54 bc	7 c	0 b	0 b	0 b	54 b	8 b	5 c	52 b	0 b	0 c	0 b
4	41 c	1 c	0 b	0 b	0 b	0 c	0 b	0 d	23 c	1 b	0 c	0 b
5	60 b	0 c	0 b	0 b	0 b	44 b	3 b	0 d	33 c	0 b	0 c	0 b

Values are averaged across three locations in Mississippi and Louisiana. Means within a species followed by the same letter are not significantly different at the 0.05 level of probability. Species codes are listed in Table 1 germinative capacity of other species rapidly declined shortly after burial. Species were classified into five groups based on their similarity of response.

The first group of species maintained relatively high levels of germinative capacity throughout the 5 years of burial and consisted of American beautyberry, muscadine grape, and sugarberry (Fig. 1). Germinative capacity of all three species generally declined gradually as length of burial time increased, but remained above 30 percent even after 5 years. Haywood (1994) also reported high germination rates for American beautyberry through 5 years of storage under forest canopy. Initial germinative capacity of muscadine grape seeds was only 27 percent (Table 2), but germinative capacity after the first year of burial was 76 percent. The internal seed dormancy exhibited by muscadine grape may have affected the initial TZ staining test to the extent that the test was inadequate to accurately assess initial germinative capacity of muscadine grape. The lack of viability observed in muscadine grape seeds after 4 years of burial cannot be explained. Haywood (1994) found that buried seeds of a similar species, summer grape, remained viable for 5 years. The ability of sugarberry to produce large seed crops nearly every year (Kennedy 1990) combined with its ability to maintain high germinative capacity for up to 5 years in the forest floor ensures that sugarberry will remain a stable component of the regeneration layer of most southern bottomland forests.

The second group of species exhibiting similar responses to seed burial consisted of American hornbeam and shining sumac. Seeds of these two understory species maintained high germinative capacity for up to 2 years of burial in the forest floor, but germinative capacity dropped to very low levels during subsequent years (Fig. 2). Retention of seed viability for up to 2 years in the forest floor may at least partially compensate for American hornbeam's ability to produce large seed crops only every 3–5 years (Rudolf and Phipps 1974). On the other hand, shining sumac is known to produce large seed crops nearly every year. Similar to our

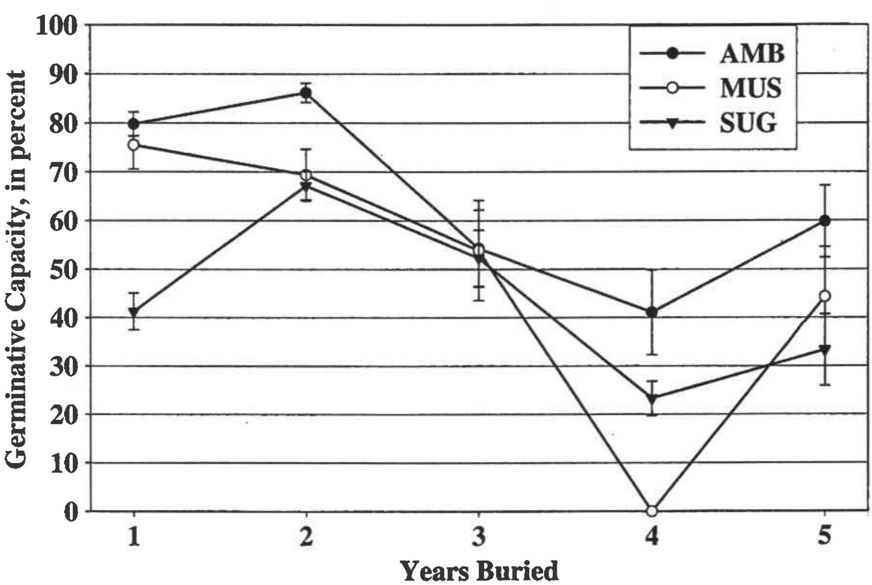

Fig. 1 Germinative capacity, averaged across three locations in Mississippi and Louisiana, of seeds of American beautyberry (AMB), muscadine grape (MUS), and sugarberry (SUG) after burial in the forest floor for up to 5 years. Error bars represent standard error of the mean

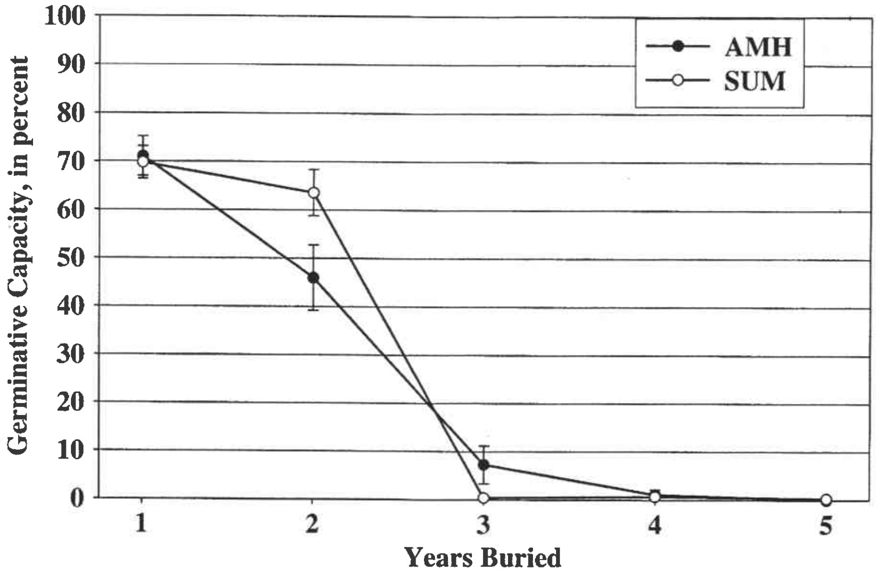

Fig. 2 Germinative capacity, averaged across three locations in Mississippi and Louisiana, of seeds of American hornbeam (AMH) and shining sumac (SUM) after burial in the forest floor for up to 5 years. Error bars represent standard error of the mean

observations, Haywood (1994) also found that germinative capacity of buried shining sumac seeds was highest during the first 2 years, but decreased after that. Seeds of other species of sumac are known to remain viable for up to 10 years in the forest floor (Brinkman 1974b).

The third group of species consisted of sassafras (*Sassafras albidum* (Nutt.) Nees) and southern bayberry. Both species exhibited high initial germinative capacity (prior to burial) that declined rapidly during the first year of burial in the forest floor; germinative capacity of both species remained low for up to 3 years in the forest floor (Fig. 3). Germinative capacity of seeds buried more than 3 years was very low, but some seeds germinated even after 5 years in the forest floor. Germinative capacity of buried southern bayberry seeds has been reported to be the highest during the first year (Haywood 1994). On the other hand, sassafras seeds have been reported to remain viable in the forest floor for up to 6 years in New England hardwood forests (Wendel 1977) and for up to 4 years buried in an upland hardwood forest in Louisiana (Haywood 1994), but we found only very low germinative capacity (3 percent) of sassafras seeds after 5 years in the forest floor. The high temperatures and high moisture conditions found at our sites in the South likely contributed to a more rapid decrease in germinative capacity and may have prevented the long-term retention of viability of sassafras seeds reported by Wendel (1977) in New England.

For the fourth group of species, which consisted of boxelder (*Acer negundo* L.), green ash, and sweetgum, germinative capacity was moderate after the first year of burial in the forest floor, but dropped significantly thereafter (Fig. 4). In fact, no seeds of any of these three species were able to germinate beyond the second year of burial in the forest floor. Haywood (1994) found very high germinative capacity of buried sweetgum seeds after the first year in the forest floor, but almost none beyond the first year. All three species produce relatively large seed crops nearly every year (Bonner 1974a, c; Olson and Gabriel 1974), so that retention of viability of seed stored in the forest floor is not a necessary survival mechanism. Bonner (1974a) reported that seeds of green ash may lie dormant in the litter

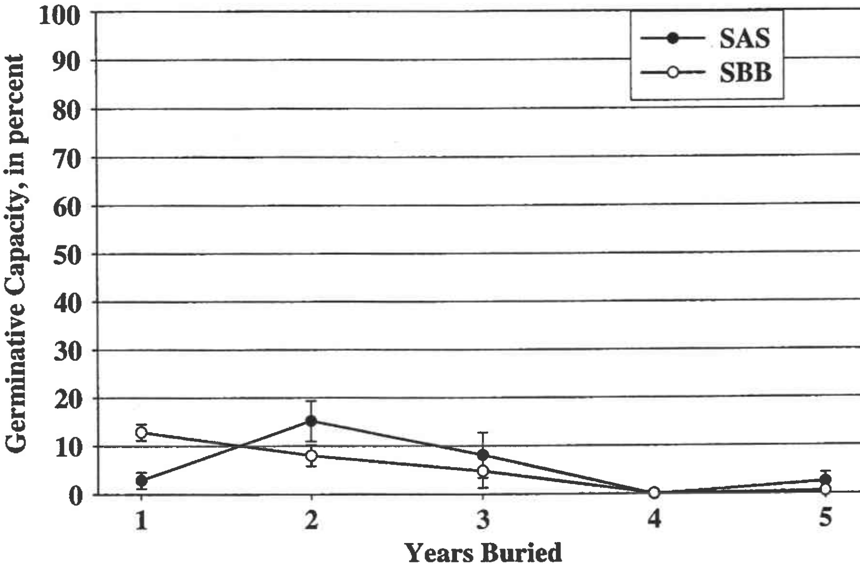

Fig. 3 Germinative capacity, averaged across three locations in Mississippi and Louisiana, of seeds of sassafras (SAS) and southern bayberry (SBB) after burial in the forest floor for up to 5 years. Error bars represent standard error of the mean

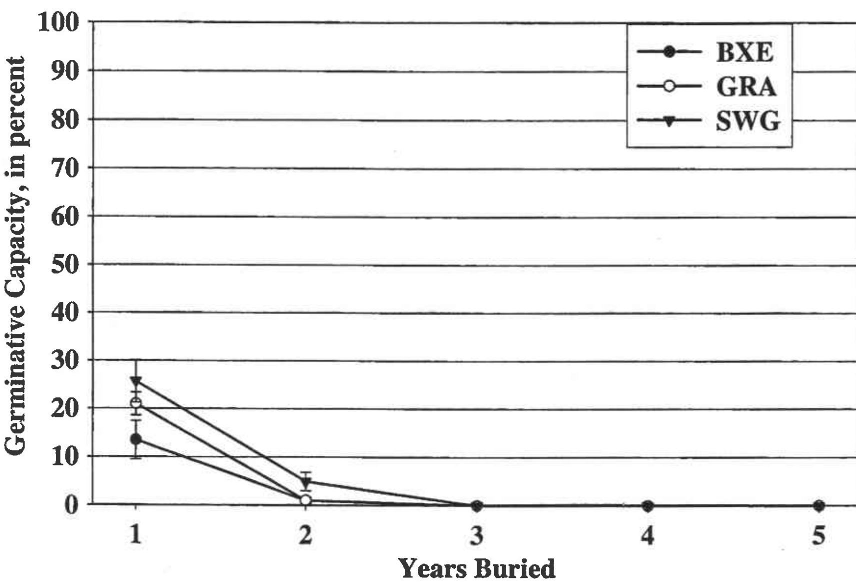

Fig. 4 Germinative capacity, averaged across three locations in Mississippi and Louisiana, of seeds of boxelder (BXE), green ash (GRA), and sweetgum (SWG) after burial in the forest floor for up to 5 years. Error bars represent standard error of the mean

for several years before germinating, but our results do not substantiate this assertion. All three of these species have relatively soft seedcoats, which may have been a factor in the rapid loss of viability after the first year of burial in the forest floor.

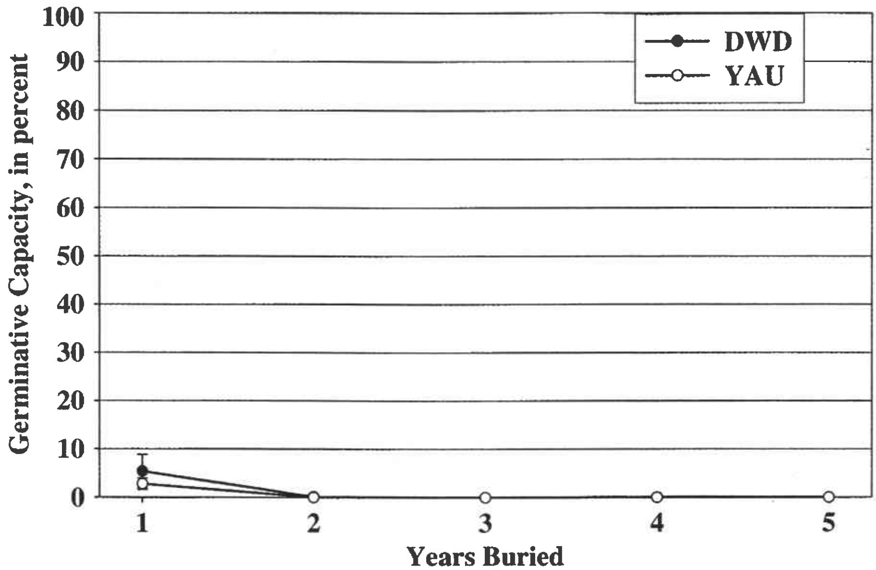

Fig. 5 Germinative capacity, averaged across three locations in Mississippi and Louisiana, of seeds of flowering dogwood (DWD) and yaupon (YAU) after burial in the forest floor for up to 5 years. Error bars represent standard error of the mean

The final group of species consisted of flowering dogwood and yaupon. Both of these species are characterized by deeply dormant seeds that commonly exhibit delayed germination and low rates of germinative capacity. In fact, only a very low percentage (less than 6 percent) of seeds of both species germinated after 1 year of burial in the forest floor; no seeds of either species germinated in subsequent sampling years (Fig. 5). Flowering dogwood generally produces large seed crops nearly every year, but excessive heat has been reported to severely reduce germination (Brinkman 1974a).

Our results indicate that there is wide variation in the viability of seeds of different species stored for long periods in the forest floor. Overall site conditions may be an important factor because seeds generally remained viable longer at the upland pine site in Louisiana than at the two bottomland hardwood sites in Mississippi. It is also conceivable that the close proximity of seeds in the pouches could have influenced germinative capacity during the study, but clumped distributions of seeds often occur during natural primary and secondary dispersal.

Species whose seeds are capable of long-term soil-seed bank storage, such as American beautyberry, muscadine grape, and sugarberry, have a reproductive advantage over other species. However, seed storage in the forest floor is only one of many factors that affect the ability of a species to reproduce. Other factors include frequency of large seed crops, seed dissemination, germination, seed predation, reliance on vegetative propagation, and many others. A more complex, holistic research approach is needed to fully understand the reproductive strategies of woody species in southern forests.

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References

Association of Official Seed Analysts (1988) Rules for testing seeds. J Seed Technol 12:1–109

Bonner FT (1974a) *Fraxinus* Ash. In: Schopmeyer CS (Tech Coord) Seeds of woody plants in the United States. USDA Forest Serv., Washington, DC. Agric. Handb. 450 pp 411–416

Bonner FT (1974b) *Ilex* L. Holly. In: Schopmeyer CS (Tech Coord) Seeds of woody plants in the United States. USDA Forest Serv., Washington, DC. Agric. Handb. 450 pp 450–453

Bonner FT (1974c) *Liquidambar styraciflua* L. Sweetgum. In: Schopmeyer CS (Tech Coord) Seeds of woody plants in the United States. USDA Forest Serv., Washington, DC. Agric. Handb. 450 pp 505–507

Bonner FT, Crossley JA (1974) *Vitis labrusca* L. Fox grape. In: Schopmeyer CS (Tech Coord) Seeds of woody plants in the United States. USDA Forest Serv., Washington, DC. Agric. Handb. 450 pp 853–854

Bonner FT, Summerville KO (1999) Production and quality of Atlantic white-cedar seed in coastal North Carolina. In: Shear TH, Summerville KO (eds) Proceedings: Atlantic white-cedar: Ecology and Management Symposium. USDA Forest Serv., South. Res. Sta., Asheville, North Carolina. Gen. Tech. Rep. SRS-27 pp 76–79

Bonner FT, Vozzo JA, Elam WW, Land SB Jr. (1994) Tree seed technology training course. Instructor's manual. USDA Forest Serv., South. Forest Exp. Sta., New Orleans, Louisiana. Gen. Tech. Rep. SO-106. 160 p

Brinkman KA (1974a) *Cornus* L. Dogwood. In: Schopmeyer CS (Tech Coord) Seeds of woody plants in the United States. USDA Forest Serv., Washington, DC. Agric. Handb. 450 pp 336–342

Brinkman KA (1974b) *Rhus* L. Sumac. In: Schopmeyer CS (Tech Coord) Seeds of woody plants in the United States. USDA Forest Serv., Washington, DC. Agric. Handb. 450 pp 715–719

Hanlon TJ, Williams CE, Moriarity WJ (1998) Species composition of soil seed banks of Allegheny Plateau riparian forests. J Torrey Bot Soc 125:199–215

Haywood JD (1994) Seed viability of selected tree, shrub, and vine species stored in the field. New For 8:143–154

International Seed Testing Association (1985) International rules for seed testing. Seed Sci Technol 13:299–520

Kennedy HE Jr. (1990) *Celtis laevigata* Willd. Sugarberry. In: Burns RM, Honkala BH (Tech Coords) Silvics of North America, vol 2. Hardwoods. USDA Forest Serv., Washington, DC. Agric. Handb. 654 pp 258–261

Neter J, Wasserman W (1974) Applied linear statistical models. Richard D. Irwin, Inc., Homewood, Illinois, 842 p

Olson DF Jr, Gabriel WJ (1974) *Acer* L. Maple. In: Schopmeyer CS (Tech Coord) Seeds of woody plants in the United States. USDA Forest Serv., Washington, DC. Agric. Handb. 450 pp 187–194

Roberts TL, Vankat JL (1991) Floristics of a chronosequence corresponding to old field-deciduous forest succession in southwestern Ohio. II. Seed banks. Bull Torrey Bot Club 118:377–384

Rudolf PO, Phipps H (1974) *Carpinus* L. Hornbeam. In: Schopmeyer CS (Tech Coord) Seeds of woody plants in the United States. USDA Forest Serv., Washington, DC. Agric. Handb. 450 pp 266–268.

Schiffman PM, Johnson WC (1992) Sparse buried seed bank in a southern Appalachian oak forest: implications for succession. Am Midl Nat 127:258–267

Simpson RL, Leck MA, Parker VT (1989) Seed banks: general concepts and methodological issues. In: Leck MA, Parker VT, Simpson RL (eds) Ecology of soil seed banks. Academic Press, San Diego, pp 3–8

Tierney GL, Fahey TJ (1998) Soil seed bank dynamics of pin cherry in a northern hardwood forest, New Hampshire, USA. Can J For Res 28:1471–1480

Titus JH (1991) Seed bank of a hardwood floodplain swamp in Florida. Castanea 56:117–127

Wendel GW (1977) Longevity of black cherry, wild grape, and sassafras seed in the forest floor. USDA Forest Serv., Northeast. Forest Exp. Sta., Upper Darby, Pennsylvania. Res. Pap. NE-375. 6 p