# Potential carry-over of seeds from 11 common shrub and vine competitors of loblolly and shortleaf pines

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**Abstract:** Many of the competitors of the regeneration of loblolly and shortleaf pines (*Pinus taeda* L. and *Pinus echinata* Mill., respectively) develop from seed disseminated on the site after reproduction cutting or from the seed bank. To evaluate the potential carry-over of the seeds from 11 shrub and vine competitors of these two important southern pines, we designed packets so that fruits could be deposited on the forest floor and subsequently extracted over a 3-year period. After extraction, repeated cycles of 60 days of germination testing followed by 60 days of stratification were conducted over a maximum of 42 months to determine the potential for seed carry-over and the germination characteristics of the species. Seeds of privet *(Ligustrum vulgare* L.) showed no viability after the first winter of field storage, while seeds of rattan vine *(Berchemiu scandens* (Hill) K. Koch) and Japanese honeysuckle *(Loniceru japonica* Thunb.) had low viability (1–3%) after the third year. In contrast, seeds of smooth sumac (*Rhus glabra* L.), devils-walkingstick *(Arulia spinosu* L.), pepper vine (*Ampelopsis arborea* (L.) Koehne), and blackberry (*Rubus argutus* Link) were moderate in viability (7-19%) after the third year of field storage, while seeds of beautyberry (*Callicarpa americana* L.), common greenbrier (*Smilax rotundifolia* L.), and summer grape *(Vitis aestivulis* Michx.) showed a high viability (31–55%). Cumulative germination of seeds of deciduous holly (*Ilex decidua* Walt.) was greater after 3 years of field storage (8%) than after only 1 year (4%); for the first removal from field storage, no germination occurred until the ninth germination cycle. Results indicate that new seedlings of some species of shrubs and vines rely mostly on seeds dispersed shortly before or after disturbance, while seedlings of other species appear to develop from seeds that have been stored for long periods in the seed bank. Results of this study can be useful in developing ecologically sound strategies for controlling competing vegetation in forest stands of the southeastern United States.

**Résumé** : Plusieurs plantes qui entrent en competition avec la regeneration du pin à encens (*Pinus taeda* L.) et du pin à courtes feuilles (*Pinus echinatu* Mill.) se developpent à partir de graines disséminées sur le site apres une coupe de regeneration ou à partir de la banque de graines. Afin d'évaluer la persistance potentielle des graines de 11 arbustes et vignes qui entrent en competition avec ces deux pins importants du Sud, nous avons créé des amoncellements de telle sorte que les fruits puissent se deposer sur le parterre forestier et être subséquemment extraits sur une période de 3 ans. Après extraction, des cycles répétés de 60 jours d'essais de germination suivis de 60 jours de stratification ont été effect& sur un maximum de 42 mois pour determiner la persistance potentielle des graines et les caractéristiques germinatives de chaque espèce. Les graines du troène commun *(Ligustrum vulgare* L.) n'étaient pas viables apres un premier hiver passe sur le terrain tandis que les graines du rotang *(Berchemiu scandens* (Hill) K. Koch) et du chèvrefeuille du Japon *(Loniceru japonica* Thunb.) avaient une faible viabilité (1–3%) apres la troisième année. Par contre, les graines du sumac glabre (*Rhus glabra* L.), de l'aralie Cpineuse *(Arulia spinosu* L.), de la vigne arborescente (*Ampelopsis arborea* (L.) Koehne) et de la ronce Cpineuse (*Rubus argutus* Link) Ctaient modérément viables (7-19%) apres la troisième année sur le terrain tandis que les graines du callicarpe d'Amérique (*Callicarpa americana* L.), de la smilax à fleurs rondes (*Smilax rotundifolia* L.) et de la vigne d'été *(Vitis aestivalis* Michx.) avaient une forte viabilité (31–55%). La germination cumulative des graines de houx décidu (*Ilex deciduu* Walt.) Ctait meilleure aprbs 3 ans sur le terrain (8%) qu'après 1 an (4%); avec la premiere extraction, il n'y a eu aucune germination avant le neuvibme cycle de germination. Les résultats indiquent que les nouveaux semis de certaines espèces d'arbustes et de vignes comptent principalement sur les graines dispersées peu de temps avant ou apres une perturbation, tandis que les semis d'autres espèces semblent se developper à partir de graines entreposées depuis longtemps dans la banque de graines. Les résultats de cette etude peuvent Ctre utiles pour mettre au point des strategies écologiquement valables pour contrôler la végétation compétitrice dans les peuplements forestiers du sud-est des États-Unis.

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## Introduction

Loblolly and shortleaf pines (*Pinus taeda* L. and *Pinus echinatu* Mill., respectively) are widely distributed in the southeastern United States and are well known for their commercial importance and their ability to be regenerated successfully in numerous ways. In many studies of different natural reproduction methods, we have observed a fairly common group of hardwood, shrub, and vine competitors to loblolly and shortleaf pines over a wide array of different stand and site conditions (Cain and Barnett 1994; Shelton and Murphy 1994; Cain and Shelton 2001). Most hardwood competitors appear to develop from existing rootstocks that became established in the stand before reproduction cutting. However, much of the shrub and vine competition appears to develop from seeds either stored in the seed bank or disseminated on the site after disturbance (Shelton 1998).

In forest stands, the seed bank includes seeds stored in both the forest floor and the mineral soil. The ability of seeds to remain viable in the seed bank over many years is well known for some species. Common examples of trees include yellow-poplar (*Liriodendron tulipifera* L.) (Clark and Boyce 1964), hackberry (*Celtis occidentalis* L.), white ash (*Fruxinus americana* L.) (Clark 1962), black cherry (*Prunus serotina* Ehrh.) (Wendel 1977), and sassafras (*Sassafras albidum* (Nutt.) Nees) (Haywood 1994). Considerable research has been conducted on the longevity of seeds in the seed bank for herbaceous species that compete with agronomic crops (e.g., Darlington and Steinbauer 1961; Egley and Chandler 1983). However, much less is known about the carry-over of seeds from the shrubs and vines that compete with tree regeneration during stand establishment. Wendel (1977) found that some summer grape (*Vitis aestivalis* Michx.) seeds remained viable after 8 years of field storage. Haywood (1994) reported on the seed viability of seven common shrubs and vines in the southeastern United States and found that some southern bayberry (*Myrica cerifera* L.) and tree sparkleberry (*Vaccinium arboreum* Marsh.) seeds were viable after 4 years, while some seeds of beautyberry (*Callicarpa americana* L.), hawthorn (*Crataegus uniflora* Muenchh.), shining sumac (*Rhus copallina* L.), and summer grape were still viable after 5 years.

The seed bank is an important element of the regeneration ecology of species with seeds that remain viable. The seed bank is a dynamic reservoir for seeds (Chambers and MacMahon 1994). Inputs come from dispersal of current seed crops, and losses occur because of reduced viability through senescence, consumption by seed predators, death from pathogens, and germination. Because of its dynamic nature, the seed bank is difficult to study. Farmer (1997) describes several well-established methods used to extract or germinate existing seeds in the seed bank. Although these methods indicate the current contents of the seed bank, they do not enable determining seed carry-over, because seed age is not known. To track seeds of a known age, researchers have devised a clever array of different devices that enable recovery of seeds from the forest floor or soil at some later point in time (Clark and Boyce 1964; Wendel 1977; Egley and Chandler 1983). In this paper, we investigated the potential carry-over and germination characteristics of 11 common early competitors of loblolly and shortleaf pines by depositing packets containing their fruits in the forest floor and tracking subsequent germination over 3 years of field slorage.

## Methods

### Species studied

Eleven species were selected for study based on *(i)* our experience that they were common competitors to loblolly and shortleaf pines in the West Gulf Coastal Plain (Cain and Barnett 1994; Shelton and Murphy 1994; Cain and Shelton 2001), and *(ii)* their fruit production was good during the summer and fall of 1996 when the study began. Four tall shrubs or small trees were selected: deciduous holly (*Ilex decidua* Walt.), devils-walkingstick (*Aralia spinosa* L.), privet (*Ligustrum vulgare* L.), and smooth sumac (*Rhus glabra* L.). These species normally begin fruiting when about 2 m tall, and they attain a maximum height of about 7 to 8 m (Radford et al. 1968). Two species of low shrubs were selected: beautyberry and blackberry (*Rubus argutus* Link); these species reach heights of about 2 m and typically have multiple stems. Stems of blackberry are both erect and arching. The classification of blackberry as a shrub is somewhat arbitrary; it has been classified as a semiwoody plant by some authors and as a vine by others. In this paper, we chose to follow the designation of Radford et al. (1968) and group blackberry with the shrubs. The five vines in this study (common greenbrier (*Smilax rotundifolia* L.), Japanese honeysuckle (*Lonicera japonica* Thunb.), pepper vine (*Ampelopsis arborea* (L.) Koehne), rattan vine (*Berchemiu scandens* (Hill) K. Koch), and summer grape) are classified as being high climbing vines, but Japanese honeysuckle is also described as potentially being a trailing vine (Radford et al. 1968). Privet and Japanese honeysuckle are escaped exotics, while all other species are indigenous to the West Gulf Coastal Plain. The studied species are very common throughout southeastern Arkansas and frequently occur along roadsides and in recently disturbed areas. These species generally occur on both upland and bottomland sites.

Fruits of the studied species are either berries or berrylike drupes, except for smooth sumac which is described as a hairy drupe (Radford et al. 1968; Young and Young 1992). Birds and small mammals are the most important means of dissemination for the studied species (Hunter 1989). Fruit mass varied from as little as 0.02 g/fruit for smooth sumac to as much as 1.56 g/fruit for blackberry (Table 1). With the exception of smooth sumac, fruits had a high moisture content ranging from 160% for common greenbrier to 700% for blackberry. In contrast, fruits of smooth sumac contained only 12% moisture. The number of seeds per fruit was greatest for blackberry (63 seeds/fruit) and smallest for rattan vine, smooth sumac, and privet (1 seed/fruit). The heaviest seeds were from common greenbrier, averaging 50.2 mg/seed, and the lightest seeds were from beautyberry and blackberry, averaging 1.6 mg/seed.

### Study area

The study was located on forest lands of the School of Forest Resources, University of Arkansas at Monticello. The study site is in the West Gulf Coastal Plain at 91°46′W, 33°37′N. Elevation is 98 m with a rolling topography. The

**Table 1.** Mean characteristics of the fruits and seeds of the species tested for potential carry-over in the forest floor

| Life form and species | Fruit mass (g/fruit) | | No. of seeds/fruit | Seed soundness (% of total) | Seed mass (mg) (air dry) | No. of fruit/packet | Placement date in 1996' |
|---|---|---|---|---|---|---|---|
| | Fresh | Ovendry* | | | | | |
| Shrubs | | | | | | | |
| Beautyberry | 0.095 | 0.017 | 3.8 | 88 | 1.6 | 80 | Oct. 11 |
| Blackberry | 1.560 | 0.195 | 63.1 | 89 | 1.6 | 20 | Aug. 13 |
| Deciduous holly | 0.213 | 0.095 | 3.7 | 76 | 10.8 | 50 | Oct. 22 |
| Devils-walkingstick | 0.144 | 0.031 | 4.6 | 74 | 3.9 | 50 | Sept. 30 |
| Privet | 0.143 | 0.045 | 1.0 | 94 | 41.1 | 50 | Dec. 3 |
| Smooth sumac | 0.018 | 0.016 | 1.0 | 71 | 9.5 | 100 | Aug. 13 |
| Vines | | | | | | | |
| Common greenbrier | 0.349 | 0.133 | 2.5 | 100 | 50.2 | 50 | Oct. 11 |
| Japanese honeysuckle | 0.186 | 0.057 | 6.2 | 73 | 3.4 | 50 | Oct. 16 |
| Pepper vine | 0.438 | 0.100 | 2.8 | 90 | 19.5 | 50 | Aug. 13 |
| Rattan vine | 0.150 | 0.047 | 1.0 | 89 | 24.5 | 50 | Nov. 18 |
| Summer grape | 0.141 | 0.049 | 1.2 | 96 | 22.1 | 50 | Sept. 3 |

"At 75°C for 48 h.

'Fruits of all species were collected shortly before their placement date except for blackberry, which were collected during mid-June, air-dried, and stored at 21 °C until placement.

soil is a Sacul loam (clayey, mixed, thermic, Aquic Hapludult), which is a moderately well-drained upland soil with a site index of 24 m for loblolly pine and 21 m for shortleaf pine at 50 years (Larance et al. 1976). The growing season is about 240 days with seasonal extremes being wet winters and dry autumns. Annual precipitation averages 134 cm. The study site was located in a mature stand, principally composed of loblolly and shortleaf pines with a midstory and understory of mixed hardwoods. A mature stand was selected for study, because it represents the stage of development when a buildup of viable seeds within the seed bank could result in competing vegetation after reproduction cutting. Basal area in trees >9 cm diameter at breast height (DBH) averaged 25.7 $m^2$/ha for pines and 6.4 $m^2$/ha for hardwoods; there were also 2.8 $m^2$/ha in hardwoods ≤9 cm DBH. Light intensity at 1.37 m in height averaged 7% of full sunlight at noon during a clear summer day, and the canopy exerted 97% ground coverage.

## Field and laboratory procedures

Mature fruits were collected for each species during 1996 in Ashley and Drew counties, Arkansas, from a minimum of 20 individuals for each species. General ripening dates for fruits were obtained from Schopmeyer (1974), Radford et al. (1968), and Young and Young (1992), but dates were adjusted by local observations. Immediately after collection, fruits were transferred to the laboratory for processing. Fleshy fruits were air-dried until they reached a consistency at which they could be processed without damage. Fruits were weighed after counting the number given in Table 1.

Storage packets were made by uniformly spacing the fruits between two pieces of nylon netting (openings approximately 0.03 x 0.05 mm) and two pieces of fiberglass window screen (openings 1.3 x 1.3 mm) that were held in place by two pieces of 1.3-cm mesh hardware cloth. Packets were devised to protect fruits from predation and to minimize cross contamination from pathogens that may have infected individual fruit. Each packet measured 14 x 15 cm. There were four packets of each species for each of three removal dates (early spring of 1997, 1998, and 1999).

In 1996, fruit-filled packets were placed on top of the forest floor at designated dates (Table 1) inside wire frames that were buried within the soil and forest floor. Fruits were deposited on top of the forest floor to mimic natural dispersal mechanisms. These frames were 0.5 x 0.5 m and made of 0.35cm mesh galvanized hardware cloth. They were designed to protect packets from small mammals and birds. After removal of the existing forest floor by litter and fermentation layers and the surface 5 cm of mineral soil, the fruit-storage frame was positioned within the depression, and the soil surface and forest floor were reconstructed. A top constructed of 1.3-cm mesh hardware cloth was used to cover each frame. Packets were placed in the frames through late summer and autumn as fruits matured (Table 1), and any litter that had fallen on the frame's top was moved to the inside of the frame to cover existing packets in a natural manner. After all packets had been placed, litter was moved to the inside of frames approximately monthly during peak litterfall (October through December) but less frequently thereafter. Sixteen frames were located in a square pattern in the study area with about 30 cm separating adjacent frames. Nine packets could be stored in each frame. The 11 packets representing a replicate for a removal date (i.e., a full complement of the 11 species) were always located in adjacent frames, but the replicates for a removal date were randomly located within the matrix of frames. Frames were installed about 1 month before the first placement of packets so that the soil and forest floor would have ample time to settle.

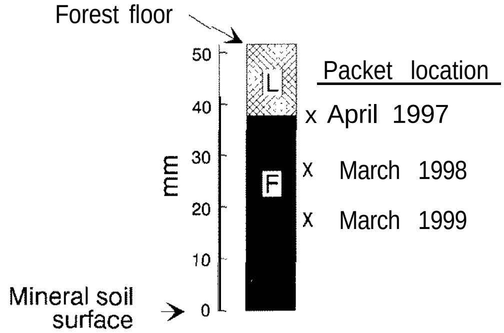
While packets were being constructed for each species, a subsample of fruits was collected to determine dry mass at 75°C. Another subsample of fruits (at least twice the number of fruits in a packet) was obtained to determine the number of seeds per fruit. The fruits were distributed among five subsamples so that variation could be detected. Fruits were weighed and then were macerated by hand under a stream of water using a sieve of the proper size to prevent seed loss. Seeds and the residual pulp were transferred to a glass beaker filled with water and floating (empty) seeds were separated from sinking (filled) seeds. Seeds were counted after drying, and a cut test (Bonner 1974*a*) was conducted to determine if any floating seeds were filled or any sinking seeds were empty. Usually, a total of 50 sinking seeds and 25 floating seeds were cut tested for a species. A 20x microscope was used as an aid when cutting small seeds. Results of the cut test were used to adjust the results of the float test. Overall, the cut test revealed an error rate of 4% for sinking seeds and 2% for floating seeds. The air-dry mass of sinking seeds was determined.

After the specified period of field storage in wire frames, packets were removed for seed extraction on April 4, 1997; March 15, 1998; and March 17, 1999. After removal, the depth of the forest floor from the packet's location to mineral soil was determined for four packets per replicate. Any apparent insect damage to packets was recorded. After removal from packets, the residual fruit material was maceratcd by hand under a stream of water using a sieve of the proper size to prevent seed loss. Seeds and residual material were then transferred to moist, sterile sand in 10 x 10 cm plastic cups with drainage holes. The 60-day germination cycles were conducted with 16 h of full-spectrum fluorescent light and 8 h of dark, and temperature in the germination room was maintained at 21 "C. Gross (1990) considered these conditions to provide peak germination. A seed was considered to have germinated when the seed coat lifted off the sand by three times the seed's length or in the case of common greenbrier, which has hypogeal germination, when the epicotyl was three times the seed's width. After the 60-day germination test, the cups containing seeds were refrigerated at 4°C for 60 days to provide stratification; cups were loosely covered with paper to reduce drying but also to provide good aeration. Alternating germination-stratification cycles have been used by others to provide thorough germination of dormant species (Onaindia and Amezaga 2000). During stratification, cups were watered approximately biweekly. The germination-stratification cycle was repeated 11 times (42 months) for the 1997 removal, nine times (34 months) for the 1998 removal, and six times (22 months) for the 1999 removal.

### Statistical analysis

Percentage germination for each species was calculated from the germination counts and the number of sound seeds, which was estimated from the mass of fruit in each packet and the subsample of fruit that was weighed before seed extraction and float and cut testing. Homogeneity of treatment variances was tested by Levene's test (Levene 1960). When the hypothesis of homogeneity of variance was rejected at $a \leq 0.05$, data were arcsine syuare-root proportion transformed, which provided homogeneity in some cases. For species and germination periods with homogeneous treatment variance, analysis of variance was conducted within each species to detect differences among removal dates for the first, third, and sixth germination cycles. A Kruskal–Wallis test, which is a nonparametric procedure based on treatment ranks, was conducted when homogeneity was not achieved through transformation (Lehmann 1975). Replications for all statistical analyses were the germination of each of the four packets of a species that was removed from field storage at specific dates. Significance was accepted at $\alpha \leq 0.05$.

**Fig.** 1. Approximate location of packets (X) containing fruits at the time of their removal from litter (L) and fermentation (F) layers of the forest floor over a 3-year period. Packets were deposited on top of the forest floor during the late summer and fall of 1996.




## Results

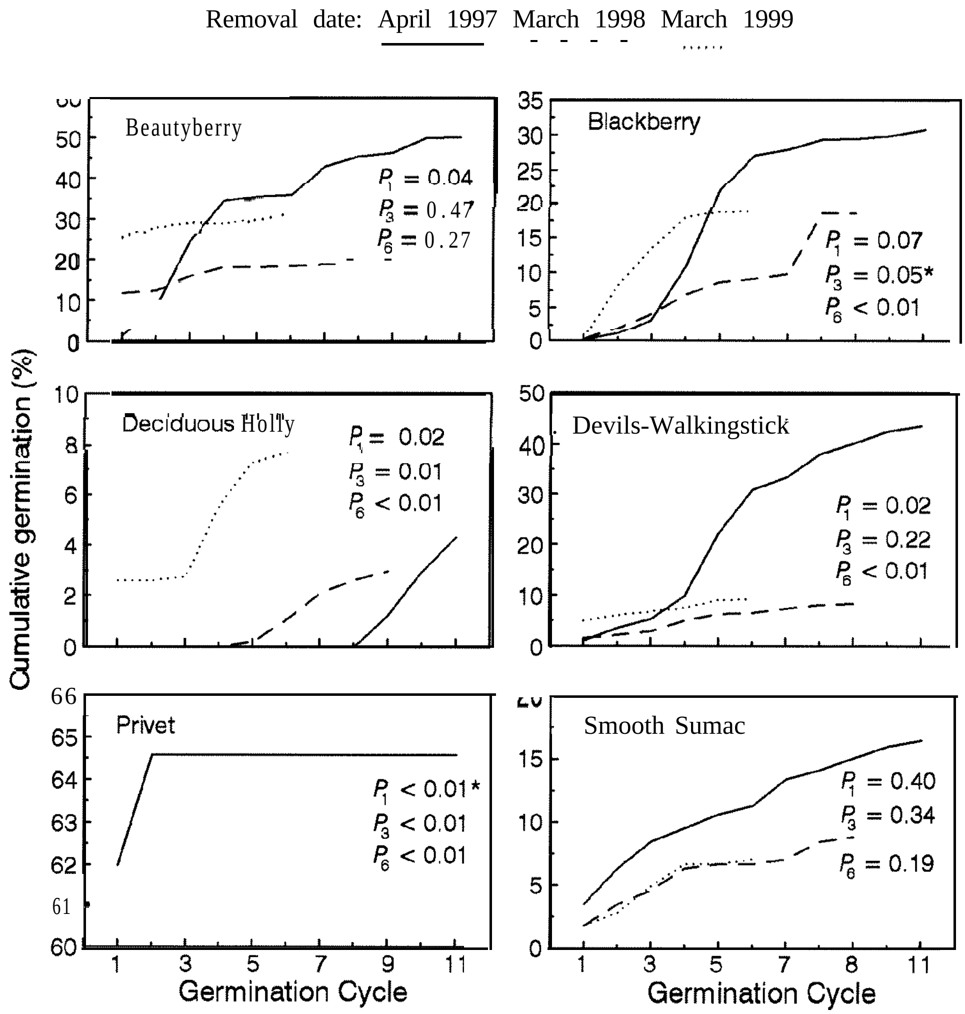
The position of the packets within the forest floor changed through time because of inputs from litterfall and losses from decomposition. The packets of most species were deposited before the autumn pulse of litterfall, and thus, most packets were at the boundary between the litter and fermentation layer by spring 1997 (Fig. 1). However, packets were well within the F layer during 1998 and 1999.

Germination characteristics of the shrubs are shown in Fig. 2. Cumulative germination of the seeds removed in 1997 was greatest for privet (65%) and least for deciduous holly (4%). Privet had the fewest dormant seeds, because 96% of the germination for the 1997 removal occurred during the first germination cycle and only 4% thereafter. Potential carry-over was also lowest for privet, because no seeds germinated from the 1998 and 1999 removals.

For the 1997 removal, devils-walkingstick, beautyberry, and blackberry had a fairly similar pattern of germination, and the highest cumulative germination observed was 42, 50, and 30%, respectively. For all three species, germination for the 1997 removal was almost zero for the first germination cycle. During the second and third cycles, germination accelerated, and some germination was even observed during the 11 th cycle. For the same number of cycles, germination for the 1998 removal was consistently below that of the 1999 removal, and the reason for that pattern was not clear. For blackberry, germination of the 1998 removal was considerably slower than the 1999 removal, but the cumulative germination after nine cycles of the 1998 removal equaled that of six cycles of the 1999 removal. For all three species, germination for the 1999 removal was initially more rapid than the 1997 removal. At the end of the sixth cycle, cumulative germination was approximately equal for the 1997 and 1999 removals for beautyberry and blackberry, but the 1997 removal exceeded the 1999 removal by four times for devils-walkingstick. These results indicated a high degree of seed dormancy. The potential for seed carry-over after 3 years was high for beautyberry (3 1%) and was moderate for blackberry (19%) and devils-walkingstick (9%).

Germination of smooth sumac seeds from the 1997 removal was greatest for the first cycle (3%), and cumulative germination increased at a fairly constant rate of about 1%

Fig. 2. Cumulative germination of seeds of six shrubs common to southeastern United States during alternating cycles of 60 days of germination testing followed by 60 days of stratification. Fruits were deposited on the forest floor of a mature pine-hardwood stand in the late summer and autumn of 1996 and were removed at the indicated dates. Probabilities with no asterisk were from analysis of variance comparing three removal dates for cumulative germination, while those with an asterisk were from a Kruskal–Wallis test; subscripts (1, 3, and 6) give the specific germination cycle of the comparison among removal dates.



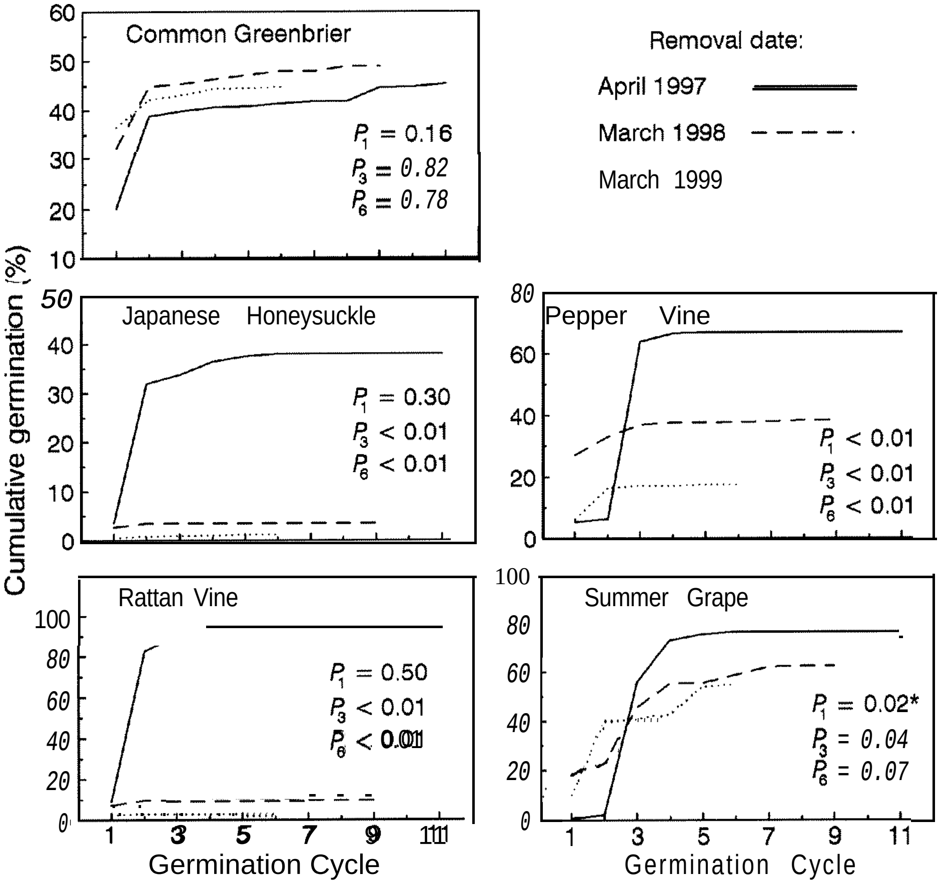

per cycle thereafter. At the end of the sixth cycle, cumulative germination of the 1998 and 1999 removals were 42% lower than the 1997 removal, but differences were not significant. Results indicated a fairly high dormancy that can be broken by multiple germination-stratification cycles and a moderate potential for carry-over (7% after 3 years) in the seed bank.

Germination characteristics of deciduous holly were unique when compared with the other shrubs. The greatest and most rapid germination occurred after 3 years of field storage. The slowest germination was for the 1997 removal, which had no germination whatsoever until the ninth cycle. According to Bonner (1974*b*), holly (*Ilex* spp.) seeds are very dormant, which is partly due to the hard endocarp surrounding the seed coat and partly due to conditions in the embryo. The seeds of some hollies have an immature embryo that must complete its development after apparent fruit maturity. Thus, carry-over in the seed bank appears to be a necessary step in the germination of deciduous holly seeds.

For the 1997 removal, the germination characteristics of vine seeds (Fig. 3) displayed much more uniformity than the shrubs. All cumulative germination curves increased rapidly during the second or third cycles but showed little increases thereafter. In addition, the range in cumulative germination was much higher for vines (38-95%) than for shrubs (4-65%). Germination of common greenbrier seeds was unique as the first germination cycle of the 1997 removal (20%) was higher than any other vine and was exceeded only by privet (65%). The potential for carry-over was high for common greenbrier and summer grape, where cumulative germination after 3 years of field storage averaged 45 and 55%, respectively. Seeds of pepper vine showed a moderate potential for carry-over with 17% germination after 3 years of storage. In contrast, rattan vine and Japanese honeysuckle seeds showed little gemination (3 and 1%, respectively) after 3 years of field storage, indicating a low potential for carryover under the tested conditions.

Although our use of packets allowed tracking changes in seed viability through time, they did not enable determination of the reason that viability changed. There was some recorded insect damage to the packets suggesting consumption can even occur in our protected conditions. Some seeds also

Fig. 3. Cumulative germination of seeds of five vines common to southeastern United States during alternating cycles of 60 days of germination testing followed by 60 days of stratification. Fruits were deposited on the forest floor of a mature pine-hardwood stand in the late summer and autumn of 1996 and were removed at the indicated dates. Probabilities with no asterisk were from analysis of variance comparing three removal dates for cumulative germination, while those with an asterisk were from a Kruskal–Wallis test; subscripts (1, 3, and 6) give the specific germination cycle of the comparison among removal dates.




germinated while in the packets. For example, when packets were removed after 2 years of field storage, Japanese honeysuckle (1.5%), rattan vine (1.1%), devils-walkingstick (0.3%), and pepper vine (0.2%) seeds were observed to be actively germinating.

## Discussion

The degree of dormancy displayed by the seeds of a species is central to the potential for carry-over in the seed bank. Dormancy is the result of the interaction of imposed environmental conditions and the hereditary properties of the species (Krugman et al. 1974). Dormancy can result from both morphological and physiological conditions, and the specific mechanisms involved vary greatly among species. Seeds of privet and common greenbrier provide an interesting contrast. Both species have fairly large seeds, and we observed while conducting the cut tests and processing seeds that the seed coat of these two species appeared to provide little protection to the seed's contents. The seed coat of privet was soft and easily torn, while the seed coat of common greenbrier appeared to be a thin membrane that was easily cut. Both species display a fairly low dormancy as they had the highest germination rates after the first field removal and during the first germination cycle. However, no privet seed were viable after more than one winter in storage, while there was very little difference in the viability of common greenbrier seeds over the entire 3 years of field storage. Thus, a thick and protective seed coat does not appear to be necessary for the carry-over ability of some species. Krugman et al. (1974) pointed out that it is not necessarily the thickness of the seed coat that affects dormancy, but it is the seed coat's permeability to gasses and water. In contrast, the high potential for carry-over of smooth sumac and blackberry seeds appears to be related to their thick and resistant seed coats, as scarification has been shown to significantly improve germination. For example, Brinkman (1974*a*) suggested soaking smooth sumac seeds for 1 to 3 h in concentrated sulfuric acid as a pregermination treatment, and Brinkman (1974*b*) listed acid soaking for up to 1 h as one of several pregermination treatments for blackberry (*Rubus* spp.) seeds. When we soaked seeds of smooth sumac in concentrated sulfuric acid for 1.5 h and blackberry for 20 min, cumulative germination averaged 57 and 49%, respectively, in two germination-stratification cycles, compared with 7 and 1%, respectively, for the 1997 field removal for the same number of cycles.

Birds and mammals are the principal dispersal agents of the species in our study, but we do not know what effect passing through an animal's gut would have on germination characteristics. Farmer (1997) pointed out that many birds and small mammals accidentally drop or dislodge fruits during foraging, and some birds regurgitate the larger seeds. Thus, not all seeds from fruits that are berries or berrylike drupes actually pass through an animal during dispersal. In addition, Farmer (1997) concluded that the effect of passing through an animal on seed germination has been largely overstated. For example, Lautenschlager (1997) found no improvement in the germination of red raspberry (*Rubus idaeus* L.) seeds after passing through the gut of several types of animals.

Disturbance, whether from natural or human causes, has a pronounced effect on the successional development of a forest stand. Foresters use the relationship between disturbance and succession to create an environment favorable to the species being targeted in management. Loblolly and shortleaf pines are both early successional species that thrive following stand manipulations that provide a disturbed seedbed and high light intensities near the ground. However, the environmental conditions that favor the regeneration of loblolly and shortleaf pines also favor many of their competitors. Loblolly and shortleaf pines become established mainly from seeds dispersed on the site after the disturbance, although some seedlings may become established before reproductive cutting. Cain and Shelton (1997) have shown that the potential for seed carry-over from one year to the next is very low for loblolly and shortleaf pines. In contrast, the competitors of the pines originate from multiple sources: from advanced regeneration established before reproduction cutting, from seeds dispersed on the site shortly before or after disturbance, and from seeds from earlier seed crops that remain viable in the seed bank for years. Of the 11 species evaluated in this study, only privet showed no carry-over beyond the first winter of field storage. The potential for carry-over through 3 years of field storage was low (<5%) for two species (rattan vine and Japanese honeysuckle), moderate (5–25%) for live species (pepper vine, devils-walkingstick, deciduous holly, smooth sumac, and blackberry), and high (>25%) for three species (beautyberry, common greenbrier, and summer grape).

## Management implications

Results of our study are useful in planning control strategies for competing species. According to Farrar et al. (1984), competition from privet resulted in the regeneration failure on about 20% of the area of a stand of loblolly and shortleaf pines in southwestern Arkansas that had been managed using uneven-aged silviculture for three decades. In addition, Cain (1992) reported that competition from Japanese honeysuckle resulted in severe regeneration problems in uneven-aged stands of loblolly and shortleaf pines in southeastern Arkansas. Knowledge that seeds of these two species do not remain viable in the seed bank is important in developing an effective control strategy; if existing plants can be eliminated using herbicides, then there is no reserve of viable seeds to repopulate the stand. In contrast, complete control of a species with a large reservoir of viable seeds in the seed bank would be very difficult. Cain and Barnett (1994) found that sumacs and beautyberry were the most aggressive competitors in young, even-aged stands of loblolly pine in southeastern Arkansas. Results of our study showed that seeds of these species have a high potential for carry-over, and thus, viable seeds in the seed bank could potentially repopulate the stand even if existing plants were eliminated using herbicides. Repeated herbicide applications would probably be needed for complete control. In such situations, a realistic goal of releasing an adequate number of pines to grow into dominant positions may be more feasible than a futile attempt to arrest succession. Land managers should also recognize some of the beneficial features of species with seeds that persist in the seed bank. Competing vegetation obscures logging debris and provides food and cover for wildlife; some species, like beautyberry and smooth sumac, are aesthetically pleasing because of autumn colors. Our results on the germination characteristics of the 11 species of shrubs and vines also have implications for their regeneration for ecosystem restoration, visual enhancement, or wildlife habitat.

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