

Effects of the amount and composition of the forest floor on emergence and early establishment of loblolly pine seedlings

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Abstract: Five forest floor weights (0, 10, 20, 30, and 40 Mg/ha), three forest floor compositions (pine, pine-hardwood, and hardwood), and two seed placements (forest floor and soil surface) were tested in a three-factorial, split-plot design with four incomplete, randomized blocks. The experiment was conducted in a nursery setting and used wooden frames to define 0.145-m² subplots. Forest floor composition had no significant effect on emergence or establishment of loblolly pine (*Pinus taeda* L.) seedlings. Numbers of emerging and established seedlings displayed a negative exponential relationship with forest floor weight (fit indices of 0.62 and 0.62, respectively). Seed placement significantly affected the number of emerging seedlings (forest floor > soil surface) and their survival (forest floor < soil surface). However, seed placement had no overall significant effect on the number of established seedlings because effects on emergence and survival essentially canceled out. Germination of herbaceous seeds in the soil bank also displayed a negative exponential trend with forest floor weight (fit indices of 0.46 and 0.50 for the weight of grasses and forbs, respectively) and was not significantly affected by forest floor composition. Results indicate that forest floor composition is not a factor in the natural regeneration of the pine component of mixed pine-hardwood stands and suggest that when pine seed production is adequate, moderate amounts of forest floor material will improve pine seedling development because of suppression of herbaceous vegetation.

Résumé : Cinq masses de couverture morte (0, 10, 20, 30 et 40 Mg/ha), trois compositions de couverture morte (pin, pin-feuillus, feuillus) et deux positions des semences (couverture morte et surface du sol) ont été testées à l'aide d'un dispositif en tiroirs avec quatre blocs aléatoires incomplets, selon un plan factoriel à trois facteurs. L'expérience a été menée dans une pépinière en utilisant des cadres de bois pour délimiter des sous-parcelles de 0,145 m². La composition de la couverture morte n'a pas eu d'effet significatif sur l'émergence ou l'établissement des semis de pin à encens (*Pinus taeda* L.). Le nombre de semis émergés et établis a démontré une relation exponentielle négative avec la masse de la couverture morte (indices d'ajustement de 0,62 et 0,62 respectivement). La position de la semence a influencé significativement le nombre de semis émergés (couverture morte > surface du sol) de même que leur survie (couverture morte < surface du sol). Toutefois, la position de la semence n'a pas eu d'effet d'ensemble significatif sur le nombre de semis établis parce que les effets sur l'émergence et la survie tendaient à s'annuler. La germination des semences des herbacées de la banque du sol présentait aussi une tendance exponentielle négative avec la masse de la couverture morte (indices d'ajustement de 0,46 et 0,50 pour la masse des graminées et autres herbacées, respectivement) et n'était pas significativement influencée par la composition de la couverture morte. Les résultats indiquent que la composition de la couverture morte ne constitue pas un facteur important dans la régénération naturelle du pin des peuplements mixtes et suggèrent que, lorsque la production de semences du pin est adéquate, une importance moyenne de la couverture morte favorisera le développement des semis de pin en réduisant l'importance de la végétation herbacée.

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Introduction

Pines and hardwoods are common associates throughout most of the South, and recent interest has been expressed in silvicultural methods that create and maintain these mixtures (Waldrop 1989). Competition between these two groups is most significant and apparent during stand regeneration. It is well known that hardwood competition severely reduces the establishment and developmental rates of pine regeneration. However, little is known about the effects of hardwood litter on the suitability of the seedbed for pine germination. Each plant species has particular seedbed requirements, and a basic tenet of the natural regeneration of forest stands is to favor the target species by creating a favorable seedbed (Smith 1986). The inhibitory effects of the forest floor on germination and establishment are well documented for the small, wind-disseminated seeds of loblolly pine (*Pinus taeda* L.) (Clark 1948; Grano 1949; Pomeroy 1949; Trousdell 1950; Dougherty 1990; Cain 1991). Loblolly pine seeds have a greater chance for successful germination and establishment in seedbeds of exposed mineral soil than in those composed of forest floor material. Other tree species (Koroleff 1954; Burton and Bazzaz 1991) and herbaceous species (Harper et al. 1965; Gross and Werner 1982; Winn 1985; Reader and Buck 1991) have similar requirements. Some incidental evidence suggests that a hardwood forest floor has more of an inhibitory effect than a pine forest floor (Brender 1973; Grano 1949); however, in a stand setting it is difficult to isolate the effects of the forest floor from the trees that produced it. Therefore, a controlled experiment was conducted in a nursery setting to determine whether the amount and composition of the forest floor and seed placement affect the emergence and early establishment of loblolly pine seedlings.

Methods

Study site

Nursery beds were established in the Crossett Experimental Forest in southeastern Arkansas in a field that was periodically mowed. During the summer of 1991, herbaceous vegetation on the study site was killed with foliar-applied glyphosate, and dead vegetation was burned to remove residual organic materials. The soil series is Providence silt loam (fine-silty, mixed, thermic Typic Fragiudalfs), which is a moderately well-drained soil. A perched water table often occurs in the winter and early spring. Site index for loblolly pine is 26 m at 50 years. Study installation was completed in mid-November 1991, and termination was in early July 1992.

Climate of the study site is subtropical humid. Winter and spring weather of 1991–1992 was considerably milder than normal. Winter temperatures averaged 12.0°C during 1991–1992 compared with a long-term mean of 9.6°C; a similar comparison for spring was 19.6 versus 17.6°C. There were only 8 days in December and January, and none thereafter, when the minimum temperature fell below 0°C. Precipitation was slightly above normal during the winter of 1991–1992 (13.7 versus a long-term mean of 12.6 cm/month) and below normal during the spring (9.9 versus a long-term mean of 13.6 cm/month).

Table 1. Characteristics of the stands providing the forest floor material used in the study.

Property	Stand type	
	Loblolly pine	Mixed oaks
Forest floor		
Foliage (Mg/ha)	17.2	9.6*
Woody material (Mg/ha)	2.3	2.0
Total (Mg/ha)	19.5	11.6*
Depth (cm)	3.2	2.3*
Vegetation		
Stand age (years)	22.0	74.6*
Basal area (m ² /ha)		
Pines	32.5	0.9*
Red oaks	0.0	13.7*
White oaks	0.0	7.8*
Other trees	0.0	3.2
Woody understory	2.1	2.8
Total	34.6	28.5*

*A significant difference occurred between stands by analysis of variance at the 0.05 probability level.

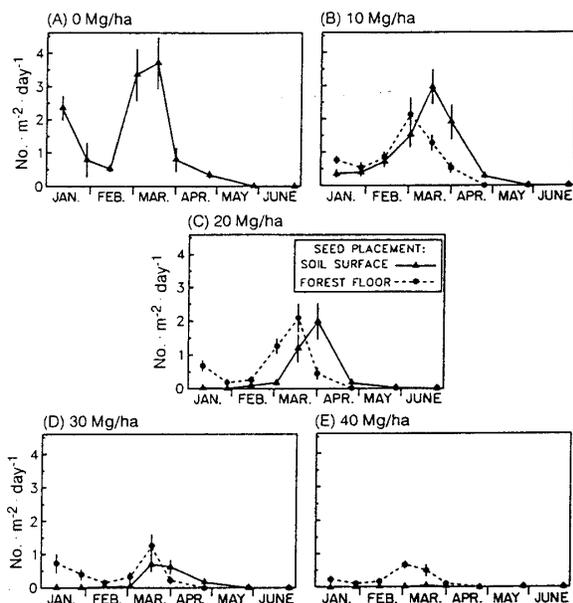
Treatments and implementation

Treatments were arranged in a three-factorial, split-plot design; forest floor weights (0, 10, 20, 30, and 40 Mg/ha) and compositions (pine, pine-hardwood, and hardwood) were the whole plots, and seed placements (forest floor vs. soil surface) were the subplots. Because composition and seed placement are meaningless when there is no forest floor, only one plot of the 0 Mg/ha weight (i.e., exposed mineral soil) was established in each of the four randomized, incomplete blocks.

Forest floor material used in the study came from a loblolly pine plantation and an upland oak (*Quercus* spp.) stand (Table 1). These forest floors are typical of similar stand conditions found elsewhere in the South (Switzer et al. 1979). Stand vegetation was characterized by inventorying five points with a 10 basal area factor prism. Understory stems (≤ 10 cm in diameter at breast height) were inventoried on a 40-m² circular plot at each prism point. The forest floor of each stand was characterized by sampling five 0.1-m² plots for weight and depth. The bulk forest floor material was collected in September 1991 before the onset of pine seedfall. The forest floor was collected by litter and fermentation layers to facilitate reconstruction. Material was dried to a constant weight at 50°C. Several 100-g subsamples were dried at 105°C to determine the residual moisture content.

Forest floors were reconstructed within wooden frames equipped with removable tops constructed from window-screen wire to keep out unwanted seeds and seed-consuming animals. Each subplot was 0.145 m² in area with dimensions of about 26 by 55 cm. Forest floor material was weighed by layer to yield the designated weights and compositions. The proportion of litter and fermentation material was the same as observed in the respective stand condition; a mean value was used for the pine-hardwood forest floor. The

Fig. 1. Effect of date, seed placement, and forest floor weight (0, 10, 20, 30, and 40 Mg/ha) on the emergence of loblolly pine seedlings. Symbols are treatment means \pm 1 SE.



pine-hardwood composition contained equal amounts of pine and hardwood material. Small adjustments were made to yield an equivalent weight at a drying temperature of 105°C. After treatments were randomly assigned, subplots that were designated for seed placement on top of the forest floor were established during mid-October. These plots received several heavy rains, which allowed the material to settle.

During mid-November 1991, seeds were sown at the rate of 40 per subplot (276/m²). Seeds were placed on top of the litter layer for subplots with the previously established forest floors. On adjacent split plots, seeds were placed on the soil surface and lightly pressed into the soil; then, a forest floor of the designated weight and composition was reconstructed.

The woods-run seeds used in the study came from southern Arkansas and had been in cold storage since 1981. Seven 40-seed groups that had been stratified for 45 days and four groups of unstratified seeds were tested for germination in sand flats in a laboratory. Germination after 100 days averaged 93.2 and 89.4% for stratified and unstratified seeds, respectively. Germination rates of 25, 50, and 75% were achieved in an average of 6, 8, and 10 days, respectively, for the stratified seeds and in 16, 24, and 38 days, respectively, for the unstratified seeds.

Measurements and data analysis

Emerging seedlings were counted at approximately 2-week intervals once emergence had begun; monthly intervals were used during the latter part of the observation period when emergence had nearly ceased and counts were essen-

tially made to determine mortality. Emerging seedlings were marked with small rubber bands to distinguish them from future cohorts; this also allowed the determination of mortality. Each subplot was examined for additional emerging seedlings that may have died during the same observation interval. Subplots were periodically weeded by hand; the last weeding was done in early May 1992. The last seedling count was made in early July 1992. Living seedlings during the final count were considered to be established. After counts were completed, pine seedlings, grasses, and forbs were cut at groundline, and their respective weights were determined after drying to a constant weight at 105°C.

Data were initially analyzed with analysis of variance (restricted to treatments with a forest floor), which indicated no significant effect of forest floor composition. Regression analysis was then used to test the quantitative effects of forest floor weight (W), entering seed placement (P) as an indicator variable (0 = soil surface, 1 = forest floor) as follows:

$$[1] \quad Y = b_0 + b_1W + b_2P + b_3WP$$

Response variables (Y) were the number, survival, and weight of established seedlings. Variables were dropped from the full model if their coefficients did not significantly differ from zero at a probability level (p) of 0.05. Several linear and nonlinear modifications of eq. 1 were tested in an attempt to improve the fit. Equations were fitted using linear and nonlinear least squares regression provided in SAS procedures REG and MODEL (SAS Institute Inc. 1988, 1989). The reported fit index (FI) for nonlinear equations is analogous to the coefficient of determination (R^2) reported for linear equations. Several outliers for grass and forb weights were eliminated from the data.

Results

Emergence of loblolly pine seedlings began in early January 1992, about 50 days after sowing, and was virtually completed by the end of April (Fig. 1). Emergence of loblolly pine normally begins in March in this area. The early emergence observed in this study probably reflected: (i) a moderated temperature regime caused by the screens covering the seedbeds and (ii) the exceptionally mild winter of 1991-1992, when temperatures averaged 2.4°C above normal. However, a few emerging pine seedlings were also observed in January 1992 in nearby areas being naturally regenerated.

Emergence rate was affected by date, forest floor weight, and seed placement, but not forest floor composition. The overall mean emergences were 0.43, 0.37, and 0.42 seedlings·m⁻²·day⁻¹ for the pine-hardwood, and hardwood forest floors, respectively ($p = 0.58$). Emergence rate was greatest on exposed mineral soil (0 Mg/ha), which had peaks in both January and March (Fig. 1A). The January peak was suppressed by the presence of a forest floor, especially when seed placement was on the soil surface. Emergence rate decreased as forest floor weight was increased (Figs. 1B-1E). Emergence from seeds placed on top of the forest floor occurred earlier than those placed on the soil surface; respective peaks were generally separated by about 2 weeks.

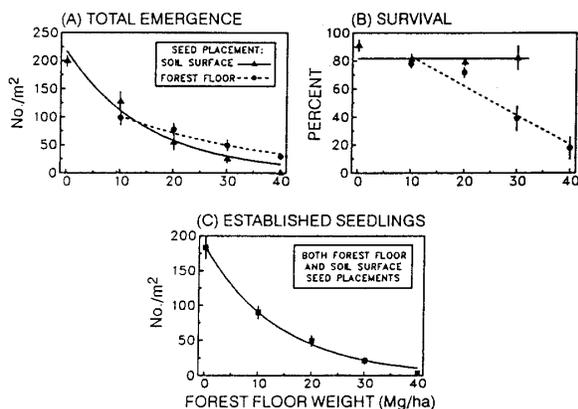
Table 2. Equations and associated statistics for predicting emergence, survival, and weight of loblolly pine seedlings and weight of herbaceous vegetation.

Equation No.	Equation*	Fit index or R^2	RMSE [†]	Mean of Y	df
1	EMERG = $\exp(5.38 - 0.0662W - 0.388P + 0.0297WP)$	0.62	37.2	63.4	96
2	SURV = $81.8 + 22.2P - 2.09WP$	0.62	17.3	66.6	68
3	ESTAB = $\exp(5.22 - 0.0714W)$	0.66	31.0	46.4	98
4	GRASS = $\exp(4.90 - 0.0709W)$	0.46	35.5	31.9	95
5	FORB = $\exp(4.42 - 0.140W)$	0.50	17.0	10.1	96
6	PINE = $\exp(3.08 + 0.0657W - 0.00384W^2)$	0.48	11.1	13.6	97

*EMERG, total pine emergence (no./m²); SURV, pine survival (%); ESTAB, established pine seedlings at study termination (no./m²); GRASS, grass weight (g/m²); FORB, forb weight (g/m²); PINE, pine seedling weight (g/m²); W, forest floor weight (Mg/ha); P, seed placement (0, soil surface; 1, forest floor).

[†]Root mean square error.

Fig. 2. Effect of forest floor weight and seed placement on (A) total emergence of loblolly pine seedlings, (B) seedling survival (limited to subplots with >2 emerging seedlings), and (C) the number of established seedlings at study termination. Symbols are treatment means \pm 1 SE. Curves or lines are calculated from Table 2, eq. 1 for (A), eq. 2 for (B), and eq. 3 for (C).

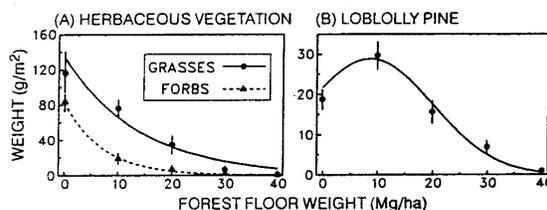


Total emergence displayed a negative exponential relationship with forest floor weight, which explained 62% of the variation (Fig. 2A, Table 2, eq. 1). Emergence from seeds placed on the forest floor was slightly less than that from seeds placed on the soil surface for the 10 Mg/ha forest floor, but the reverse occurred for greater weights.

Survival of emerging seedlings was about 80% for seeds placed on the soil surface, regardless of the forest floor weight (Fig. 2B). Survival of emerging seedlings from seeds placed on the forest floor decreased linearly for weights greater than 10 Mg/ha, and only 20% of the emerging seedlings survived for a forest floor of 40 Mg/ha.

The number of established seedlings reflected the combined effects of seed placement on the total emergence of seedlings and their survival. The opposing effects of seed placement on total emergence (forest floor > soil) and survival (forest floor < soil) essentially canceled out, so that seed placement did not significantly affect the number of established seedlings (Fig. 2C). Forest floor weight

Fig. 3. Effect of forest floor weight on the weight of (A) herbaceous vegetation and (B) loblolly pine seedlings at study termination. Herbaceous vegetation is the 2-month regrowth following an earlier weeding. Symbols are treatment means \pm 1 SE. Curves are calculated from Table 2, eqs. 4 and 5 for (A) and eq. 6 for (B).



accounted for 66% of the variation in the number of established seedlings (Table 2, eq. 3). Establishment ranged from 67% of the seeds on exposed mineral soil to 4% for a forest floor of 40 Mg/ha.

The amount of competing vegetation was also related to forest floor weight (Fig. 3A, Table 2, eqs. 4 and 5). The reported weights for competing vegetation represent a 2-month regrowth following hand weeding in early May 1992. These values are undoubtedly lower than those that would have occurred without weeding and are presented to illustrate the overall trend observed throughout the study. Grasses and forbs growing on exposed mineral soil weighed two and four times, respectively, more than that for a forest floor of 10 Mg/ha. Forest floor composition did not significantly affect this relationship.

Weight of pine seedlings peaked for a forest floor weight of 10 Mg/ha (Fig. 3B). This result reflects the treatment effects on both number of seedlings and their size. Seedling size was apparently suppressed by the large amounts of herbaceous vegetation present on exposed mineral soil. Seedling weight averaged 0.09 g for exposed mineral soil compared with 0.34 g for a forest floor of 10 Mg/ha.

Discussion

This study demonstrates the strong effect of the forest floor on germination and establishment, a finding that has considerable support from existing literature for loblolly

pine and many other species. Results of this study indicate that increasing forest floor weight decreases the number of established loblolly pine seedlings, delays their emergence, and reduces amounts of competing vegetation. Grano (1949) described a similar relationship between forest floor depth and the number of loblolly and shortleaf (*Pinus echinata* Mill.) seedlings. Peterson and Facelli (1991) reported that the forest floor significantly delayed the emergence of yellow birch (*Betula alleghaniensis* Britton) seedlings, and Facelli and Pickett (1991) observed that the forest floor reduced the amount of herbaceous vegetation. The effect that the forest floor exerts on the complicated process of germination and establishment undoubtedly involves a number of environmental, physical, biological, and chemical mechanisms.

The forest floor modifies environmental conditions during dormancy, germination, and establishment. The forest floor moderates the daily fluctuations in temperature (Kittredge 1948), affects light intensity and quality, and goes through numerous wetting-drying cycles. Moisture (Pomeroy 1949), temperature (McLemore 1966; Dunlap and Barnett 1982), and light (Toole et al. 1962; Woods and Mollish 1963; McLemore 1971) are all known to affect the germination of loblolly pine seeds. Although dormant pine seeds have been shown to be unaffected by repeated drying cycles of short duration (Adams 1975), moisture relationships are known to be crucial during certain stages of germination and early seedling establishment (Trousdel and Wenger 1963; Larson and Smith 1969).

The forest floor is a physical barrier that interferes with development of the radicle and (or) shoot. For example, Pomeroy (1949) observed that 83% of the mortality of loblolly pine seeds germinating in the forest floor resulted from failure of the radicle to contact a penetrable substrate. Critical physical features of the forest floor affecting the establishment of loblolly pine seedlings appear to be restricted to amount (i.e., weight and depth). Despite broad differences in foliar structure (i.e., a needle leaf versus a broad leaf), the pine and hardwood forest floors had the same effect on the emergence of loblolly pine seedlings. The fragmentation that occurs during decomposition undoubtedly reduces the initial differences in the structure of pine needles and hardwood leaves. Bark, branches, and wood fragments are also significant forest floor components (about 10 to 20% of total weight in this study), and contribute to the barrier imposed by the forest floor.

The forest floor is teeming with life, some of which may be unfavorable to dormant and germinating seeds (Vaartaja 1952). For example, damping-off of southern pine seedlings in nursery beds increases with appreciable quantities of organic matter (Wakeley 1954). In addition, Reader (1991) observed that the forest floor could potentially affect emergence of some species by harboring seed consumers. It seems reasonable that the biological effects of the forest floor would be correlated with the amount of material present.

The forest floor also has distinctive chemical properties, such as pH, nutrients, and organic compounds (Pritchett and Fisher 1987; Hinesley et al. 1991). These factors may affect germination in certain situations (DeBell 1971; Fisher 1980), but they were apparently not very important in the

conditions tested in this study because forest floor composition had no significant effect on the emergence and establishment of loblolly pine seedlings. However, composition may indirectly affect seedling establishment through its influence on forest floor amounts. Hardwood forest floors tend to be lighter and thinner than those of pine (Switzer et al. 1979). Thus, the yield of established loblolly pine seedlings is predicted to be 29% of the seeds for the hardwood forest floor presented in Table 1 compared with 17% for the pine forest floor.

Results of this study indicate that the initial placement of seeds within the forest floor has no net effect on the number of established seedlings. Apparently, a seed placed on the forest floor and separated from the soil surface has the same probability to develop into an established seedling as a seed placed on the soil surface and covered by forest floor material. The fate of seeds that did not produce a seedling, such as in the treatments with heavy forest floors, is unknown. These seeds may have germinated and died without producing a visible seedling, or the microsite may not have been suitable for the initiation of germination. It is also possible that seeds placed on the forest floor and those placed on the soil surface were affected by different factors. For example, emergence from seeds located on the forest floor may have been restricted by a fluctuating moisture regime and the physical barrier imposed by the forest floor on radicle development. Emergence from seeds on the soil surface but covered by the forest floor may have been restricted by saturated conditions during wet periods, the absence or reduction of light (light is beneficial to germination), and the barrier imposed by the forest floor to shoot development.

Although the forest floor inhibits germination, the effects are far from complete. Some seedlings were established even on the heaviest forest floors tested in this study. A few suitable microsites can apparently exist within a generally unfavorable seedbed. In addition, the effects of the forest floor are likely to vary with prevailing weather conditions that occur during stratification, germination, and establishment (e.g., wet vs. dry spring weather or cold vs. warm weather).

After termination of the study, plots with the heaviest forest floors were examined for ungerminated seeds, which were split and their contents examined. No potentially viable seeds were found; some were void and others had decomposed contents. Little and Somes (1959) and Barnett and McGilvray (1991) have also reported that there is virtually no carry-over of viable loblolly pine seeds from one year to the next.

Seedbed conditions after implementing a reproduction cut are very heterogeneous and range from exposed mineral soil to deep accumulations of forest floor material and logging debris (Shelton and Wittwer 1992). Thus, all the seedbed conditions tested in this study could probably be found after a typical natural reproduction cut; exposed mineral soil occurs where traffic scrapes the forest floor away, and heavy accumulations occur where the material is deposited. In addition, the seed placements tested in this study might occur when logging is conducted during or immediately after pine seedfall (October through February). From a regeneration standpoint, the areal extent of each

condition and its spatial distribution are the critical features of the seedbed and will govern the need for seedbed preparation treatments. In addition, the impact of seedbed conditions on the success of natural loblolly pine regeneration will undoubtedly vary with the seed supply. Moderate forest floor amounts would be favorable to lessen problems with overstocking when the seed supply is high, but would be detrimental when the seed supply is marginal.

Many studies have noted the dramatic increase in herbaceous vegetation following reproduction cutting, which has principally been attributed to increases in available resources (especially light and moisture). However, as this study indicates, seedbed conditions after harvest can strongly influence the germination and development of a wide assortment of seeds stored in the soil. The longevity of seeds in the soil bank is well known for many species (Livingston and Alessio 1968; Roberts and Feast 1973). Clearly, loblolly pine and many of its herbaceous competitors have similar seedbed requirements. Thus, when the loblolly pine seed supply is adequate, the forest floor may actually be favorable to the natural regeneration of loblolly pine because it suppresses the development of herbaceous vegetation.

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