

Effects of leaf litter depth on the emergence and seedling growth of deciduous forest tree species in relation to seed size¹

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KOSTEL-HUGHES, F., T. P. YOUNG, AND J. D. WEHR. (Louis Calder Center—Biological Field Station and Department of Biological Sciences, Fordham University, P.O. Box 887, Armonk, NY 10504). Effects of leaf litter depth on the emergence and seedling growth of deciduous forest tree species in relation to seed size. *J. Torrey Bot. Soc.* 132: 50–61. 2005.—Leaf litter has a major impact on soil microenvironmental conditions and so can be an important influence on seedling recruitment and hence plant community structure. We conducted a greenhouse experiment to examine the impact of leaf litter from temperate deciduous forests on the emergence and growth of tree seedlings in relation to seed size. Our treatments were bare (no litter), shallow (1–2 cm deep, 140 g·m⁻²), and deep (ca. 5 cm deep, 420 g·m⁻²) litter. Seed sizes ranged from 0.7–3636 mg. For *Betula lenta* (seed mass = 0.7 mg), emergence on bare soil was greater than 50%, approximately 12% in shallow litter, and no emergence in deep litter. Percent emergence for *Liquidambar styraciflua* (seed mass = 6 mg) was highest in bare soil and shallow litter treatments (64–69%) and was reduced by more than 80% in the deep litter treatment. *Ailanthus altissima* (seed mass = 30 mg) and *Quercus velutina* (seed mass = 1900 mg) exhibited no significant differences in emergence among litter depth treatments whereas, for *Quercus rubra* (seed mass = 3636 mg), percent emergence was over 50% greater under deep litter than under shallow litter. Seedling growth also differed in response to the litter treatments. For the two smallest-seeded species, *B. lenta* and *L. styraciflua*, seedling robustness (aboveground biomass divided by seedling height) was greatest in the bare treatment. Seedling robustness of *Q. velutina* decreased with increased litter depth while *Q. rubra* had its greatest seedling robustness in the shallow litter treatment. For *A. altissima*, seedling robustness and root:shoot ratio both decreased with increased litter depth. Our results suggest that the two smallest-seeded species are better adapted to colonizing post-disturbance sites where there is likely to be less litter, whereas the two largest-seeded oak species are better suited to establishing in forests with a thicker litter layer. This is consistent with the communities in which these species typically are found. The enhanced seedling growth of *A. altissima* in bare-to-shallow litter conditions may be one of the attributes that accounts for the success of this highly invasive non-native species in urban forests in the New York City metropolitan area which have shallower litter than nearby rural forests.

Key words: germination, recruitment, regeneration, urban forests, non-native species.

Leaf litter has long been recognized for its importance in the nutrient dynamics of plant communities (see review in Facelli and Pickett 1991a). More recently, researchers have begun to focus on how litter directly and indirectly influences abiotic conditions and biotic interactions, thus playing a major role in structuring

many plant communities (Facelli and Pickett 1991a, Xiong and Nilsson 1997, Xiong and Nilsson 1999). Studies have concentrated on the effects of leaf litter on seed germination and seedling establishment because of the potential importance of this life stage for determining future community composition (Grubb 1977, Harper 1977) and because of the sensitivity of this life stage to the soil microenvironmental conditions (light, temperature, and moisture) on which litter can exert major impacts.

Leaf litter can reduce diurnal and annual thermal amplitude in forests by decreasing the amount of solar radiation reaching the soil and by providing insulation for the soil (MacKinney 1929, Molofsky and Augspurger 1992). Soil moisture is typically greater (Beatty and Sholes 1988) and fluctuates less (Tao et al. 1987) under leaf litter than when bare. Larger patches of litter have been found to have greater soil organic matter and lower soil bulk density than smaller litter patches (Dighton et al. 2000). Leaf litter intercepts and changes the quality of light reach-

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ing the soil (Vazquez-Yanes et al. 1990, Facelli and Pickett 1991b, Schimpf and Danz 1999). Litter also presents a physical barrier that can interfere with seeds reaching the soil, the emergence of seedlings, and seed visibility to predators (Shaw 1968, Facelli and Pickett 1991a, Myster and Pickett 1993, Vellend et al. 2000).

Leaf litter is heterogeneously distributed within and across forests. The distribution of leaf litter on the forest floor can differ due to slope and aspect (Frankland et al. 1963), canopy cover (Molofsky and Augspurger 1992), topography (Dwyer and Meriam 1981, Beatty and Sholes 1988), fire (Enright and Lamont 1989), urbanization (Kostel-Hughes et al. 1998), successional stage (Persson et al. 1987, Facelli and Carson 1991), understory (George and Bazzaz 1999, Dighton et al. 2000), and edge effects (Facelli and Carson 1991, Matlack 1993, Didham and Lawton 1999, Haskell 2000). Differences in microenvironmental conditions created by litter are thus likely to be similarly heterogeneous. Seeds, which are also patchily distributed (Bigwood and Inouye 1988), are species-specific in their response to these conditions. Microenvironmental conditions, seed availability, and species response to microenvironmental conditions, can therefore differ greatly and together determine seedling germination and establishment in the community (Grubb 1977, Harper 1977).

The relationship between seed size and germination under different litter conditions has been studied in both herbaceous species (Gross 1984, Winn 1985, Reader 1993, Metcalfe and Turner 1998, Froberg 2001) and woody species (Tao et al. 1987, Molofsky and Augspurger 1992, Peterson and Facelli 1992, Myster 1994, Facelli and Ladd 1996, Seiwa and Kikuzawa 1996, Cintra 1997, Metcalfe and Turner 1998, Green 1999, Lopez-Barrera and Gonzalez-Espinosa 2001, Dzwonko and Gawronski 2002) in a variety of community types (e.g. temperate deciduous and coniferous forests, tropical forests, and old fields). While there are exceptions (Facelli and Ladd 1996, Green 1999), most studies have found that smaller-seeded species generally have reduced germination as litter depth increases while germination of larger-seeded species is usually unaffected or increased by leaf litter (Tao et al. 1987, Molofsky and Augspurger 1992, Peterson and Facelli 1992, Reader 1993, Myster 1994, Seiwa and Kikuzawa 1996, Cintra 1997, Metcalfe and Turner 1998, Lopez-Barrera and Gonzalez-Espinosa 2001, Dzwonko and Gawronski 2002). However, the range of seed sizes

and the type and amount of litter treatments varies enormously among studies depending on the community being studied.

Peterson and Facelli (1992) and Myster (1994), to the best of our knowledge, have conducted the only studies testing the interaction of litter and seed size on temperate deciduous forest tree species. Myster (1994) compared four species but only with regard to germination and emergence and within the context of old field invasion. Peterson and Facelli (1992) compared germination, as well as measures of seedling growth and morphology as indicators of seedling fitness. However, their study included only two species with a fairly narrow range of seed sizes compared to those that typically occur in nature.

The objective of our study was to examine the impact of leaf litter from temperate deciduous forests on the emergence and growth of tree seedlings representing a wide range of seed sizes. Our interest in litter depth was two-fold. As previously demonstrated, litter depth and distribution varies naturally in temperate deciduous forests based on factors such as topography, canopy cover, understory, and proximity to edge. Leaf litter also increases over the course of succession with mature old growth forest having the greatest amount of leaf litter (Facelli and Carson 1991). Therefore, we predict that the response of different species to variation in litter conditions could affect forest stand development over the long-term. Secondly, we were particularly interested in the impact of litter depth differences in temperate deciduous forests along an urban-to-rural gradient in the New York City metropolitan area (Kostel-Hughes et al. 1998). Among these forests, litter depth across microsites range from 0–5.5 cm (Kostel-Hughes, 1995). Across the forests along this gradient, the average litter depth increases by about 30% and the average litter mass increases by 2.85 times from the urban end to the rural end, largely due to the presence of non-native earthworms in the urban and, increasingly, the suburban forests (Kostel-Hughes et al. 1998). These local and regional differences in litter depth may be large enough to have profound impacts on seedling success, with these effects differing among species with different seed sizes, with the potential to influence the long-term species composition of these forests.

The specific objectives of this study were (1) to compare seedling emergence and growth of deciduous tree species across three leaf litter depths, and (2) to contrast these responses

Table 1. Tree species included in this study (in order of seed size) and their respective mean seed masses (Young and Young 1992). Included are the experimental sets to which each species was assigned within each experimental block and the total percent emergence for each species.

| Species | Seed mass (mg) | Native vs. non-native | Set | Total percent emergence |
|--|----------------|-----------------------|-----|-------------------------|
| <i>Betula lenta</i> | 0.7 | Native | B | 21 |
| <i>Liquidambar styraciflua</i> | 6 | Native | A | 49 |
| <i>Acer palmatum</i> (small-seeded var.) | 18 | Non-native | A | 0 |
| <i>Acer palmatum</i> (large-seeded var.) | 28 | Non-native | B | 0 |
| <i>Ailanthus altissima</i> | 30 | Non-native | A | 69 |
| <i>Liriodendron tulipifera</i> | 32 | Native | B | 4 |
| <i>Acer saccharum</i> | 65 | Native | A | 10 |
| <i>Acer pseudoplatanus</i> | 88 | Non-native | B | 1 |
| <i>Acer platanoides</i> | 159 | Non-native | B | 7 |
| <i>Quercus velutina</i> | 1900 | Native | A | 73 |
| <i>Quercus rubra</i> | 3636 | Native | B | 63 |
| <i>Quercus alba</i> | 3788 | Native | A | 8 |

among tree species as a function of seed size. We predicted that under deeper litter, the smaller-seeded tree species would have lower percent emergence than the larger-seeded tree species. We also predicted that the smaller-seeded species would exhibit more differences in seedling growth (i.e. resource allocation) when subjected to deeper leaf litter while seedling growth of the larger-seeded species would be relatively unaffected by litter.

Materials and Methods. EXPERIMENTAL DESIGN. This greenhouse experiment was a randomized complete block design with three treatments consisting of (1) no litter (BARE), (2) thin/low amount of litter (SHALLOW), and (3) thick/high amount of litter (DEEP). Blocking was established to control for the possible effects of light and temperature differences due to placement on the greenhouse bench. In early March 1994, we collected leaves from the forest floor at the Louis Calder Center in Armonk, NY, air dried them, and separated out leaves of *Quercus rubra* (co-dominant canopy species) for use in this experiment. We used only one species of leaf in order to control for physical and chemical properties of leaves, which differ among tree species (Facelli and Pickett 1991a). These leaves dominate the litter layer and are known to be particularly resistant to decay (McClougherty et al. 1985, Blair 1988) and so are more likely to exert an influence on seeds in nature than would leaves of many other deciduous species that occur in the forest.

The amount of leaves used in the litter treatments was based on surveys of litter input in oak forests along an urban-to-rural land-use gradient in the New York City metropolitan area.

These forests have been the focus of numerous studies of the effect of urbanization on forests (McDonnell et al. 1997), particularly the effects on litter decomposition (Pouyat et al. 1994, Pouyat et al. 1997, Steinberg et al. 1997, Carreiro et al. 1999). According to Pouyat and Carreiro (unpublished data) the mean annual litter input in the forests along this gradient ranged from 257 to 402 g·m⁻². Our goal was to measure the effects of litter depth on tree seedlings, but we varied litter mass to assure consistency within treatments. The deep litter treatment was ca. 5 cm deep and received 420 g·m⁻²; shallow litter treatment was 1–2 cm deep and received 140 g·m⁻².

The seeds of tree species included in this study, their mean seed mass, and experimental set to which they were assigned are listed in Table 1. We chose for our study both native and non-native tree species that occur in and around the forests along an urban-rural gradient northward from New York City, and that represented a large range of mean seed sizes. All the seeds were obtained from F.W. Schumacher Co., Inc., Sandwich, MA, where they were reported to have been stored cold (about 0–1.5 °C) and dry. Prior to stratification, the seeds were surface sterilized with dilute bleach (1:10) for five minutes followed by several thorough rinses with water (D. Schumacher, F.W. Schumacher Co., pers. comm). The seeds were then soaked in water for 48 hours (changing the water after 24 h), drained, transferred to plastic bags with moistened vermiculite, and stored in a refrigerator at 3–5 °C for approximately three months. Following instructions from the supplier, the seeds of *Betula lenta*, *Quercus alba*, and *Liquidambar styraciflua* were not surface sterilized. *Betula*

lenta seeds only needed to be soaked for a few hours prior to stratification. Seeds of *Acer palmatum* (large- and small-seeded) were soaked in near boiling water for 48 h (with several changes of water) prior to stratification, as per the instructions from the supplier.

We used large flats (33 X 43 cm) to ensure at least 4 cm distance from the edges of each flat based on a pilot study showing leaf litter avoidance by seedlings near edges. Flats were filled with commercial sterilized potting soil and wetted thoroughly. A few species that were difficult to distinguish as seedlings (*Acer saccharum* and *Acer platanoides*; large-seeded *Acer palmatum* and small-seeded *Acer palmatum*; *Quercus velutina* and *Quercus rubra*) were separated into two experimental sets (A and B, see Table 1) which were treated concurrently. On 14 March 1994, we interspersed the seeds of each of six tree species (set A) on the soil surface in each of nine flats and followed the same procedure for six other tree species (set B) in another set of nine flats, for a total of 18 flats. We then added 20 g leaf litter to six of the flats for the shallow litter treatment and added 60 g litter to another six flats for the deep litter treatment. The last six flats had no litter added for the bare treatment. This resulted in three replicate blocks, each including bare, shallow, and deep litter treatments, with species sets A and B in two different flats. Seeds of each species were sown 15 to a flat, which resulted in a total of 45 seeds/species for each treatment and for each block for an overall total of 135 seeds/species, or 1620 seeds total.

The seeds were subjected to 12 hours of light each day from commercial plant growth bulbs and room temperatures ranging between 20–30 °C. Flats were watered twice a week at a rate that simulated spring rainfall, based on records at the Westchester Airport, White Plains, NY (mean = 127 mm per month for April and May 1993). This regime kept the soil consistently moist in all treatments. The position of the flats was rearranged each time they were watered. Flats were monitored daily for seedling emergence and mortality. The experiment was concluded after eight weeks, at which time we removed the litter to see if any seeds germinated but had not emerged through the litter. We then removed each surviving seedling, washed the soil from the roots, and recorded height to the apical meristem, hypocotyl length, number of leaves, and leaf area. For *Quercus* seedlings, the distance between the base of the stem and the

first true leaf was substituted for the hypocotyl length. The trends for differences in hypocotyl length in response to our treatments were the same as those for stem height, therefore we report only the data for stem height. Plants were dried to a constant weight at 105 °C for 48 h. After drying, we weighed the stem, leaves, and roots separately and calculated root:shoot ratio and “robustness” (aboveground biomass divided by height, after Peterson and Facelli 1992).

DATA ANALYSES. We compared percent emergence in each flat among treatments for each species using one-way ANOVA, followed by Tukey’s HSD multiple comparisons test. Percent emergence data were arcsine transformed to approximate normality (based on skewness: g_1). However, there were no important differences in significance levels of the ANOVAs between the untransformed and transformed data. We compared growth measures of individual seedlings only for those species that exhibited substantial total emergence rates (> 10%). Comparisons of individual seedlings between treatments were made using one-way ANOVA, followed by Tukey’s HSD multiple comparisons test. Growth data were log transformed and skewness (g_1) was calculated for both transformed and untransformed data to assess the normality of each dataset. Leaf number and leaf area were square root transformed and skewness calculated (Sokal and Rohlf 1981). For each dependent variable, one-way ANOVAs were performed on either the untransformed or transformed data depending on which was more normally distributed (as determined by the formula: $g_1 < (6/n)^{-2}$ with n = sample size; Snedecor and Cochran 1980). As ratios, the derived variables (robustness and root:shoot ratio) are prone to skewness and are biased estimates of means (Sokal and Rohlf 1987), and so were analyzed using Kruskal-Wallis one-way analysis of variance. For all tests, we chose an *a priori* significance level of $P < 0.05$.

Results. PERCENT EMERGENCE. Tree species exhibited great differences in emergence in response to the different litter treatments. Of the twelve species included, only five exhibited overall emergence rates exceeding 10% (Table 1). These included *Betula lenta* (21%), *Liquidambar styraciflua* (49%), *Ailanthus altissima* (69%), *Quercus velutina* (73%), and *Quercus rubra* (63%). Those seven species with very low emergence rates ($\leq 10\%$) were not included in

Table 2. Summary of independent one-way ANOVA results testing the effect of litter depth on seedling emergence (analyses conducted on untransformed data unless indicated.)

| Species | df | MS | F | P | Response to increased litter depth |
|---|----|-------|---------|--------|------------------------------------|
| <i>Betula lenta</i> | 2 | 0.210 | 178.198 | <0.001 | decrease |
| <i>Liquidambar styraciflua</i> | 2 | 0.283 | 38.881 | 0.002 | decrease |
| <i>Ailanthus altissima</i> ^a | 2 | 0.095 | 2.016 | 0.248 | |
| <i>Quercus velutina</i> ^a | 2 | 0.362 | 5.826 | 0.065 | |
| <i>Quercus rubra</i> | 2 | 0.085 | 7.564 | 0.044 | increased |

^a Arcsine transformed.

further analyses of seedling growth. Across species, there was no significant relationship between percent emergence and seed size (Spearman's $r = 0.20$, $P > 0.50$) or between percent emergence and species' origin (native vs. non-native) (Pearson's Chi-square = 1.6, $P = 0.20$).

Betula lenta emergence, which was greater than 50% in the bare soil treatment, was reduced to about 12% in shallow litter and no emergence at all in deep litter (ANOVA: $P < 0.001$; Table 2; Fig. 1). Mean percent emergence in *Liquidambar styraciflua* was highest in bare soil and shallow litter treatments (64–69%) and was reduced by more than 80% in the deep litter treatment (ANOVA: $P = 0.002$; Table 2; Fig. 1). In contrast, mean percent emergence of *Ailanthus altissima* and *Quercus velutina* showed no significant differences among litter depth treatments (ANOVA: $P = 0.25$ and $P = 0.65$, respectively; Table 2; Fig. 1). Unlike all other species tested, *Quercus rubra* mean percent emergence was over 50% higher under deep litter than under shallow litter (ANOVA: $P = 0.044$;

Table 2; Fig. 1) but variation between bare and deep litter responses was judged to be non-significant.

Despite efforts to ensure that all seeds were subjected to the same initial litter depths, depths were later somewhat modified by the seedlings themselves. As *Quercus* spp. seedlings emerged, they tended to lift the leaves around them, creating openings in the litter layer. Some seedlings of *B. lenta*, *L. styraciflua*, and *A. altissima* emerged through these openings. These seedlings bent their stems, sometimes severely, in order to emerge.

SEEDLING GROWTH AND MORPHOLOGY. The five species with emergence rates greater than 10% were next analyzed for seedling traits. No seeds of *B. lenta* germinated in the deep treatment, therefore litter effect comparisons for *B. lenta* could only be made between the bare and shallow treatments. Seedlings of all five species had stems significantly longer in deep litter (shallow for *B. lenta*) than in the bare treatment (Table 3; Fig. 2). Aboveground biomass did not differ significantly among treatments for *Betula lenta*, *Quercus velutina*, and *Quercus rubra* (Table 3) but for *Liquidambar styraciflua* it was approximately one-third lower in the shallow litter than in the bare treatment (ANOVA: $P = 0.038$, Table 3; Fig. 3) but variation between deep and bare or shallow litter responses was judged to be non-significant. For *Ailanthus altissima* aboveground biomass was approximately 25% lower in the deep litter compared to bare treatment (ANOVA: $P = 0.027$, Table 3; Fig. 3). Leaf biomass of *Ailanthus altissima* seedlings was highest in the bare treatment and lowest in the shallow litter for *Liquidambar styraciflua* seedlings (Table 3). The two oak species had greatest stem biomass in the deep litter treatment (Table 3; Fig. 4). Root biomass did not differ significantly among litter treatments for any species (Table 3) except *Ailanthus altissima*, which

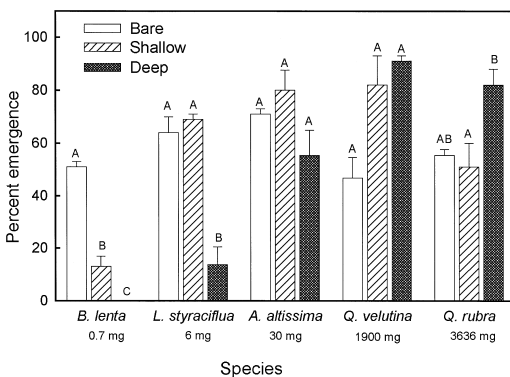


FIG. 1. Percent emergence (mean \pm SE) of tree seeds in response to bare, shallow, and deep litter treatments. Treatment means within each species not sharing a letter differ significantly (ANOVA: $P < 0.05$). Numbers below each species name represent the average seed mass for that species.

had about 70% (ANOVA: $P < 0.001$) lower root mass in the deep treatment than in bare soil (Table 3; Fig. 3). Seedling robustness was greatest in the bare treatment for all species except *Quercus rubra* which had the greatest seedling robustness in shallow litter (Kruskal-Wallis: $U = 6.957$, $P = 0.031$; Table 4). Only *Ailanthus altissima* exhibited a significant difference in root:shoot ratio, which decreased as litter depth increased (Kruskal-Wallis: $U = 33.345$, $P < 0.001$; Table 4).

In summary, for the two smallest-seeded species, *B. lenta* and *L. styraciflua*, percent emergence and seedling robustness both decreased with increased litter depth. For the two largest-seeded species, percent emergence of *Q. velutina* was unaffected and seedling robustness decreased with increased litter depth, while *Q. rubra* had its greatest percent emergence and seedling robustness in the deep and shallow litter treatments, respectively. For *A. altissima*, with intermediate size seeds, percent emergence was unaffected by litter depth but seedling robustness and root:shoot ratio both decreased with increased litter depth.

Discussion. EMERGENCE RATES AND SEED SIZE. Our results generally support the prediction that emergence of small-seeded species, but not large-seeded species, is reduced in deeper litter. *Betula lenta* and *Liquidambar styraciflua* were the two smallest-seeded species used in this study and exhibited the greatest reduction in emergence in response to deeper leaf litter. The two largest-seeded *Quercus* species had unaffected or improved emergence in the deep litter. The lack of significant differences in emergence among treatments for *Ailanthus altissima* could be related to its intermediate seed size or a neutral effect of the presence of litter on germination.

One of our original goals for this study had been to compare the responses to litter depth between native and non-native species. We were interested in non-native species because of their increasing encroachment into forests in the Northeast U.S., particularly in urban and suburban areas (Whitney and Adams 1980, Dorney et al. 1984, McDonnell and Pickett 1990, Yost et al. 1991, Pickett et al. 2001). Rejmanek and Richardson (1996) have suggested that seed size may be a useful characteristic for predicting the invasiveness of species. We sought to test if response to leaf litter would be associated with the known invasive ability of a species in these for-

ests. However, the very low emergence rates of all but one of the non-native species prevented us from making any such comparisons.

In their investigation of the effect of leaf litter on emergence of tree species, Peterson and Facelli (1992) compared wind-dispersed *Betula alleghaniensis* seeds (1 mg) with bird-dispersed *Rhus typhina* seeds (8.5 mg). The pattern for *B. alleghaniensis* was maximum emergence rate in the absence of litter, lower in thin litter treatments, and almost no emergence in deep litter; this is similar to the pattern for *B. lenta* (seed wt. = 0.7 mg) observed in our study. This was in contrast to *Rhus typhina* which showed no significant differences in emergence in response to litter amount. They suggest that this difference could be due to a light requirement for seeds of *B. alleghaniensis*, while *Rhus* seeds chiefly require scarification as a pretreatment to germination. In their study, *B. alleghaniensis* seeds beneath litter that did not emerge also did not germinate, therefore Peterson and Facelli (1992) conclude that reduced establishment in response to litter was due to lack of germination rather than an inability to penetrate the litter layer.

Among those tree species compared in the present study, *B. lenta* is regarded to be most dependent on light as a germination cue (Young and Young 1992). Field-sown seeds of *L. styraciflua*, *Q. velutina*, and *Q. rubra* benefit from light mulching, while *Q. velutina* and *Q. rubra* germinate best in partial shade (Young and Young 1992) therefore these species may benefit from being under some leaf litter in forest conditions. Similar to the findings of Peterson and Facelli (1992), none of the *B. lenta* seedlings in our study that germinated did not emerge through the litter. These results suggest that litter negatively affects establishment of *Betula* spp. by obstructing light that is apparently needed for germination, more so than by presenting a physical barrier to emergence.

Liquidambar styraciflua emergence was reduced only in deep litter conditions. Many of the seedlings that emerged in both shallow and deep litter did so through openings in the litter created by *Quercus* seedlings. Thus, our results may overestimate this species' ability to germinate and emerge in litter, although all tree species in forests coexist with other taxa. While all seeds that had germinated also emerged, some seedlings of *L. styraciflua* had not yet developed leaves by the end of the experiment (eight weeks). The percentage of leafless seedlings in-

Table 3. Summary of independent one-way ANOVA results for factors affecting seedling growth (analyses conducted on untransformed data unless indicated.) Comparisons were among the bare (B), shallow (S), and deep (D) litter treatments for each species except for *B. lenta* for which there was no emergence in the deep litter treatment (ND = not measured for *B. lenta* due to negligible biomass).

| Species | Seedling height | | | Aboveground biomass | | |
|--------------------------------|--------------------|--------|-----------|---------------------|-------|-------------------|
| | F | P | Response | F | P | Response |
| <i>Betula lenta</i> | 40.6 ^a | <0.001 | B < S | 0.109 ^a | 0.75 | |
| <i>Liquidambar styraciflua</i> | 48.4 | <0.001 | B < S, D | 3.497 ^a | 0.038 | B > S D ≈ B, S |
| <i>Ailanthus altissima</i> | 170.4 ^a | <0.001 | B < S < D | 3.783 ^a | 0.027 | B > D S ≈ B, D |
| <i>Quercus velutina</i> | 53.5 | <0.001 | B < S < D | 1.292 | 0.28 | |
| <i>Quercus rubra</i> | 20.3 | <0.001 | B, S < D | 1.011 | 0.37 | |

^a Log transformed.

creased directly in relation to the amount of litter with 3.6% in the bare soil, 22.6% in shallow litter, and 50% in deep litter. This may indicate that emergence in the presence of litter, even with the presumed advantage of these openings, was either delayed or placed a greater demand on the initial reserves of these seeds and slowed seedling development. Whether small-seeded species actively exploit such openings in the field seems worthy of further study.

In our experiments, percent emergence of *A. altissima* did not differ significantly among treatments. In greenhouse studies, Facelli and Pickett (1991c) found that litter delayed the emergence of *A. altissima* by approximately two days but it did not affect percent emergence. In a follow-up field experiment, Facelli (1994) found no significant differences in emergence of *A. altissima* among litter treatments in plots pro-

tected from herbivory. Our results and these previous studies suggest that *A. altissima* has the ability to germinate in a wide range of litter conditions, which could be one attribute that has enabled it to be such a successful invasive species.

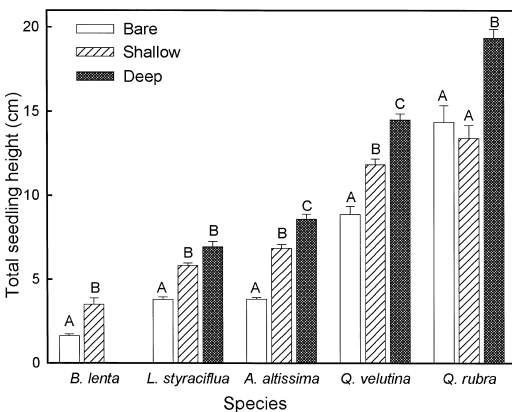


FIG. 2. Total seedling height (mean ± SE) of tree seedlings in response to bare, shallow, and deep litter depth treatments (no *Betula lenta* seedlings germinated in deep litter). For each dependent variable, treatment means not sharing a letter differ significantly (ANOVA: $P < 0.05$).

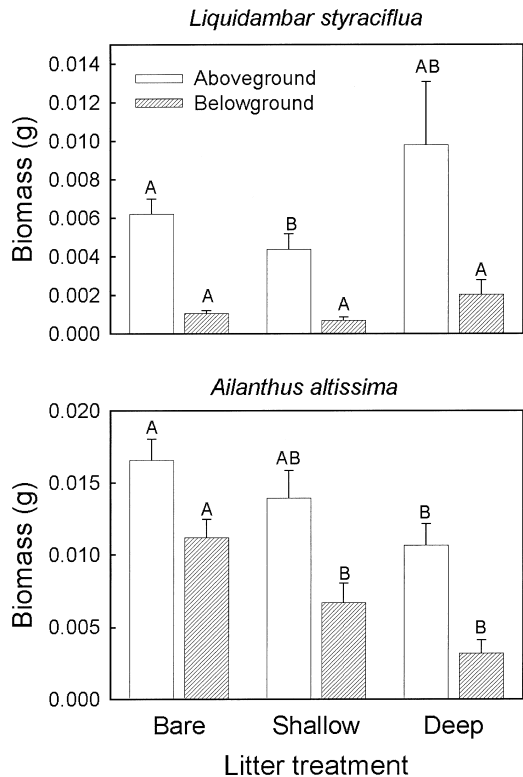


FIG. 3. Above- and belowground biomass (mean ± SE) of *Liquidambar styraciflua* seedlings (bare, $N = 27$; shallow, $N = 24$; deep $N = 3$) and *Ailanthus altissima* seedlings (bare, $N = 31$; shallow, $N = 35$; deep, $N = 22$) in response to litter depth treatments. Treatment means not sharing a letter differ significantly (ANOVA: $P < 0.05$).

Table 3. Extended.

| Belowground biomass | | | Stem biomass | | | Leaf biomass | | |
|---------------------|----------|-------------------------|--------------------|----------|-----------|--------------------|----------|----------|
| <i>F</i> | <i>P</i> | Response | <i>F</i> | <i>P</i> | Response | <i>F</i> | <i>P</i> | Response |
| 0.32 ^a | 0.58 | | ND | | | ND | | |
| 3.37 ^a | 0.0444 | no pairwise differences | 1.219 ^a | 0.30 | | 9.250 ^a | <0.001 | B, D > S |
| 13.50 ^a | <0.001 | B > S, D | 0.905 ^a | 0.409 | | 6.581 ^a | 0.002 | B > S, D |
| 0.54 | 0.58 | | 15.154 | <0.001 | B < S < D | 0.635 | 0.53 | |
| 1.13 | 0.33 | | 9.953 | <0.001 | B, S < D | 0.553 | 0.58 | |

Previous studies have shown that other *Quercus* species have greatest emergence under litter greater than 2 cm deep. In a field experiment, Shaw (1968) found that seeds of *Q. petraea* had the greatest percent emergence when covered with 2.5–4 cm litter, compared with surface sown seeds and seeds buried in the soil. Barrett (1931) conducted a field survey of leaf litter

depth, sprouted, and unsprouted acorns of *Q. montana*. He found that quadrats with no litter had the lowest percent emergence (35%) of *Q. montana* seeds. Quadrats with approximately 1.25 cm litter had 65% emergence while quadrats with approximately 2.5–10cm litter had 90% emergence. In our experimental study, percent emergence of *Q. rubra* was 50% greater in the deep (ca. 5 cm) litter treatment than it was in the shallow (1–2 cm) litter treatment.

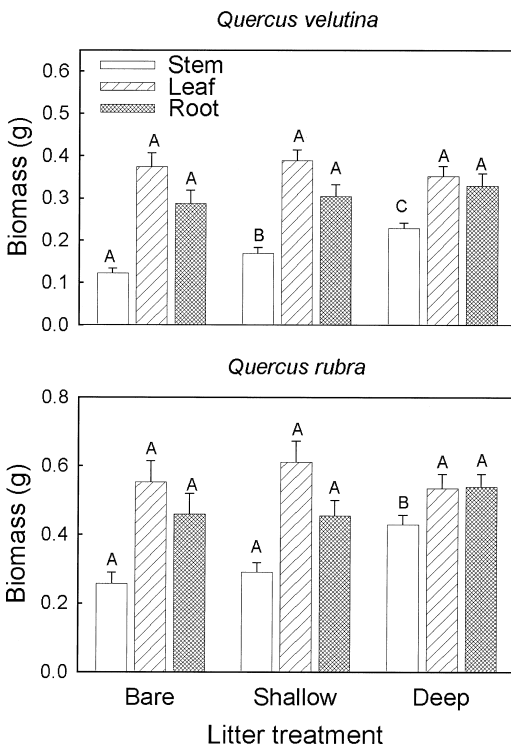


FIG. 4. Stem, leaf, and root biomass (mean \pm SE) of *Quercus velutina* seedlings (bare, $N = 22$; shallow, $N = 36$; deep, $N = 42$) and *Quercus rubra* seedlings (bare, $N = 25$; shallow, $N = 23$; deep, $N = 37$) in response to litter depth treatments. Treatment means not sharing a letter differ significantly (ANOVA: $P < 0.05$).

BIOMASS ALLOCATION AND SEED SIZE. Seedlings of smaller-seeded species tended to be more negatively affected by leaf litter depth than were seedlings of larger-seeded species (Tables 3 and 4; Figs. 2–4). Larger seeds have greater energy reserves which may make them less sensitive to certain physical conditions, such as shade or leaf litter. These patterns suggest that larger-seeded species can establish and grow under a wider range of physical conditions than smaller-seeded species.

ROBUSTNESS AND ETIOLATION. Robustness, based on aboveground biomass/seedling height, was used as an indicator of the sturdiness of seedlings and may be regarded as the inverse of etiolation. Greater litter cover resulted in reduced robustness (and therefore increased etiolation) especially in smaller-seeded species (Table 4). All five species for which seedling measurements were taken exhibited increased height and hypocotyl length with increased litter depth. The extent of this increase, however, tended to be inversely related to seed size. Also, as height increased, *B. lenta*, *L. styraciflua*, and *A. altissima* seedlings had the same amount or less biomass allocated aboveground (Table 3, Fig. 3). As a result, these three species had significantly reduced robustness in conditions with litter than on bare soil. Seedling robustness declined with deeper litter for *Q. velutina*, as well, however *Q.*

Table 4. Results of Kruskal-Wallis Tests of factors affecting the derived variables expressing relative seedling growth. Comparisons are among bare, shallow and deep treatments unless indicated (1 = bare vs. shallow only, Mann-Whitney *U*-test statistic reported).

| Species | Robustness (aboveground biomass/height) | | | Root:shoot | | |
|----------------------------------|--|----------|--|------------|----------|--|
| | <i>U</i> | <i>P</i> | Litter treatment with highest mean biomass | <i>U</i> | <i>P</i> | Litter treatment with highest mean biomass |
| <i>Betula lenta</i> ¹ | 81.5 | 0.013 | bare | 43.5 | 0.60 | |
| <i>Liquidambar styraciflua</i> | 15.961 | 0.003 | bare | 4.018 | 0.134 | |
| <i>Ailanthus altissima</i> | 36.086 | <0.001 | bare | 33.345 | <0.001 | bare |
| <i>Quercus velutina</i> | 12.152 | 0.002 | bare | 0.843 | 0.66 | |
| <i>Quercus rubra</i> | 6.957 | 0.031 | shallow | 1.91 | 0.38 | |

velutina seedlings were still able to produce comparatively sturdy stems in deep litter because there was an increase in stem biomass that accompanied the increased height. Robustness of seedlings of *Q. rubra* was improved by the presence of shallow but not deep litter. These results suggest that seedlings of the three smaller-seeded species tend to be weaker-stemmed with increased litter. The oak species, with their large seeds, apparently have sufficient energy reserves to support the longer stems without sacrificing sturdiness. These patterns may have implications for population survival and recruitment in forests. Although the adaptive advantage of increased robustness has not been demonstrated, it has been suggested that more robust seedlings may be more resistant to physical damage (Peterson and Facelli 1992, Ellsworth et al. 2004). In any case, the oak species appear to be better adapted for recruitment in forests with substantial litter than the other three species.

AILANTHUS ALTISSIMA—A NON-NATIVE SPECIES. *Ailanthus altissima* seedlings tended to be more flexible in their ability to allocate biomass than some of the native species, and were less affected by litter depth (including emergence rates) than other small-seeded species. *Ailanthus altissima* is the only species in this study that exhibited a difference in root:shoot ratio in response to litter depth treatments. Seedlings of *A. altissima* grown in deep litter allocated relatively less to roots than those seedlings in the shallow litter or bare treatments. Seedlings may have a reduced ability to absorb water and nutrients from the soil, making them less competitive than seedlings of other species. However, if the seedlings of this species can survive this way in the short-term, they may be able to compensate later in the growing season. Facelli and Pickett

(1991c) found that hypocotyl length and stem biomass were significantly increased and leaf area and biomass were significantly decreased in litter treatments for *A. altissima* seedlings 8–12 days old, but by 40–44 days after emergence, hypocotyl length was the only significantly different variable. This suggests that with time, seedlings of *A. altissima* may be able to overcome most of the initial negative effects of leaf litter which we identified in our study. Ellsworth et al. (2004) found that a non-native vine species, *Celastrus orbiculatus*, is also able to shift the allocation of resources in response to a dense litter layer.

The redistribution of biomass in response to litter tended to occur primarily in the aboveground biomass for the other species. The size and strength of the stem and the leaf biomass were quite variable among species in this study. It may be that the ability to overcome an initial disadvantage of reduced root biomass is uncommon among species and that this contributes to *A. altissima*'s invasive ability. Among the small-seeded species, our data suggest a competitive advantage for *A. altissima*. However, when comparing seedlings grown in different litter depths, all measures indicate potentially reduced survivorship of *A. altissima* in deeper litter than in shallow litter or no litter. This may explain, at least in part, the successful invasion of this species into urban forests in the New York City metropolitan area, which tend to have a shallower litter layer than relatively nearby rural forests (Kostel-Hughes et al. 1998).

Conclusions. *Betula lenta* and *L. styraciflua*, the two smallest-seeded species in our study exhibited both reduced emergence and greatly modified seedling growth (suggesting potentially reduced fitness) in the presence of leaf litter. The

two largest-seeded species, *Q. velutina* and *Q. rubra*, exhibited little overall difference (or an increase) in emergence or seedling growth due to the presence of leaf litter. Oaks are thus better-suited to establishment in more mature woods, whereas birch and sweetgum are better suited to colonizing younger, post-disturbance sites where there is likely to be less litter. This is consistent with the classification of red oak and black oak as intermediate in shade tolerance and mid-to-late-successional forest species whereas birch and sweetgum are shade intolerant pioneer species (Burns and Honkala 1990). *Ailanthus altissima* seedlings, while able to germinate well regardless of litter depth, exhibited reduced robustness, root:shoot ratio, and root biomass with increased litter depth. However, *A. altissima* may be able to respond to different conditions in ways that allow it to allocate resources that improve its ultimate survivorship and fitness. Such attributes could contribute to the invasiveness of *A. altissima* in forests with shallower litter layers, such as the urban and suburban forests in the New York City metropolitan area. In contrast, this shallower litter layer may result in reduced recruitment of red oak in the urban forests compared to their rural counterparts along this gradient. Lastly, the patterns of responses to litter depth demonstrated in our study may have implications for temperate deciduous forests that are unaffected by non-native earthworms but which may have reduced litter depth due to edge effects created by forest fragmentation (Matlack 1993) and forest roads (Haskell 2000).

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