Vegetatio **114**: 169–174, 1994.

Contrasting litter effects on old field tree germination and emergence

Randall W. Myster
Terrestrial Ecology Division, University of Puerto Rico, P.O. Box 363682, San Juan, PR 00936, USA

Accepted 12 January 1994

Key words: Seed mass, Forest regeneration, New Jersey, USA

Abstract

Because the fate of seeds is critical to understanding the invasion of old fields by trees, and plant litter is an important component defining the old field microsite of dispersed seeds, I investigated the effects of litter type (*Solidago* spp./goldenrod, *Quercus* spp./oak, mixed) and litter amount (100–800 g/m^2) on tree seed germination and seedling emergence. I found that at all densities both *Solidago* and *Quercus* litter greatly reduced emergence of the small-seeded, bird-dispersed species, *Juniperus virginiana* and *Cornus florida*. For one of the large-seeded, mammal-dispersed species, *Carya tomentosa*, high density *Solidago* litter and high density mixed litter treatments reduced emergence. For the other large-seeded species, *Quercus rubra*, the high density mixed litter treatment and all levels of *Solidago* litter reduced emergence. *Quercus* seedlings emerged twice as often as the other three species in control pots without litter. *Carya* emerged before the other species but the high density oak treatment delayed the expansion of its cotyledons. My results suggest that litter may contribute to the slow rate of tree invasion and the low probability of tree establishment in old fields. However, old field litter studies taken together point to the difficulty in drawing general conclusions about any 'net effect' of litter on old field tree establishment.

Introduction

Forests in the eastern United States are disturbed by a variety of natural and human activities (e.g. tree fall gaps, clear-cutting, fires, mine spoils, agriculture). After many of these disturbances, saplings or seedlings remain and trees can regenerate from these or sprout from living roots and stumps (Gholz *et al.* 1985; Runkle 1985). However, in an old field left fallow after agriculture, the woody vegetation is no longer present and trees can only reestablish from seeds (Buell *et al.* 1971; Myster & Pickett 1992). The tree seeds of the eastern USA commonly have short viability (Schopmeyer 1974) and little persistent old field seed bank (Oosting & Humphreys 1940; Livingston & Allessio 1968; Myster & Pickett 1992), and, therefore, tree establishment must come from seeds dispersed from outside the old field and the fate of these seeds influences invasion dynamics, rate of succession, growth, and spatial pattern of trees (Myster & Pickett 1992, 1993).

The influence of litter on seed and seedling processes is well documented (Grime 1979; Sydes & Grime 1981; Spence 1982; Van der Valk 1986; Vazquez-Yanes *et al.* 1990; Facelli & Pickett 1991a; Peterson & Facelli 1992). Litter is a dominant feature of the old field microhabitat, and interactions between litter and old field plants are potentially complex (Gross & Werner 1982, Monk & Gabrielson 1985; Facelli & Pickett 1991a). For example, interactions between the ground microhabitat and seed characteristics greatly influence old field tree establishment (Myster & Pickett 1992, 1993). Litter may increase germination by decreasing moisture and temperature extremes (Burton & Bazzaz 1991) for large seeds (Barrett 1931; Sork 1983), or by increasing soil nitrate through decomposition (Pons 1989) for small seeds. Conversely, litter may present a physical barrier to the germination and emergence of small seeds (Facelli & Pickett 1991a; Peterson & Facelli 1992). In addition, litter may increase (Abbott & Quink 1970; Price & Jenkins 1986) or decrease seed predation (Myster & Pickett 1993), prevent seed dehydration on bare soil, or foster fungal (Fenner 1985) and micro-organism growth (Florence 1965).

In the old fields of New Jersey, wind- and bird-dispersed species are the first trees to invade with mammal-dispersed trees present in the second decade after abandonment (Bard 1952; Myster & Pickett 1992). Here, tree invasion is tied to the forest edge and its oak litter accumulation, with extensive clumping of the bird-dispersed species occurring later in succession (Myster & Pickett 1992). A previous study (Myster & Pickett 1993) found that litter affected predation on tree seeds differentially between species, areas and ages of old fields. Here I focus on a later regeneration filter, the fate of seeds that survive predation, by asking in a greenhouse study (1) Is tree seed germination affected by the presence of litter?, (2) Is the timing of tree seedling emergence affected by litter? and (3) How do these effects differ between amount and type of litter, species and dispersal agent/seed mass of tree?

Methods

The study was conducted in a greenhouse located on the Cook College Campus, Rutgers University in New Brunswick, Middlesex County, New Jersey, USA (40° 30′N, 74° 34′W). Seeds of four autumn-dispersing tree species were used in the January–April 1991 experiment when they would normally be on the ground ready to germinate. The species were the bird-dispersed, small-seeded species *Juniperus virginiana* (Nomenclature follows Gleason & Cronquist 1963; 0.005 grams/seed fresh mass) and *Cornus florida* (0.08 g/seed), and the mammal-dispersed, large-seeded species *Quercus rubra* (3.5 g/seed) and *Carya tomentosa* (4.4 g/seed). These are abundant tree species during the first 32 years of old field succession in New Jersey (Buell *et al.* 1971, Pickett 1982, Myster & Pickett 1992) and include the dominant species in New Jersey old-growth forests (Bard 1952). These seeds were collected locally in New York, New Jersey and Pennsylvania by Sheffield Seed Co. of Locke, New York. Their tests yielded greater than 90% germination and they scarified all *Juniperus* and *Cornus* seeds used. Seeds from the most abundant New Jersey old field wind-dispersed tree species *Acer rubrum* (0.015 g/seed) and *Fraxinus americana* (0.043 g/seed; Myster & Pickett 1993) were not available from local trees at the start of the experiment, or from Sheffield Seed Co. *Quercus* spp. and *Solidago* spp. litter was used because they are the most common litter types in New Jersey old fields (Facelli & Carson 1991). The litter was collected in local old fields, dried at room temperature for a week before use and then broken by hand into pieces.

I tested the effect of amount and type of litter on germination, emergence, and seedling morphology in pots using a randomized 2 × 3 factorial experiment and a control treatment in which no litter was used. Amount of litter was either low or high, while the type of litter was oak (*Quercus* spp.) leaves, goldenrod (*Solidago* spp.) stems, fruits and leaves, or a mix of the oak and goldenrod litter. The resulting treatments were therefore control, low oak, high oak, low goldenrod, high goldenrod, low mix and high mix. The amount of litter added to the pots reflected naturally occurring densities of these dominant litter types in New Jersey old fields (Facelli & Carson 1991). The low oak density was 100 grams/m^2, high oak 200 g/m^2, low goldenrod 400 g/m^2, high goldenrod 800 g/m^2, low mix was a combination of 50 g/m^2 oak with 200 g/m^2 goldenrod and high mix was a combination of 100 g/m^2 oak with 400 g/m^2 goldenrod. The pot surface area was 126.7 cm^2 and litter was added proportionally to preserve these densities. In January 1991, each pot was filled with standard greenhouse potting mix, and five seeds of each test species were spread over the soil surface of an individual pot (the maximum possible number of the large *Carya* seeds that could fit without touching the pot) and then covered by litter. The treatments were replicated six times for each species making a total of 168 pots. During the following 10 weeks of the experiment, the pots were sprayed with a fine mist every ten minutes during the daylight hours. A natural light regime was maintained in the greenhouse during the experiment and the temperature range was between 18–25 °C.

I counted and identified seedlings (the epicotyl or other part of an emerging seedling; Burton & Bazzaz 1991) as they emerged above the litter every week. I also recorded status (alive or dead) of all seedlings and presence of cotyledons. Because the range of distinct values for seedling number per pot (0 to 5) was too narrow to approximate a continuous function (Dr. Peter Morin, Rutgers Ecology Program, personal communication), logistic regression analysis (LGA, a maximum likelihood regression based on categorical data modeling; SAS 1985, Gaines & Rice 1990) was used to compute treatment effects. In addition, I compared per-pot emergence between treatments using one-way analysis of variance (ANOVA; Dr. Javier Cabrera, Rutgers Statistics Department, personal communication). To analyze for interaction between litter amounts and

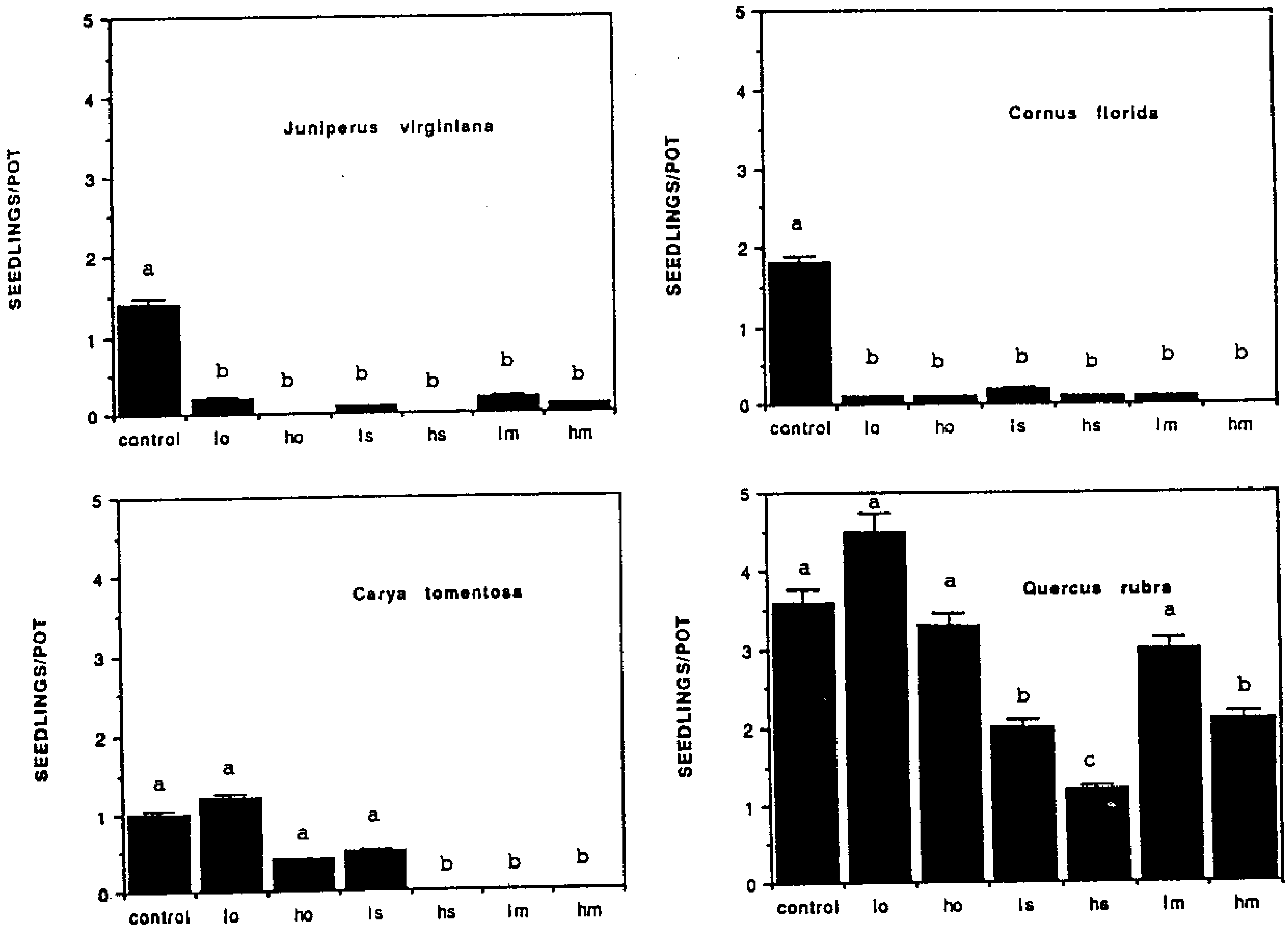

Fig. 1. Mean number of emerged seedlings per pot from various litter treatments for each of the four test tree species. Error bars are one standard error. Treatments: Control - no litter; lo - low density oak (*Quercus* spp.) leaves; ho - high density oak leaves; ls - low density goldenrod (*Solidago* spp.) leaves, fruits and stems; hs - high density goldenrod leaves, fruits and stems; lm -low density mix of oak and goldenrod litter; hm - high density mix of oak and goldenrod litter. See text for details of treatments. Means sharing the same letters are statistically indistinguishable using the Turkey-Kramer separation test.

types, I used two way factorial ANOVAs, excluding the control, using pots as experimental units. P-values from both analyses are presented in the results section, with ANOVA always *first*. Tukey-Kramer separation procedures were used as a common method to detect differences among means.

Results

The presence of litter significantly reduced seedling emergence (df = 5, ANOVA P = 0.030, LGA P = 0.032, Fig. 1) and this effect was most obvious when comparing the small-seeded species, *Juniperus* and *Cornus*, with the large-seeded species *Carya* and *Quercus*. In particular, every litter treatment greatly reduced germination and emergence of *Juniperus* and *Cornus* (df = 5, P<0.001, P<0.001) and for a number of treatments, no seedlings emerged at all. For these small-seeded species, there was no significant interaction between type and amount of litter because few seedlings emerged in any of the litter treatments. These effects on emergence are probably equivalent to effects on germination because I did not observe any germination in which the seed did not penetrate the physical obstruction of the litter (Grime 1979).

Litter also significantly reduced emergence for *Carya* and *Quercus* (df = 5, P = 0.041, P = 0.045, Fig. 1), with the high density goldenrod and both mix treatments preventing *Carya* emergence completely. For *Quercus*, high density goldenrod reduced emergence most (to ~ 1/3 of control density) with the low density goldenrod and high density mix treatments also reducing emergence (to ~ 1/2 of control density). However, contrasting litter effects were seen because in the low density oak litter treatment, more *Carya* and *Quercus* seedlings emerged compared with the control (also see Burton & Bazzaz 1991), and this was significant when compared to other litter treatments (Fig. 1). All other treatments showed less emergence compared with the control and observed seed loss due to fungus was minimal for all species. In the control pots without litter, *Cornus*, *Juniperus*, and *Carya* emerged at a mean density of 1–2 seedlings per pot whereas *Quercus* had twice that emergence. Similarly in the treatment pots, *Quercus* (having the seed with the largest mass) showed the most emergence compared to the other species. In addition, litter significantly reduced above-ground biomass for *Carya* and *Quercus* (df=4, P=0.041, P=0.044) where the greatest reduction occured for *Carya* under the high oak treatment. In general as seeds increased in mass, litter had less of an inhibition effect and may even have facilitated emergence for some *Carya* and *Quercus* seeds.

The mean day of cotyledon opening for seedlings in control pots was 48 days for *Juniperus*, 54 days for *Cornus*, 41 days for *Carya* and 49 days for *Quercus*. Control seedlings of *Carya* opened their first leaf/cotyledon significantly sooner than all other species (df = 3, P = 0.027, P = 0.039). In addition, the date of opening for *Carya* was significantly delayed by the high density oak treatment (to approx. 66 days) when compared with controls (df = 5, P = 0.04, P = 0.032). Although there were not enough seedlings in the *Juniperus* and *Cornus* treatment pots to assess litter effects on timing of cotyledon opening for those species, the timing for *Quercus* was very close to 49 days regardless of treatment.

Discussion

Because high density treatments always produced either the same or lower emergence compared to the low density treatments within the same litter type, and because the effect of litter type regardless of density did not form a clear trend, the inhibition mechanism may have been physical rather than chemical (Peterson & Facelli 1992). This implies that germination is light sensitive (Burton 1982) or that the hypocotyl (esp. of small seeded species) cannot physically penetrate the litter layer (Grime 1979; Facelli & Pickett 1991a, b), and agrees with the observation that there may be a direct recruitment relationship between depth of litter and the mass of the seed (van der Valk 1974). The larger seeds of *Carya* and *Quercus* could penetrate the litter layer, perhaps because of sufficient carbohydrate reserves, and, therefore, ranges of litter density where germination and emergence occurs (implied by the pattern of increased emergence at some densities and a decrease at others) may represent important filters to establishment for these species.

Combining my results with other studies on litter and old field tree establishment (for a review see Myster 1993) shows how difficult it may be to find a 'net effect' (sensu Connell *et al.* 1987) of litter on tree establishment in old fields. For example, seed predation on *Quercus rubra* is reduced by litter (Myster & Pickett 1993), but results here show a pattern that suggests that *Quercus* germination may be enhanced by some litter treatments while being inhibited by others. In addition, for *Quercus* seedlings, litter may reduce the effect of drought (Fowells 1965). Because the seeds of most old field tree species overwinter (Fowells 1965), litter may prevent early emergence and loss of seedlings to frost-heaving (Buell *et al.* 1971), although it may also increase seedling risk from physical damage (Barrett 1931; McCarthy & Facelli 1990) and from competition with neighboring vegetation (Peterson & Facelli 1992). Similarly, Hamrick & Lee (1987) found that even if species emerge better under litter, seedling mortality may be high because of energy lost penetrating the litter mat.

In conclusion, the large number of litter inhibition studies suggest that litter may contribute to a low probability of tree establishment especially when, as they often do, litter fall and seed dispersal coincide. In addition, litter effects on germination, emergence and growth may help explain the slow rate of tree succession in eastern U.S. old fields (Bard 1952; Bazzaz 1968; Gill & Marks 1991), and, because of the extensive variation in litter effects at the regeneration level, litter may influence relative abundances of species (Facelli & Pickett 1991a) and spatial heterogeneity (Myster & Pickett 1992) in old fields.

Acknowledgments

The author wishes to thank Ms. Nikki Graf and the rest of the staff of the Floriculture greenhouse, Cook College, Rutgers University, New Brunswick, New Jersey 08854 USA for the use of their facility and helpful advice during this experiment. I also wish to thank M. Aide, L. Walker, J. Zimmerman and C. Peterson for commenting on earlier drafts of the manuscript.

References

Abbott, H. G. & Quink, T. F. 1970. Ecology of eastern white pine seed caches made by small forest mammals. Ecology 51: 271–278.

Bard, G. E. 1952. Secondary succession on the Piedmont of New Jersey. Ecological Monographs 22: 195–215.

Barrett, L. I. 1931. Influence of forest litter on the germination and early survival of chestnut oak, *Quercus montana* Willd. Ecology 12: 476–484.

Bazzaz, F. A. 1968. Succession on abandoned fields in the Shawnee Hills, Southern Illinois. Ecology 49: 924–936.

Buell, M. F., Buell, H. F., Small, J. A. & Siccama, T. G. 1971. Invasion of trees in secondary succession on the New Jersey piedmont. Bulletin of the Torrey Botanical Club 98: 67–74.

Burton, P. J. 1982. The effects of temperature and light on *Metrosideros polymorpha* seed germination. Pacific Science 36: 229–240.

Burton, P. J. & Bazzaz, F. A. 1991. Tree seedling emergence on interactive temperature and moisture gradients and in patches of old-field vegetation. American Journal of Botany 78: 131–149.

Connell, J. H., Noble, I. R. & Slatyer, R. O. 1987. On the mechanisms producing successional change. Oikos 50: 136–137.

Facelli, J. M. & Carson, W. P. 1991. Heterogeneity of plant litter accumulation in successional communities. Bulletin of the Torrey Botanical Club 118: 62–66.

Facelli, J. M. & Pickett, S. T. A. 1991a. Plant litter: Its dynamics and effects on plant community structure. The Botanical Review 57: 1–32.

Facelli, J. M. & Pickett, S. T. A. 1991b. Plant litter: light interception and effects on an oldfield plant community. Ecology 72: 1024–1031.

Fenner, M. 1985. Seed Ecology. Chapman and Hall, New York, USA.

Fowells, H. A. 1965. Silvics of forest trees of the United States. USDA Forest Service Agricultural Handbook No. 271, 762 p.

Florence, R. G. 1965. Decline of old-growth redwood forests in relation to some soil microbiological processes. Ecology 46: 52–64.

Gaines, S. D. & Rice, W. R. 1990. Analysis of biological data when there are ordered expectations. American Naturalist 135: 310–317.

Gill, D. S. & Marks, P. L. 1991. Tree and shrub seedling colonization of old fields in central New York. Ecological Monographs 61: 183–206.

Gholz, H. L., Hawk, G. M., Campbell, A., Cromack, K. & Brown, A. T. 1985. Early vegetation recovery and element cycles on a clearcut watershed in western Oregon. Canadian Journal of Forestry Research 15: 400–409.

Gleason, H. A. & Cronquist, A. 1963. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. D. Van Nostrand Company, New York, USA.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley and Son, New York.

Gross, K. L. & Werner, P. A. 1982. Colonizing abilities of biennial plant species in relation to ground cover: Implications for their distributions in a successional sere. Ecology 63: 921–931.

Hamrick, J. L. & Lee, J. M. 1987. Effect of soil surface topography and litter cover on the germination, survival and growth of musk thistle (*Carduus nutans*). American Journal of Botany 74: 451–457.

Livingston, R. B. & Allessio, M. L. 1968. Buried viable seed in successional field and forest stands, Harvard Forest, Massachusetts. Bulletin of the Torrey Botanical Club 95: 58–69.

McCarthy, B. C. & Facelli, J. M. 1990. Microdisturbances in old fields and forests: Implications for woody seedling establishment. Oikos 58: 27–33.

Monk, C. D. & Gabrielson, F. C. 1985. Effects of shade, litter and root competition on old field vegetation in South Carolina. Bulletin of the Torrey Botanical Club 112: 383–392.

Myster, R. W. & Pickett, S. T. A. 1992. Effects of palatability and dispersal mode on spatial patterns of trees in old fields. Bulletin of the Torrey Botanical Club 119: 145–151.

Myster, R. W. & Pickett, S. T. A. 1993. Effects of litter, distance, density and vegetation patch type on postdisperal tree seed predation in old fields. Oikos 66: 381–388.

Myster, R. W. 1993. Tree invasion and establishment in old fields at Hutcheson Memorial Forest. The Botanical Review 59: 251–272.

Oosting, H. J. & Humphreys, M. E. 1940. Buried viable seeds in a successional series of old field and forest soils. Bulletin of the Torrey Botanical Club 67: 253–273.

Peterson, C. & Facelli, J. M. 1992. Contrasting germination and seedling growth of *Betula alleghaniensis* and *Rhus typhina* subjected to various amounts and types of plant litter. American Journal of Botany 79: 1209–1216.

Pickett, S. T. A. 1982. Population patterns through twenty years of oldfield succession. Vegetatio 49: 45–59.

Pons, T. L. 1989. Breaking of seed dormancy by nitrate as a gap detection mechanism. Annals of Botany 63: 139–143.

Price, M. V. & Jenkins, S. H. 1986. Rodents as seed consumers and dispersers. In: Murray DR (ed) Seed dispersal. Academic Press, New York. pp 191–236.

Runkle, J. R. 1985. Disturbance regimes in temperate forests. In: Pickett, S. T. A. & White, P. S.(eds) The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, FL. pp 17–34.

SAS 1985. SAS/STAT User's Guide. Release 6.03 Edition. SAS Institute Inc., CARY, NC

Schopmeyer, C. S. 1974. Seeds of woody plants in the United States. Handbook no. 450. Forest Service, USDA, Washington, D.C, USA.

Sork, V. L. 1983. Distribution of pignut hickory *Carya glabra* along a forest to edge transect and factors affecting seedling recruitment. Bulletin of the Torrey Botanical Club 10: 494–506.

Spence, D. H. 1982. The zonation of plants in fresh water lakes. Advances in Ecological Research 12: 37–125.

Sydes, C. & J. P. Grime. 1981. Effects of tree litter on herbaceous vegetation in the deciduous woodlands. II An experimental investigation. Journal of Ecology 69: 249–262.

Van der Valk, A. G. 1974. Environmental factors controlling the distribution of forbs on coastal foredunes in Cape

Hatteras National Seashore. Canadian Journal of Botany 52: 1057–1073.

Van der Valk, A. G. 1986. The impact of litter and annual plants on recruitment from the seed bank of a lacustrine wetland. Aquatic Botany 24: 13–26.

Vazquez-Yanes, C., A. Orozco-Segovia, E. Rincon, M. E. Sanchez-Coronado, P. Huante, J. R. Toledo & V. L. Barradas. 1990. Light beneath the litter in a tropical forest: Effect on seed germination. Ecology 71: 1952–1958.