

Canopy type, forest floor, predation, and competition influence conifer seedling emergence and early survival in two Minnesota conifer–deciduous forests

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Abstract: There is concern that the conifer component of mixed conifer–deciduous forests in the Great Lakes region is on the decline, possibly the result of insufficient conifer regeneration. Limitations on conifer regeneration that occur during the first 18 months of seedling emergence and establishment were examined for *Abies balsamea* (L.) Mill. and *Pinus strobus* L. in two mixed conifer–deciduous forest types in northeastern Minnesota. We hypothesized that the removal of potential barriers to regeneration, including forest floor, seed predation, and competition with understory vegetation, will enhance conifer regeneration. We also hypothesized that the importance of the above regeneration barriers, and early regeneration success of each species, will differ beneath deciduous and conifer canopy types. The study was conducted under conifer and deciduous canopy types for two sites of each forest type: *Abies balsamea* – *Populus tremuloides* Michx. forest and *Thuja occidentalis* L. – *Betula papyrifera* Marsh. Germination experiments were conducted with seeds of *A. balsamea* and *P. strobus*. Experimental treatments included forest floor removal, caging to exclude seed predators and herbivory, and weeding to study the effects of understory competition. *Abies balsamea* and *P. strobus* responded differently to experimental treatments at different developmental stages. The best conditions for early regeneration of both *A. balsamea* and *P. strobus* included reduction of seed predation ($p < 0.0001$) and competition with understory vegetation ($p \leq 0.001$). *Abies balsamea* additionally benefited from a conifer overstory ($p < 0.0001$) and a reduction in thickness of the forest floor ($p < 0.01$).

Résumé : Le déclin de la composante coniférienne des forêts mixtes conifériennes–décidues dans la région des Grands Lacs devient préoccupant. Il pourrait être dû à une régénération coniférienne insuffisante. Les obstacles à la régénération des conifères, qui se manifestent pendant les premiers 18 mois de l'émergence et de l'établissement des semis, ont été examinés pour *Abies balsamea* (L.) Mill. et *Pinus strobus* L., dans deux types forestiers mixtes conifériens–décidus du nord-est du Minnesota. Les auteurs ont émis l'hypothèse que l'élimination des barrières potentielles à la régénération, incluant la litière, la prédation des semences et la compétition de la végétation du sous-bois, améliorera la régénération des conifères. Ils ont aussi émis l'hypothèse que l'importance des barrières mentionnées, ainsi que la réussite de chaque espèce, tôt au cours de la régénération, seront différentes sous les types de couvert décidu et coniférien. L'étude a été réalisée sous les types de couvert décidu et coniférien dans deux sites de chacun des types forestiers suivants : forêt d'*Abies balsamea* – *Populus tremuloides* Michx. et de *Thuja occidentalis* L. – *Betula papyrifera* Marsh. Les essais de germination ont été réalisés avec les semences de *A. balsamea* et de *P. strobus*. Les traitements expérimentaux comprenaient l'enlèvement de la litière, l'utilisation de cages pour exclure les prédateurs des semences et les herbivores, ainsi que le sarclage pour étudier les effets de la compétition du sous-bois. *Abies balsamea* et *P. strobus* ont répondu différemment à ces traitements expérimentaux, à différents stades de leur développement. Les meilleurs conditions, tôt au cours de la régénération, aussi bien d'*A. balsamea* que de *P. strobus*, comprenaient la réduction de la prédation ($p < 0,0001$) et la compétition de la végétation du sous-étage ($p \leq 0,001$). En plus, *A. balsamea* a bénéficié du couvert coniférien ($p < 0,0001$) et de la réduction de l'épaisseur de la litière ($p < 0,01$).

[Traduit par la Rédaction]

Introduction

Forests dominated by conifers were once a widespread component of the northern Great Lakes landscape (Ontario, Minnesota, Michigan, and Wisconsin). Extensive logging and ensuing fires at the time of European settlement have resulted

in a Great Lakes landscape that is vastly changed. The forests of this region likely have been homogenized in structure and composition by past management practices (Mladenoff and Pastor 1993). Where a wide variety of forest types once intermingled on various spatial scales, today many areas are dominated by even-aged, early-successional deciduous forests, particularly of *Populus tremuloides* Michx. and *Betula papyrifera* Marsh. (Frelich 1995).

There is concern that the conifer component will be further reduced or eliminated from managed stands, leading to a reduction of landscape-level biodiversity (Jaakko Pöyry 1992). This concern is particularly strong with respect to *Pinus strobus* L., but includes *Abies balsamea* (L.) Mill., *Thuja occidentalis* L., and other conifer species. All three species impart

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Table 1. Site characteristics.

Soil series	A-horizon texture	Drainage class	Precip. (30-year avg.) (mm)	Precip. 1994 (mm)	Max. temp. (30-year avg.) (°C)	Max. temp. 1994 (°C)	Min. temp. (30-year avg.) (°C)	Min. temp. 1994 (°C)
AP1 Ontonagon*	Silt-clay, sandy loam	Well drained	318	329	25.0	24.8	10.7	10.8
AP2 Nemadji*	Sand, loamy sand	Moderately well drained						
TB1 Hibbing†	Silt loam	Well drained	285	261	22.4	19.4	10.5	9.51
TB2 Quetico-Rock†	Silt loam	Poorly drained						

Note: Weather data are representative of both sites within a study area and are for June, July, and August.

*Lewis (1978).

†Minnesota Department of Natural Resources (1980).

timber, wildlife, and conservation value to the stands in which they occur (Franklin 1974; Krugman and Jenkinson 1974; Schopmeyer 1974; Frank 1990; Johnston 1990; Wendel and Smith 1990).

Early barriers to conifer regeneration may occur during the establishment phase, and there may be differences among regenerating species and forest types in this respect. Among the barriers to conifer regeneration may be leaf litter (Ahlgren and Ahlgren 1981; Beatty 1984; Smith and Capelle 1992), seed predation (e.g., Haeussler et al. 1995), and competition with understory vegetation (e.g., Post 1970; Goldberg and Werner 1983; Larson 1989). These factors may interact with canopy type in a feedback system (e.g., Wilson and Agnew 1992), resulting in distinct "safe sites" for each regenerating species (Harper et al. 1961). The determination of what constitutes a safe site for different conifer species will further an understanding of how the conifer component is maintained in mixed conifer-deciduous forests and contribute to better management for species diversity.

The objective of this study was to investigate the ways in which early regeneration success of *A. balsamea*, *P. strobus*, and *T. occidentalis* differ beneath deciduous and conifer canopy types in mixed conifer-deciduous forests. However, because of low seed viability, *T. occidentalis* was excluded from the study. We studied early regeneration of the two study species in two conifer-deciduous forest types in northeastern Minnesota: *A. balsamea* – *Populus tremuloides* and *T. occidentalis* – *B. papyrifera* forests. We chose these forest types because they are of conservation interest and are dominated by a mixture of species of contrasting successional stages: *A. balsamea* and *T. occidentalis* are late-successional conifers and *Populus tremuloides* and *B. papyrifera* are early-successional deciduous trees. The use of two mixed conifer-deciduous forest types allowed a comparison of the regeneration requirements of two regionally important conifer species, *A. balsamea* and *P. strobus*, in a context that may be applicable to mixed conifer-deciduous forest types elsewhere in North America. (Hereafter forest and canopy types will be referred to by genus only.)

We hypothesized that the emergence and early mortality rates of the two study species would differ beneath conifer and deciduous canopy types. We further hypothesized that removal of potential barriers to regeneration, including forest floor, seed predation, and competition with understory vegetation, would enhance the early regeneration of *A. balsamea* and

P. strobus. Finally, we hypothesized that the importance of the above barriers would vary with canopy type. Testing the above hypotheses will contribute to an understanding of the role of safe sites for conifer regeneration, and its application to mixed conifer-deciduous forest management.

Study areas

The first study area included two sites of the *Abies–Populus* forest type (11 km apart) within the Nemadji River watershed, east-central Minnesota. *Abies–Populus* site 1 (AP1) is a 0.7-ha area (46°28'N, 92°35'W) with nearly level to hilly topography. *Abies–Populus* site 2 (AP2) has a total of 0.9 ha (46°27'N, 92°33'W) with hilly topography. The second study area included two sites of *Thuja–Betula* forest, which were 3 km apart on the north shore of Lake Superior, northeast Minnesota (47°N, 91°W). *Thuja–Betula* site 1 (TB1) is a 0.6-ha area, with gently sloping topography and a southwesterly aspect. *Thuja–Betula* site 2 (TB2) is a relatively level 1.2-ha area. Other site characteristics and mensurational data are presented in Tables 1 and 2, respectively. Weather data for the *Abies–Populus* study area (1994) were provided by the Cloquet Forestry Center, University of Minnesota, Cloquet, Minnesota. Weather data for the *Thuja–Betula* study area (1994) were provided by Split Rock Lighthouse State Park, Minnesota Department of Natural Resources Division of Parks and Recreation, and by the Minnesota Historical Society in Silver Bay, Minnesota. Thirty-year averages (1961–1990) for temperature and precipitation were provided by the Midwestern Climate Center, Illinois State Water Survey, Champaign, Illinois.

Methods

Field germination experiments

The experimental design consisted of a split split plot replicated at two sites for each study area (Snedecor and Cochran 1989) (Fig. 1). A subset of the randomly placed experimental plots (1.35 m²) at each site were placed half under the conifer canopy type (>50% conifer stems) and half under the deciduous canopy type (<10% conifer stems) in 1994 (Fig. 1). At each *Abies–Populus* and *Thuja–Betula* site, totals of 12 and 9 plots were installed, respectively. Three subplots (0.45 m²) were nested within each plot (first split). Subplot treatments included caging to infer seed predation effects, weeding to test for competition effects, and a control (unweeded and uncaged). Cages were constructed of a 1-cm² wire mesh. Each subplot was divided into two portions receiving different forest floor treatments (second split): forest floor removed before seeding and forest floor intact.

Seeds were purchased from the Minnesota Department of Natural Resources (MNDNR) Forestry Nursery in Willow River, Minnesota. In compliance with their Seed Source Control Guidelines, the

Table 2. Mensurational data for *Abies–Populus* and *Thuja–Betula* study areas in northeastern Minnesota.

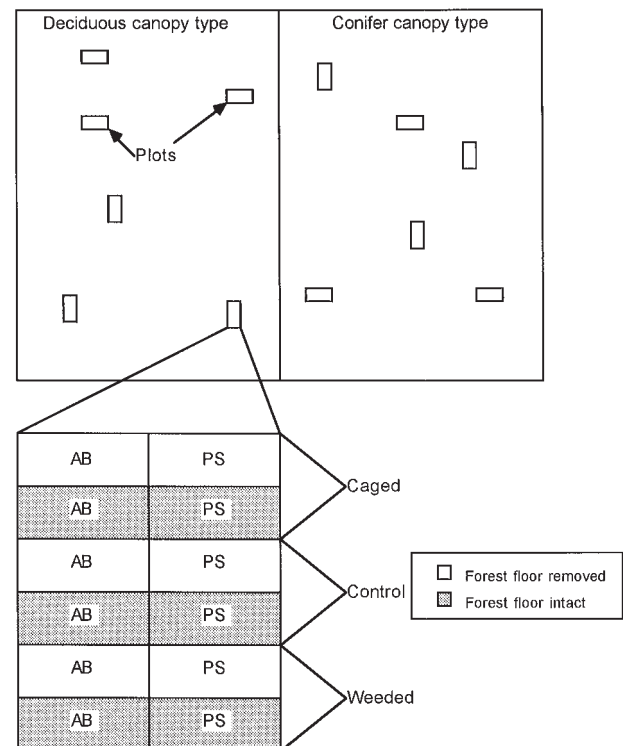
Canopy type	Basal area (m ² /ha)		% conifer stems	% deciduous stems	Age (years)	
	Mean (SE)	No. of sampling points			Mean (SE)	No. of trees
<i>Abies–Populus</i> stands						
<i>Abies</i>	25.2 (3.0)	12	52	48	43.7 (2.2)	20
<i>Populus</i>	17.5 (2.5)	12	0	100	48.3 (2.4)	21
<i>Thuja–Betula</i> stands						
<i>Thuja</i>	53.0 (7.8)	10	56	44	94.8 (3.8)	15
<i>Betula</i>	34.7 (4.0)	8	8	92	58.6 (2.2)	18

MNDNR matched our study site locations with seeds collected from Seed Zone 104. *Abies balsamea* and *P. strobus* seeds originated from Nevis and Deer River, Minnesota, respectively. Natural seed dispersal for *A. balsamea* and *P. strobus* is usually complete by late fall, hence seeds were cold-stratified to break seed dormancy (5°C for 60 days) (Krugman and Jenkinson 1974; Franklin 1974). Seed viability was determined by germinating 100 seeds of each species in a greenhouse (21°C) during April and May 1994 and was defined as number of seedlings emerged/number of seeds sown. This ratio was used to calculate seedling to viable seed ratios (S/V_S) for field experiments. Stratified seeds were sown in the field in early May 1994. The leaf litter layer was lightly agitated to permit settling of seeds. A total of 360 seeds were sown per plot, for 4320 seeds/site in the *Abies–Populus* study area (30 seeds × 2 species × 3 subplot treatments × 2 forest floor treatments × 12 plots) and 3240 seeds/site in the *Thuja–Betula* study area (30 seeds × 2 species × 3 subplot treatments × 2 forest floor treatments × 9 plots). *Abies balsamea* and *P. strobus* were direct seeded at a density of 400 seeds/m². The average annual seed input for *A. balsamea* in another mixed *Abies–Populus* stand near Lake Superior is 52.5 seeds/m² (Ghent 1958). For *P. strobus*, reported seed input for a pure stand ranges from 310 seeds/m² in a low-density stand (18.4 m²/ha) to 443 seeds/m² in an intermediate-density stand (27.6 m²/ha) during a good seed year (Graber 1970).

Emergence was defined as the presence of some growth activity, rather than cotyledon expansion. Natural germination in *A. balsamea* occurs from late May to early July (Frank 1990). *Pinus strobus* germination also generally begins in the spring (Krugman and Jenkinson 1974). Newly emerged seedlings were recorded for both species on four separate dates during the 1994 growing season (June, July, August, and September). Seedling mortality was calculated for the end of the first growing season and over winter based on the number of seedlings present from the previous life stage (e.g., Molofsky and Augspurger 1992). Overwinter mortality was defined as mortality of emerged seedlings occurring from September 15, 1994, to April 15, 1995.

Environmental conditions and seedbed factors were characterized for some variables at the scale of the individual plots and for other variables at the scale of the whole site. At the plot level, understory competition was quantified on the basis of percent cover of the herbaceous vegetation. Light availability was coarsely inferred using canopy openness measurements taken with above- and below-canopy LAI-2000 plant canopy analyzers (LI-COR Inc., Lincoln, Nebr.) under full-leaf conditions at each plot (early September 1994). Canopy openness measurements were taken at 10 cm above the ground, and thus included all the overstory and midstory vegetation, as well as some of the herbaceous vegetation. DBH (≥5.0 cm) for trees occurring within 2 m of each plot was recorded. At the site level, age of 8 to 12 canopy dominants was determined by counting growth rings from cores extracted at breast height. Data characterizing conditions under each canopy type were collected from five randomly located, undisturbed (rather than experimentally manipulated) plots in early June (1995), the time of peak emergence. Forest floor thickness, soil

Fig. 1. Schematic diagram for the experimental layout for a site (not to scale). In *Abies–Populus* sites, 30 seeds × 2 species × 3 subplot treatments × 2 forest floor treatments × 12 experimental plots were sown, for a total of 4320 seeds/site. In *Thuja–Betula* sites, 9 experimental plots were established, and a total of 3240 seeds/site were sown. *Abies balsamea* (AB) and *P. strobus* (PS) were sown in adjacent compartments for each treatment combination.

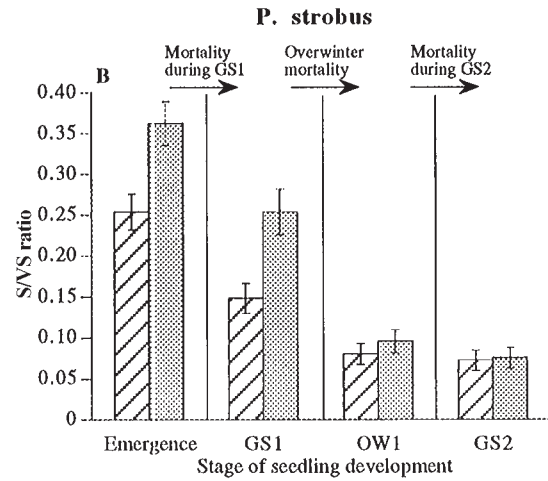
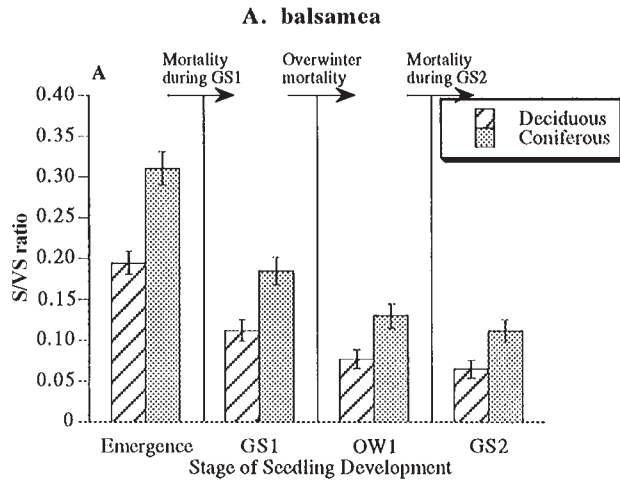


moisture, and soil temperature were the primary conditions characterized beneath each canopy type at each site. Forest floor thickness was measured thrice per plot, near the plot center. Gravimetric soil moisture was determined from a shallow core extracted from the center of each plot (depth = 4 cm, diameter = 3 cm). Cores were extracted 2 days and 7 days following the most recent rainfall at the *Abies–Populus* and *Thuja–Betula* sites, respectively. Two soil temperatures were taken near the center of each subplot by fully inserting a 15.5-cm stainless-steel thermometer with a bimetal sensor in the lower 5.2 cm into the soil, including the organic layer.

Data analyses

Seedling emergence and mortality between life stages were analyzed

Fig. 2. Canopy effects upon seedling to viable seed ratio (S/V/S) over the course of the study for *A. balsamea* (A) and *P. strobus* (B). Stages of seedling development are emergence (seedlings emerged during the 1994 growing season), GS1 (seedlings remaining by the end of the 1994 growing season), OW1 (seedlings remaining at the end of winter, 1995), and GS2 (seedlings remaining by the end of the 1995 growing season). Data were combined for the two forest types in order to show general trends. Error bars are ± 1 SE of subplot means.



separately using multiple nominal logistic regression models. Least squares methods (i.e., analyses of variance) were not appropriate because the response variables were discrete, dependent proportions with binomially, rather than normally, distributed errors (Trexler and Travis 1993). By generalizing analyses of frequency data from the ANOVA-like log-linear models to regression-like models, logistic regression often permits additional insights into data (Sokal and Rohlf 1995). Logistic regression addresses the binomial distribution of the errors by applying a logit transformation (Trexler and Travis 1993).

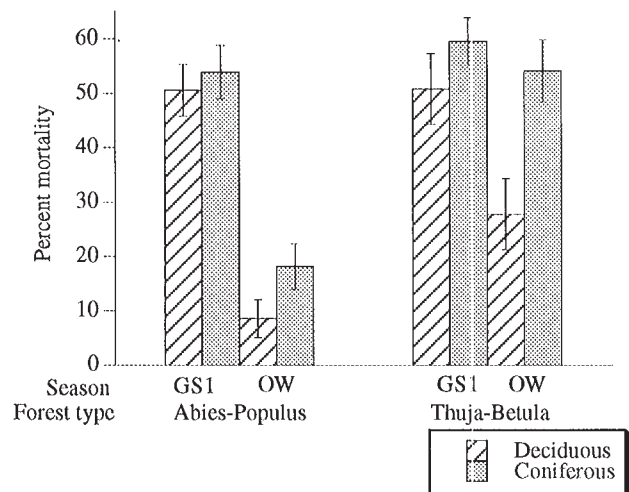
The proportion of emerged seedlings and seedling mortality were analyzed as a function of the canopy type, forest floor, caging, and weeding treatments (e.g., Molofsky and Augspurger 1992). To find general trends across both sites of each forest type (study area), data were pooled and sites were treated as replicates. Logistic regression results were followed by a likelihood ratio test, which is calculated as twice the difference of the negative log likelihoods between the saturated model and the model without the effect or interaction in question (JMP 3.0.2, SAS Institute Inc., Cary, N.C.; e.g., Walters and Reich 1996).

Differences in environmental conditions and seedbed factors beneath different canopy types were evaluated for each study area with *t*-tests. Environmental conditions included percent canopy openness, percent soil moisture, and soil temperature. Seedbed factors included percent herbaceous cover and forest floor thickness.

Results

The ratios of seedlings emerged to seeds sown in the greenhouse were 0.63 for *A. balsamea* and 0.94 for *P. strobus*. Over an 18-month postseeding period in the field, a variety of treatments resulted in mortality in both species. With lower survival rates, the initially larger S/V/S of *P. strobus* diminished over the course of the study. Thus, *A. balsamea* and *P. strobus* had a comparable S/V/S of 0.05 to 0.1 by the end of the second growing season regardless of forest type (Fig. 2). These patterns resulted from apparent differences in the effects of canopy, forest floor, competition, and predation treatments on *A. balsamea* and *P. strobus* regeneration, depending on forest type and stage of seedling development. For the sake of clarity, general trends are expressed in terms of S/V/S, while trends

Fig. 3. Canopy effects upon percent seedling mortality for *P. strobus* during the growing season of 1994 (GS1) and over the winter of 1994–1995 (OW). Percent mortality was calculated based on the number of seedlings alive during the previous life stage. Error bars are ± 1 SE of subplot means.



over shorter time periods are expressed as percent mortality based on the number of seedlings in the previous life stage.

Canopy type

Canopy type affected seedling emergence for *A. balsamea* and *P. strobus* in both forest types ($p < 0.0001$; Table 3). Seedling emergence was higher under the conifer canopy than the deciduous canopy in both cases (Fig. 2). Subsequent seedling mortality for *A. balsamea* was unrelated to canopy type (Table 3). Thus, *A. balsamea* maintained its initially higher S/V/S under the conifer canopy type over the course of the study (Fig. 2A). The S/V/S for *P. strobus* was highest under the conifer canopy type in both forest types until the end of the first growing season, but was roughly equal beneath the two canopy types thereafter (Fig. 2B). This change in pattern appears to

Table 3. Likelihood ratios and $P > \chi^2$ (in parentheses) for emergence and mortality over the first growing season (GS1) and the winter of 1994–1995 (OW).

	Canopy (1)*	Subplot treatment (2)	Forest floor treatment (1)	C × SP (2)	C × FF (1)	SP × FF (1)	C × SP × FF (2)	Full model: negative log likelihood
Abies–Populus study area								
<i>A. balsamea</i>								
Emergence	52.03 (<0.0001)	23.63 (<0.0001)	6.73 (0.01)	2.33 (0.31)	0.50 (0.48)	6.74 (0.03)	—	1508.72
GS1 mortality	0.66 (0.42)	2.33 (0.31)	29.72 (<0.0001)	5.18 (0.08)	2.18 (0.14)	0.66 (0.72)	9.22 (0.01)	281.30
OW mortality	0.35 (0.56)	7.06 (0.03)	9.98 (0.002)	1.17 (0.56)	0.07 (0.79)	1.99 (0.37)	—	147.25
<i>P. strobus</i>								
Emergence	48.88 (<0.0001)	27.17 (<0.0001)	—	2.34 (0.31)	—	—	—	1516.93
GS1 mortality	14.98 (<0.0001)	1.5467 (0.46)	0.17 (0.68)	3.43 (0.18)	3.72 (0.54)	2.15 (0.34)	9.04 (0.011)	697.39
OW mortality	21.09 (<0.0001)	4.25 (0.12)	2.01 (0.16)	2.06 (0.36)	9.41 (0.002)	3.89 (0.14)	—	395.02
Thuja–Betula study area								
<i>A. balsamea</i>								
Emergence	119.52 (<0.0001)	21.33 (<0.0001)	7.06 (0.008)	4.95 (0.08)	2.48 (0.12)	0.38 (0.83)	—	1563.58
GS1 mortality	0.18 (0.67)	13.70 (0.001)	4.77 (0.03)	6.41 (0.04)	0.15 (0.70)	2.75 (0.25)	—	441.59
OW mortality	5.29 (0.07)	21.74 (0.0002)	0.93 (0.62)	11.55 (0.02)	1.25 (0.53)	8.48 (0.08)	—	280.20
<i>P. strobus</i>								
Emergence	100.39 (<0.0001)	485.19 (<0.0001)	—	8.25 (0.02)	—	—	—	1729.13
GS1 mortality	5.01 (0.02)	11.34 (0.0034)	0.52 (0.47)	41.96 (<0.0001)	6.97 (0.008)	5.13 (0.08)	9.96 (0.007)	636.25
OW mortality	33.84 (<0.0001)	10.74 (0.03)	1.37 (0.50)	10.21 (0.04)	2.21 (0.33)	4.78 (0.31)	—	431.72

Note: Tests of likelihood ratios are calculated as twice the difference of the log likelihoods between the full model and the model without the tested effect.

*df.

have resulted from a difference in mortality rates of *P. strobus* beneath the deciduous and coniferous canopy types in both forest types (Fig. 3). For both *Abies–Populus* and *Thuja–Betula* forest types, mortality rates for *P. strobus* were generally higher under the conifer canopy type over the first growing season and over winter ($p \leq 0.02$; Table 3).

Interactions between canopy type and the experimentally manipulated variables were infrequent and occurred largely for *P. strobus*. When further explored, these two- and three-way interactions revealed no consistent pattern (Table 3).

Environmental conditions and seedbed factors

A number of seedbed factors and environmental conditions differed beneath conifer and deciduous canopy types for both forest types (Table 4). For both forest types, canopy openness was lower under the conifer than the deciduous canopy type (Table 4). In *Abies–Populus* sites, forest floor thickness and percent herbaceous cover were both greater beneath the deciduous canopy type (Table 4). In *Thuja–Betula* sites, percent soil moisture was substantially higher, and soil temperature

was lower, beneath the conifer canopy type than the deciduous canopy type (Table 4).

Forest floor

Forest floor treatments influenced seedling emergence and survival in *A. balsamea* but not *P. strobus* (Table 3). For *Abies–Populus* and *Thuja–Betula* forest types, a higher S/V/S occurred at emergence for *A. balsamea* where forest floor was removed ($p \leq 0.01$; Table 3). Once established, this initial pattern was maintained over time for *A. balsamea* by its consistently higher mortality rates for forest floor intact treatments (Fig. 4A). In contrast, *P. strobus* maintained a roughly equal S/V/S for different forest floor treatments throughout the study (Fig. 4B). Both during the first growing season and over winter, percent mortality of *A. balsamea* was higher on forest floor intact treatments in *Abies–Populus* sites ($p \leq 0.002$; Table 3; Fig. 5). For *Thuja–Betula* sites, percent mortality was higher in *A. balsamea* seedlings on forest floor intact treatments in 1994 ($p = 0.03$; Table 3), but not 1995 (Fig. 5).

Fig. 4. Forest floor treatment effects upon seedling to viable seed ratio (S/V_S) over the course of the study for *A. balsamea* (A) and *P. strobus* (B). Stages of seedling development are emergence (seedlings emerged during the 1994 growing season), GS1 (seedlings remaining by the end of the 1994 growing season), OW1 (seedlings remaining at the end of winter, 1995), and GS2 (seedlings remaining by the end of the 1995 growing season). Data were combined for the two forest types in order to show general trends. Error bars are ±1 SE of subplot means.

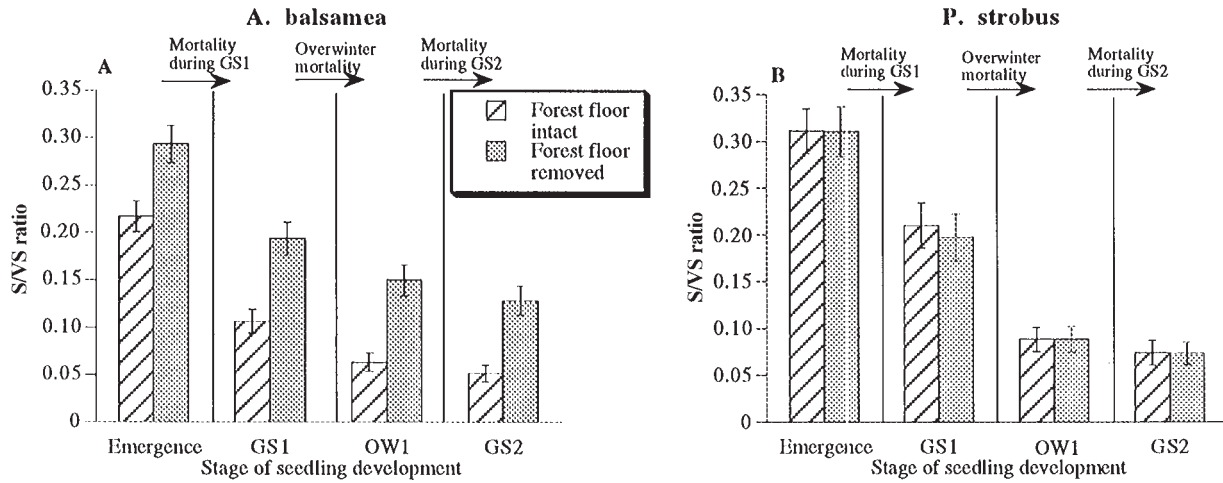
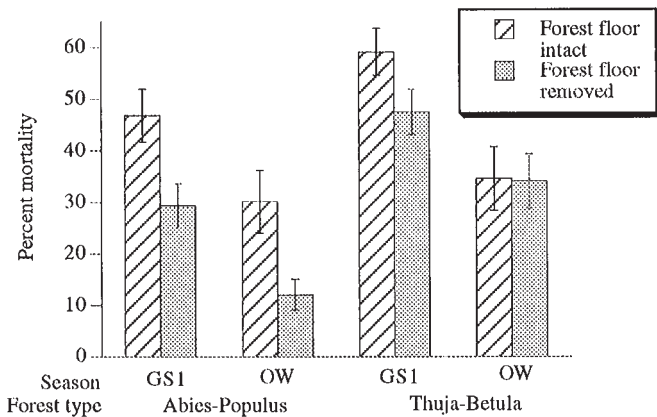


Fig. 5. Forest floor treatment effects on percent seedling mortality for *A. balsamea* during the growing season of 1994 (GS1) and over the winter of 1994–1995 (OW). Percent mortality was calculated based on the number of seedlings alive during the previous life stage. Error bars are ±1 SE of subplot means.



Predation

Caging to exclude seed predators affected emergence rates for both species in both forest types ($p < 0.0001$; Table 3). For both *A. balsamea* and *P. strobus*, S/V_S at emergence in caged treatments was high compared with that of controls in both forest types (Fig. 6). S/V_S for *A. balsamea* in caged treatments was twice as high as that of the controls by the end of the study (Fig. 6A). For *P. strobus*, the effect of caging on emergence was more dramatic than for *A. balsamea*, and a five-fold higher S/V_S was maintained over 18 months for caged treatments compared with controls (Fig. 6B).

The effects of caging on percent seedling mortality were slight (average ≈ 10% lower) for both species, except for *P. strobus* in the *Thuja–Betula* sites, where percent seedling mortality in caged treatments was ≈25% lower than in controls during the first growing season (Fig. 7). Caging did not appear to affect percent seedling mortality of *A. balsamea* in either forest type.

Table 4. Environmental conditions and seedbed factors beneath conifer and deciduous canopy types in two Minnesota conifer–deciduous forests.

Canopy type	Herbaceous cover (%)	Canopy openness (%)	Forest floor thickness (cm)	Soil moisture (%)	Soil temp. (°C)
<i>Abies</i>	24.8*** (6.2)	6.4*** (2.9)	1.6* (0.4)	51.1 (13.8)	14.9 (0.7)
<i>Populus</i>	51.0*** (8.5)	8.8*** (2.8)	2.0* (0.5)	52.3 (17.6)	14.4 (1.3)
<i>Thuja</i>	27.5 (11.9)	10.4* (6.0)	1.6 (0.6)	61.3** (16.6)	9.8*** (0.8)
<i>Betula</i>	40.8 (11.2)	16.6* (9.6)	1.8 (0.9)	35.9** (19.0)	11.5*** (0.8)

Note: Values in parentheses are standard deviations. p -values are the result of two-tailed t -tests comparing conditions and factors beneath different canopy types, but within the same study area (i.e., the *Abies–Populus* or the *Thuja–Betula* study area).

*Significantly different at $p \leq 0.05$.

**Significantly different at $p \leq 0.01$.

***Significantly different at $p \leq 0.005$.

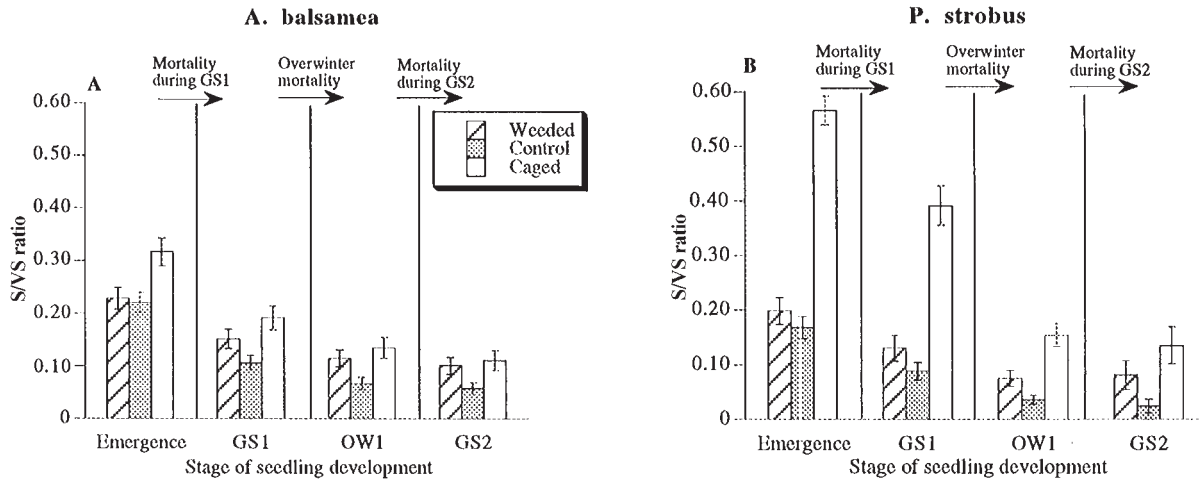
Competition

The removal of understory competition did not affect seedling emergence rates for either *A. balsamea* or *P. strobus* (Fig. 6). The absence of competition generally appeared to become more important over time for both species in the two forest types, with higher S/V_S occurring in weeded treatments relative to controls during the spring of 1995 and the second growing season (Fig. 6). Particularly in the *Thuja–Betula* sites, mortality rates for *A. balsamea* and *P. strobus* were lower in weeded treatments than in controls over the first growing season and over winter ($p < 0.05$; Table 3; Fig. 7).

Discussion

The results of the study indicated that the safe sites of *A. balsamea* and *P. strobus* differ within mixed conifer–deciduous

Fig. 6. Caging and weeding treatment effects upon seedling to viable seed ratio (S/V/S) over the course of the study for *A. balsamea* (A) and *P. strobus* (B). Stages of seedling development are emergence (seedlings emerged during the 1994 growing season), GS1 (seedlings remaining by the end of the 1994 growing season), OW1 (seedlings remaining at the end of winter, 1995), and GS2 (seedlings remaining by the end of the 1995 growing season). Data were combined for the two forest types in order to show general trends. Error bars are ± 1 SE of subplot means.



forests. Although 1-month intervals occurred between sampling dates, and additional germination and mortality may have gone unobserved, we were nonetheless able to detect ecologically important patterns. Results supported the hypothesis that canopy type influences emergence and mortality rates for the two study species. In general, seedling emergence rates in both species benefited from the presence of a conifer canopy, but the conifer canopy also contributed to increased mortality rates for *P. strobus*. The hypothesis that the removal of potential barriers to early regeneration would bolster emergence and survival rates of conifer seedlings was also upheld (forest floor, seed predation, and understory competition). It was clear, however, that the role of each of these potential barriers is complex. *Abies balsamea* and *P. strobus* were affected differently by each manipulated factor, depending upon the stage of seedling development. Although we hypothesized that the effects of the treatments would vary with canopy type, and partially explain the observed difference in seedling emergence and mortality rates beneath conifer and deciduous canopy types, no consistent trend emerged. Differences in emergence and mortality rates beneath conifer and deciduous canopy types may therefore be attributed to other variables not extensively addressed in the present study, such as light availability, soil moisture, and soil temperature.

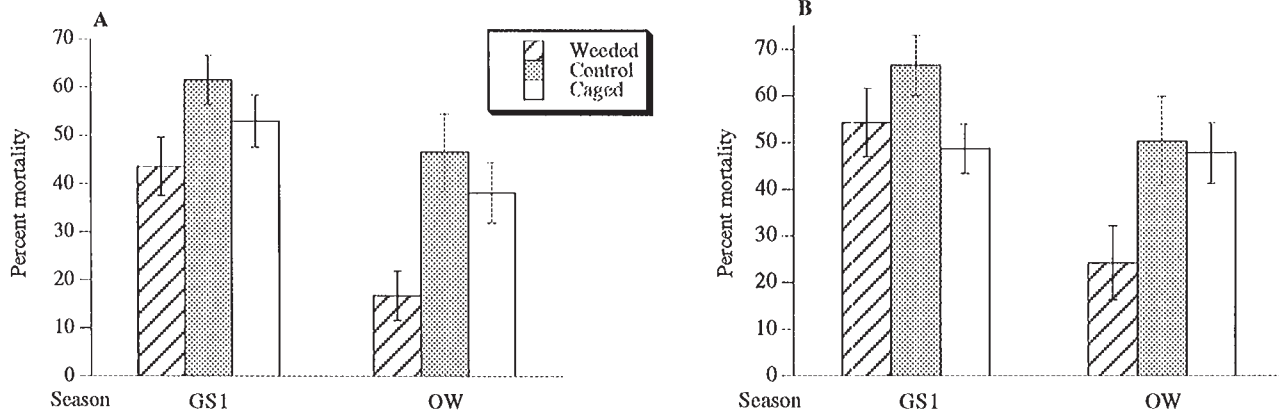
It should be noted that many environmental conditions fluctuate interannually. For example, the germination experiments were conducted during a growing season with nearly average rainfall and temperature (Table 1). In other years with higher or lower than average rainfall or temperature, emergence rates might differ from those observed in 1994. An intact forest floor might be more of a barrier to successful regeneration for both species under drier, hotter conditions. In contrast, during wetter than average years seeds might germinate at higher rates, but may also suffer higher mortality rates in response to a greater incidence of moisture-related pathogens. The emergence and mortality trends we observed in 1994 and 1995 might hold under other environmental conditions, but could shift in magnitude.

Canopy type

Higher emergence rates for both species, and higher mortality rate for *P. strobus*, occurred under conifer than deciduous canopy types. Both deciduous and conifer (Zinke 1962; Tubbs 1973; Hicks 1980) canopy tree species can influence the growth of herbs and woody seedlings in the understory. The overstory composition can contribute directly to the character of the understory for such factors as the quality of the forest floor, and indirectly for such factors as the levels of seed predation and understory competition. We initially suspected that differences in regeneration success for *A. balsamea* and *P. strobus* beneath conifer and deciduous canopy types could be explained in part by differences in the forest floor, seed predation and herbivory, and understory competition occurring beneath them. Although each of the experimentally manipulated treatments appeared to play a role in emergence, survival, or both, none of these treatments interacted in a predictable way with canopy type.

Differences in emergence and early survival rates beneath conifer and deciduous canopy types may instead be attributed to differences in light availability, soil moisture, and soil temperature (Place 1955; Górski et al. 1978; Thomas and Wein 1985a, 1985b; Canham and Burbank 1994). The present study did not directly link emergence and mortality with the above specific environmental conditions, but they were characterized at a coarse scale for each canopy type within each forest type (Table 4). Conifer canopies, for example, appear to shade the understory more than deciduous canopies at our two study sites. Shading may have created an environment more conducive to emergence for both species, for example, contributing to higher soil moisture and lower soil temperature as in the *Thuja-Betula* sites (Table 4). *Abies balsamea* is a shade-tolerant species, whereas *P. strobus* is considered midtolerant. *Pinus strobus* can benefit from shading during germination, but requires more light later during establishment (Wendel and Smith 1990). Other studies have shown higher mortality rates for *A. balsamea* than *P. strobus* seedlings under high light and high soil temperature – low moisture conditions following a burn,

Fig. 7. Caging and weeding treatment effects on percent seedling mortality for *A. balsamea* (A) and *P. strobus* (B) during the growing season of 1994 (GS1) and over the winter of 1994–1995 (OW) in *Thuja–Betula* sites. Percent mortality was calculated based on the number of seedlings alive during the previous life stage. Error bars are ± 1 SE of subplot means.



and the simulation of these harsh conditions in the greenhouse (Thomas and Wein 1985a, 1985b). Under a forest canopy as in the present study, the superior ability of *P. strobus* to cope with drought and temperature extremes may have been less of an advantage than in a more exposed environment.

Overstory species composition, then, may be important in the maintenance of the conifer component of mixed conifer–deciduous forests in a natural setting. In the case of *A. balsamea*, for example, the presence of conifers in the overstory may confer advantages for emergence and continued survival. For *P. strobus*, the role of conifers in the overstory is less clear, because higher initial emergence rates beneath the conifer canopy types were negated the following year by higher mortality rates. Managing for *A. balsamea*, *P. strobus*, or both should include a consideration of the immediate and long-term effects of canopy type on regeneration success.

Forest floor

An intact forest floor had a consistently negative effect upon *A. balsamea* emergence and survival. Higher emergence rates occurred for *A. balsamea* in forest floor removed portions than forest floor intact portions in both forest types, while *P. strobus* emergence was unaffected by forest floor treatment. Our results contrast with the idea that occasional light fires are one of the factors maintaining *P. strobus* forest, presumably in part because of seedbed preparation (e.g., Tester et al. 1997). In the present study, however, mean forest floor thickness was ≤ 2 cm at all four sites, possibly insufficient to impede *P. strobus* emergence and survival.

Differences between the two species in their response to manipulation of the forest floor may be explained in terms of their abilities to penetrate the forest floor during germination. Our results for *A. balsamea* were consistent with those of Frank (1990), who reported that shaded mineral soil is generally the best seedbed for *A. balsamea*. *P. strobus*, on the other hand, does not need mineral soil for germination (Balmer and Williston 1983; Wendel and Smith 1990). The roots of *P. strobus* seedlings can penetrate needle litter as thick as 5 cm within 2 weeks of germination (Smith 1951).

Larger seed size could also partially contribute to the ability of *P. strobus* to emerge on areas with an intact forest floor. *Pinus strobus* seeds are over twice the size of *A. balsamea*

seeds, averaging 0.017 g (Krugman and Jenkinson 1974), to *A. balsamea*'s 7.63×10^{-3} g (Franklin 1974). Given the enormous variation in seed size among all plant species, the difference in seed size between *A. balsamea* and *P. strobus* appears minor. In both herbaceous and woody plants, however, germination of smaller seeded species is generally more likely to be hindered by leaf litter than germination of larger seeded species (Gross 1984; Winn 1985; Peterson and Facelli 1992).

Hence, the forest floor may also be important in the maintenance of the conifer component of mixed conifer–deciduous forests in a natural setting. Although differences in regeneration success beneath the two canopy types did not appear to be linked to differences in the forest floor itself, *A. balsamea* was sensitive and *P. strobus* insensitive to an intact forest floor regardless of canopy type. Our results from forest floor manipulations have mixed implications for maintaining or reintroducing conifers in a mixed conifer–deciduous forest. In the case of *A. balsamea*, scarification could enhance emergence and early survival by as much as 60% by increasing safe site availability. Scarification prior to seeding could improve *A. balsamea* regeneration and would not interfere with *P. strobus* regeneration, and may be a reasonable regeneration strategy for the two species on the same site.

Predation

Caging had a strongly positive effect on emergence rates in both species (Fig. 6), suggesting that seed predation rates were high in both forest types. Predation of conifer seeds is well documented (Bakuzis and Hansen 1965; Oswald and Neuenschwander 1995). Although seed removal was inferred for controls in the present study, it would not necessarily lead to low numbers of seedlings in a natural setting. The effect of seed removal on the pool of conifer regeneration is more ambiguous than the effects of canopy type and forest floor explored above. Seeds removed by small mammals from experimental plots, for instance, could potentially be cached in another part of the forest, resulting in a redistribution rather than a net loss of seed (Abbott and Quink 1970). Caging lowered mortality rates for *P. strobus* only weakly during the first growing season and only in *Thuja–Betula* sites, and had no effect on *A. balsamea* mortality during the first growing

season. In addition, during the fall of 1994 cages probably excluded most newly senesced leaf litter, the accumulation of which is a potential cause of mortality for young seedlings (Koroleff 1954). The slightly lower rates of overwinter mortality observed for both study species in caged subplots may have resulted from partial exclusion of falling leaf litter, further diminishing the possibility that herbivores were responsible for seedling mortality occurring during the winter (Fig. 7B). Seedling mortality resulting from herbivory thus appeared to be less important than mortality resulting from seed predation.

Our results indicated that under natural conditions seed predation may hinder conifer regeneration in mixed conifer–deciduous forests. We did not track the fates of individual seeds, and it is possible that some seeds removed from experimental plots germinated elsewhere in the forest. Potentially high losses to seed predators nonetheless have implications for managing the conifer component of mixed conifer–deciduous forests. Seeding could be performed in years for which seed predator population levels are low. Other options are to seed at much higher densities than would occur naturally, in order to compensate for anticipated levels of predation. Although our results also suggest that herbivory by small mammals during the first two growing seasons may be minimal, in peak population years the problem may need to be addressed by managers.

Understory competition

Weeding had no obvious effects upon emergence in either species, but seemed to lower mortality rates of both *A. balsamea* and *P. strobus* in *Thuja–Betula* sites. The effect of competition treatments was weak compared with forest floor and predation treatments, implying that understory competition may not be as critical in the early regeneration of *P. strobus* and *A. balsamea*. Our findings were similar to those of Bartlett et al. (1991), who showed that in the Niagara Falls Escarpment ecosystem in Ontario, the negative effects of leaf litter swamped the effects of competition upon *T. occidentalis* germination. Numbers of seedlings in weeded areas and in the controls were low, however, and our comparison may simply have failed to detect real differences. Although numbers of seedlings were low for all treatment combinations by the end of the study, we believe that we used sufficient replication to detect important trends through the spring of 1995.

Competition with understory vegetation may have played a role for *A. balsamea* in mortality during the first growing season and over winter, as well as for *P. strobus* over winter. Seedlings may have been less vigorous as a result of competition with understory vegetation during the first growing season, leading to the higher mortality rates during the winter. Allelopathic, microclimatic, and other consequences of understory vegetation (Maguire and Forman 1983) also may have contributed to higher conifer seedling mortality in controls. It would have been beneficial to have obtained measurements of seedling vigor to test this explanation fully.

Under natural conditions, conifer regeneration in mixed conifer–deciduous forests may be negatively impacted by understory competition. The positive effect of weeding was less definitive for seedling survival than the effects of either canopy type or forest floor removal. If the study were continued for additional growing seasons, the importance of competition effects might increase. Although understory competition may

play a more significant role after than during emergence, site preparation prior to seeding may be prudent.

Conclusions

As we hypothesized, emergence and early survival rates of *A. balsamea* and *P. strobus* differed according to canopy type and were enhanced by removal of barriers to regeneration, including forest floor, seed predation, and understory competition. The early safe sites of the two study species differed. Within the context of our study, the ideal safe site for *A. balsamea* includes the presence of a conifer canopy, the reduction in thickness of the forest floor, seed predation, and understory competition in decreasing order of importance. For *P. strobus*, seed predators and understory competition were absent from the best safe site. The minimum regeneration requirements for both species can be met under natural conditions within the same stand. *Abies balsamea* and *P. strobus* are often associates within the same forest, possibly because their safe sites, although different, are not mutually exclusive. Although *P. strobus* was more tolerant of an intact forest floor than *A. balsamea*, removal of the forest floor did not impede its emergence or survival. An understanding of this quality of different yet partially overlapping safe sites can be applied during management practices that are conducted on a broad scale, such as scarification or weed control.

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