

Below-ground resources limit seedling growth in forest understories but do not alter biomass distribution

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Abstract – We examined the long-term growth, morphology, biomass distribution, and survival response of seedlings of five conifer species varying widely in shade tolerance to an increase in soil resources in shaded forest understories in northern Wisconsin, USA. In a 4-year experiment, trenching treatment was used to increase soil resource supply to 1-year old seedlings planted across a range of low light microenvironments. Specifically we asked: (1) does an increase in soil resources alter whole-plant growth, biomass distribution patterns, and survival in lowlight, and (2) do species differ in their responses to increasing soil resources? Increased soil resource availability increased height (+11% on average) and dry mass (+23% on average) of all species regardless of light availability. However, there was no evidence that trenching affected biomass distribution for any species, as has been previously reported. Survivorship after four years was positively related to the species' reported shade tolerance ranking and was unaltered by trenching. We concluded that soil resource availability (supply-demand) can limit tree seedling growth in deeply shaded forest understories, but that increased resource availability of the magnitude caused by trenching does not favor tolerant rather than intolerant species, or vice-versa.

long-term / trenching / northern Wisconsin / conifer species / field-grown seedlings

Résumé – Les ressources du sol limitent la croissance des semis se développant sous couvert forestier, mais ne modifient pas la distribution de leur biomasse. Nous avons examiné l'effet à long terme de l'accroissement des ressources du sol sur la croissance, la distribution de la biomasse et la survie d'espèces dont la tolérance à l'ombre est très différente, dans le sous-étage de forêts du Nord Wisconsin aux USA. On a conduit sur 4 ans une expérimentation consistant à apporter un supplément de ressources à des semis de 1 an installés dans toute une gamme de micro-environnements peu éclairés. Les questions posées étaient : (1) Est-ce que un accroissement des ressources du sol modifie la croissance totale du plant, le modèle de distribution de la biomasse et la survie, sous un faible éclairage ? (2) Est-ce que les espèces réagissent différemment à l'accroissement des ressources ? L'augmentation des disponibilités en ressources se traduit par un accroissement de la hauteur (en moyenne +11 %) et de la matière sèche (en moyenne +23 %) pour toutes les espèces et quel que soit l'éclairage. Cependant, aucun effet n'a pu être mis en évidence sur la distribution de la biomasse des différentes espèces contrairement à ce qui a été dit auparavant. La survie, après 4 ans, est liée positivement au niveau de la tolérance à l'ombre des espèces. Elle n'a pas été modifiée par le traitement. Nous concluons que le niveau des disponibilités en ressources peut limiter la croissance des plantes dans les sous-étages à faible éclairage, mais qu'un apport de l'ordre de celui adopté dans cette expérimentation, ne favorise pas plus les espèces tolérantes que celles qui ne le sont pas.

long terme / tranchées / nord-Wisconsin / espèces conifères / plants sur le terrain

1. INTRODUCTION

Light has frequently been observed to be the main factor limiting plant growth in deeply shaded understories [5, 33, 46]. However, the multiple resource limitation theory [8, 16, 17, 42] and trenching, fertilization, and gradient experiments suggest that water and/or nutrients along with light might co-limit growth in forest understories [9, 19, 27, 39, 40, 47, 49]. Neither fertilization nor trenching experiments have provided a clear understanding of how nutrients, and water interact

together with light to affect growth, biomass distribution patterns and survival of seedlings [6]. Many such studies have been performed over short time intervals (often less than a year), and have lacked whole-plant measurements of mass and morphology that included root systems.

A recent review of trenching experiments suggests that for understory plants growing in moist, nutrient rich sites, light may more strongly limit growth than do soil resources whereas, on infertile and/or drier soils, growth may be more strongly limited by soil resources than by light [10]. In addition,

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greenhouse studies have shown that tree seedlings' abilities to respond to increased soil resources diminish as light levels decrease [4, 49, 50]. Finally, we suggest that wide variation among studies [10] may, in part, be due to differences among species in their ability to respond to increased soil resources in deep shade [49, 50]. Collectively, these findings and ideas suggest that the combination of variation among species in resource tolerance, and among habitats in light and nutrient supply is likely to result in complex patterns and interactions.

Tree species differ markedly in their ability to tolerate deeply shaded forest understories. This ability, although coined shade tolerance, may be largely due to collections of traits that maximize survival via the efficient use of limiting resources in forest understories. Such resources may include both light and soil resources [26, 27, 48]. In a controlled experiment, shade intolerant species survived better in deep shade under higher than lower nutrient availability [50]. In contrast, shade tolerant species, which survived better than the intolerants in any case, were unaffected by variation in nutrient supply [50]. Thus, if species differ in their responses to soil resources in low-light forest understories, then it is likely that they will differ to the greatest degree for species comprising a broad gradient of reported shade tolerances.

Given the above-mentioned sources of variability, and our limited understanding therein, it is difficult to predict trends in growth, biomass distribution (defined here, as the mean relative fraction of biomass found in the different plant components at harvest time) and survival of plants with different shade tolerance classification. Nevertheless, based on prior findings, we can propose the following three hypotheses. First, consistent with the multiple resource limitation hypothesis [8, 16, 17, 42], we predict that trenching will generally have a positive effect on whole-plant growth and survival and will increase the proportion of leaves and stems as a fraction of whole plant mass. The second hypothesis proposes that all species response will be influenced by light, such as all species will respond more to trenching in higher light as in lower light. Finally, the third hypothesis proposes that the response will differ among species in relation to shade tolerance, such that species that are more shade tolerant will respond more to trenching than shade intolerant species. This is based on the idea that shade intolerant species will be so limited by deep shade that they will be unable to respond to changes in soil resources.

To address these hypotheses we examined the long-term responses of seedlings of five conifer species (*Pinus banksiana* Lamb., *Pinus resinosa* Ait., *Pinus strobus* L., *Picea glauca* (Moench) Voss. and *Abies balsamea* (L.) Mill.) to an increase in soil resources from trenching in shaded (3–11% of canopy openness) low fertility forest understories in northern Wisconsin, USA. In this long-term field study, we asked (1) does an increase in soil resources alter whole-plant growth, survival, or biomass distribution patterns in low-light environments and (2) do species differ in their responses to increased soil resources; and (3) if so, are these differences related to their shade tolerance classification.

Soil trenching in field experiments has been used for over a century to alter the availability of soil resources and to evaluate the impact of belowground competition [10]. Trenching is the

process of physically isolating a group of plants by installing a barrier that prevents root ingrowth from the surrounding vegetation and removes competition from the surrounding vegetation since their extant roots are severed during the trenching [22]. Trenching increases soil resource supply to residual plants largely by reducing resource demand (i.e., reducing competition) [27]. Among soil resources altered by trenching are the availability of water and of nitrogen. Several authors have reported a two-fold increase in water [11, 12, 13], and others have shown an increase in the availability of nitrogen for different forest types ([44] for deciduous and evergreen forest in North America, [21] for spruce plantations in Europe and [41] for tropical lower montane forest in the Caribbean).

2. METHODS

2.1. Sites and experimental design

We located two sites 6 km apart on moderately low fertility sandy outwash soils in northern Wisconsin, USA in the summer of 1993. At site 1, forest overstories were dominated by *Quercus rubra* L., *Acer rubrum* L. and *Populus tremuloides* Michx., and at site 2 by *Populus tremuloides*, *Quercus rubra* and scattered *Pinus strobus* L. individuals. During the four years of this experiment there was no evidence of drought in the region. Total precipitation during the growing season (May to September) was 411, 514, 465 and 388 mm for 1993, 1994, 1995 and 1996, respectively (North Temperate Lakes Long-Term Ecological Research weather records located less than 9 km from both research sites).

Across the two research sites we randomly selected 11 pairs of 5 × 3.5 m plots ($n = 12$ and $n = 10$ plots for site 1 and 2, respectively). In the spring of 1993, one plot of each pair was trenched prior to planting by digging 1-m deep and 0.3 m wide trenches around the plot and lined with root restriction cloth (Landscape Fabric, St. Paul, MN, USA). This fabric allows transfer of water and gases but does not permit root penetration. In these forests, most roots exist within the top 20-cm depth [48]. Prior to planting, the existing aboveground biomass of small vegetation was hand-pulled and allowed to decay on the surface of both trenched and control plots. After planting, all plots were weeded once a year.

For each plot, percent canopy openness was measured with the LAI-2000 plant canopy analyzer (Li-Cor, Lincoln, NB, USA). These values are a good surrogate of mean daily percent photosynthetic photon flux density [32]. During August 18 and 19, 1994, one canopy openness measurement for each corner of every plot was taken when the sky was uniformly overcast or during twilight after dawn and before dusk. Measurements were averaged to account for the spatial variation of each plot. We used one LAI-2000 at the measurement point (forest understory) while another paired unit simultaneously measured open sky values in a large clear-cut that was less than 1 km away. We averaged the four measurements of each plot. During the four years of the experiment we did not notice mortality of any large trees in the canopy.

Soil nitrogen and moisture were measured in control and trenched plots in August 1996 by extracting six soil cores (5 cm diameter × 20 cm deep) from each plot. These were subsequently pooled by plot. We oven-dried subsamples of the bulked soils at 105 °C to determine soil water content. For another subsample, 2 M KCl extractions of NH_4 and NO_3 were made on fresh soil. NH_4 and NO_3 pools in the soil were measured by conversion to salicylic acid and copper cadmium reduction to nitrite, respectively, followed by calorimetric analysis (University of Minnesota, Department of Soil Science Research Analytical Laboratory).

Table I. Light environments and soil nitrogen and water in each control and trenched plots. Canopy openness values are the mean of four measurements taken in August of 1994. Soil nitrogen and water values are single measurements taken in August of 1996, at the end of the experiment. At the bottom, for all plots ($n = 11$ for each control and trench treatments), we included the mean, standard error (S.E.) and the probability values for t -tests. Significant values < 0.1 are shown in bold.

Site	Plot #	Canopy openness (%)		Soil water (%)		NO ₃ ⁻ pool (μmol N g ⁻¹ soil)		NH ₄ ⁺ pool (μmol N g ⁻¹ soil)	
		Control	Trench	Control	Trench	Control	Trench	Control	Trench
1	1	3.2	4.1	14.8	16.2	5.7	3.4	9.9	11.5
	2	3.8	4.0	18.9	19.6	2.2	3.7	9.7	11.9
	3	7.2	6.8	17.4	18.6	5.0	3.3	10.1	17.3
	4	7.0	6.6	16.3	21.4	3.2	8.6	7.9	13.6
	5	7.6	6.4	20.2	19.0	4.2	4.7	12.2	12.0
	6	3.4	3.1	15.3	15.7	5.4	5.6	12.3	10.7
2	1	8.0	11.0	12.8	23.6	3.8	3.1	7.3	12.7
	2	11.1	10.1	12.6	17.4	2.2	3.3	4.8	7.5
	3	7.7	7.8	13.3	15.9	6.8	4.6	10.4	8.9
	4	7.6	7.4	14.8	27.0	3.4	5.9	7.5	14.9
	5	5.5	5.3	15.3	14.0	6.0	5.4	8.7	9.3
Mean		6.6	6.6	15.6	19.0	4.3	4.7	9.2	11.8
S.E.		0.72	0.74	0.73	1.15	0.46	0.49	0.67	0.84
Prob > t		0.97		0.02		0.61		0.02	

Table II. Seedling height prior to planting and a comparison between shade tolerance rankings described in the forestry literature and the distribution of juveniles (0.25 to 1.5 m of height) along light environments in the field. Seedling height values are the mean and standard error (in parenthesis). The shade tolerance scores from field data correspond to the 10th percentile of the distribution of juveniles growing in northern Minnesota [31]. Scores are inversely related to the subjective assessments of shade tolerance rankings described by North American foresters [3]. Light data for *Pinus banksiana* are not available.

Species	Seedling height prior to planting (cm)		Shade tolerance scores from field data	Shade tolerance rankings
	Control	Trench		
<i>Abies balsamea</i>	10.1 (0.3)	9.4 (0.3)	2.17	Very tolerant
<i>Picea glauca</i>	14.9 (0.4)	14.8 (0.4)	2.68	Tolerant
<i>Pinus strobus</i>	16.2 (0.3)	16.3 (0.3)	2.91	Intermediate
<i>Pinus resinosa</i>	15.0 (0.4)	13.7 (0.4)	10.11	Intolerant
<i>Pinus banksiana</i>	12.7 (0.3)	12.6 (0.3)	N.A.	Very intolerant

No significant differences among sites were found in soil nitrogen (N) pools, gravimetric soil moisture or light environments at the stand level. Trenching significantly increased KCl extractable NH₄ pools and gravimetric moisture content, while NO₃ pools and percent canopy openness did not differ between trenched and untrenched plots (Tab. I). Inorganic N pools are suggested to be a good measure of the soil solution concentration of N available for plants [43], and some authors have found a positive correlation with N mineralization [18].

2.2. Plant species and shade tolerance scores

We studied five coniferous species that vary in observed shade tolerance [2] and are common to the boreal and cold temperate forests of North America [3]. The species were: very intolerant *Pinus banksiana* Lamb., intolerant *Pinus resinosa* Ait., intermediate *Pinus strobus* L., tolerant *Picea glauca* (Moench) Voss. and very tolerant

Abies balsamea (L.) Mill. The observed shade tolerance classification was compared to the distribution of juveniles growing naturally in the field across a light gradient in Northern Minnesota [31]. The 10th percentile of the distribution of each species along the light gradient was used as an approximation of the lowest light levels tolerated by each species (Tab. II, see [30]). Scores are inversely related to the subjective assessments of shade tolerance rankings by North American foresters [3] and species rankings match exactly those of Lusk and Reich (2000). Light data for *Pinus banksiana* are not available.

One-year-old containerized seedlings were purchased from local nurseries. The seeds for these seedlings were collected from central Minnesota and northern Wisconsin forests (ca. 47° N). The seedlings were planted and labeled in May 1993. Twelve individuals of each species, for a total of 1320 seedlings, were planted at approximately 30 cm spacing in a 1 × 1 m subplot with a 0.5 m buffer that was

randomized within the larger plots. Seedling total height before planting was measured in a subset of seedlings ($n = 578$).

2.3. Seedling measurements

In September 1996, after four growing seasons we hand excavated roots and shoots of four seedlings of each species at every experimental plot ($n = 440$). Since seedling excavations were time consuming, only the above-ground portion was collected for the remaining seedlings. Seedlings were divided into needles, stems and, if collected, roots. All plant material was dried in a forced air oven (70 °C) and mass was measured. Projected area of fresh needles was determined with a video imaging system (AgVision, Decagon Devices, Inc., Pullman, WA, USA). Total nitrogen concentrations of dried and ground tissues were measured using the Kjeldahl Digestion assay (Research Analytical Laboratory, Department of Soil Science, University of Minnesota). For all seedlings, the following parameters were either measured or calculated when possible: length of terminal shoot (cm), seedling height (cm), relative main stem height ($\ln[\text{seedling height in 1996}] - \ln[\text{seedling height in 1993}] \cdot 4 \text{ yr}^{-1}$), total needle mass (g), total stem mass (g), total root mass (g), total seedling needle area (cm²), specific leaf area (SLA, cm² of needle g⁻¹ of needle), leaf area ratio (LAR, cm² of needle g⁻¹ of total plant mass), whole-plant nitrogen concentration (mg N g⁻¹ tissue).

2.4. Data analysis

Plots (11 for each control and trenched treatments for a total of 22) were considered experimental units. We analyzed for the effect of site on seedling performance but found no significant interaction among sites for canopy openness or trenching effects (data not shown). Hence, all trenching and light effects were analyzed for sites pooled. Differences in soil properties and light environments between trench and control plots were evaluated using two tailed *t*-tests.

To test effects of canopy openness and trenching on morphological and growth parameters, we used two-way mixed models where trenching (1 d.f.) and canopy openness (1 d.f.) were considered fixed nominal (trenched and control) and random (22 levels ranging from 3 to 11%, see Tab. I) effects, respectively. We tested main effects and interactions on natural log (ln)-transformed growth parameters that were computed as the mean of all individuals (per species) that were present at the end of the experiment in each plot. Number of individuals per species per plot varied from 3 to 12 as a result of variation in survival.

We used an allometric approach to test the effects of canopy openness and trenching on biomass distribution parameter, by plotting the ln-transformed biomass of root, stem or leaves against the ln-transformed biomass of the whole plant [14, 37], and testing whether these slopes or intercepts varied with trenching or light level (akin to analysis of covariance). Since the relative proportion of biomass distributed to leaves, stems or roots is sensitive to the total mass of the plant, the allometric approach enables the separation of differences in biomass distribution due to differences in size from those due to true shifts in partitioning, and is “the only routine method of showing an effect of treatment on net partitioning” [15]. To employ this approach for light, it was necessary to divide all plots into different light categories. After considering the results of the ANOVA above, we grouped canopy openness plots in two categories: (1) Very Low (mean = 4% and range = 3.1 to 5.5%) and (2) Low (mean = 8% and range = 6.4 to 11.1%).

To test for effects of canopy openness and trenching on seedling survival after four years, variables were categorized as described above and nominal logistic regression was used. All analyses were performed using JMP statistical software (SAS Institute, Cary, NC, USA).

3. RESULTS

3.1. Seedling growth

In general, trenching and light increased seedling growth of all species and these effects were generally additive since, with few exceptions, light \times trenching effects were not significant (Tab. III). Over the continuous light levels chosen (i.e., 3 to 11% of open sky), across species, trenching increased whole-plant, needle and stem mass, leaf area and height, more consistently than light, whereas light more consistently increased leaf area ratio than did trenching (Tab. III, Figs. 1, 2 and 3).

Overall, shade intolerant and tolerant species responded similarly to trenching (Figs. 1 and 2). At a common average light environment of 6.6% canopy openness (least square means), trenching significantly increased plant height (relative and total main stem height) in all five species and mass for all species except *Pinus resinosa* (Tabs. IIIa, IIIb and IIIc). Except for *Pinus resinosa* (height increased by 5.3% and mass by 14.3%), the proportional increases in height (range of 11.2–14.5%) and mass (range of 25.4–26.7%) were similar among species, regardless of the larger differences in relative main stem height (range 14–32%). In all species, increased mass was the result of similar and proportional increments of roots, stems, and needles (Fig. 1). Trenching significantly increased total needle and stem mass for all species except *Pinus resinosa* (Tabs. IIId and IIIe). Significant increments in total root mass were found only for the shade tolerant species, *Abies balsamea* and *Picea glauca* with an average increase of 11 and 20%, respectively. In addition, trenching increased total needle area for all species except *Pinus resinosa*. Trenching did not affect specific leaf area, leaf area ratio or whole-plant nitrogen concentration except that nitrogen was marginally greater as a result of trenching in shade tolerant *Abies balsamea* ($P = 0.072$, Fig. 2).

The variation in light among the plots did not have as profound effect on seedling growth characteristics as trenching (Tab. III, Fig. 3). Height was positively related to light availability in *Picea glauca*, *Pinus resinosa* and *Pinus banksiana* (Fig. 3). Total biomass and all of its components increased with light in *Picea glauca*, as did stem mass in *Pinus banksiana* and root mass in *Pinus resinosa* (Tab. III). Specific leaf area decreased significantly with light only for *Picea glauca* while leaf area ratio decreased with light in all species except *Pinus banksiana* (Fig. 3, Tab. III). Light did not affect whole plant nitrogen concentration for any species (Tab. III).

3.2. Effects of trenching and light on morphology and biomass distribution

The proportion of biomass in roots, stems and needles was not affected by trenching in any species (Tab. IV). In essence, accounting for plant size (mass basis), there was no effect of trenching on biomass distribution patterns in any species (Fig. 4). Trenching increased total height and total nitrogen per plant at a common plant mass only for shade tolerant species *Abies balsamea* and *Picea glauca* (Fig. 4). In contrast to trenching, increased light from very low (3 to 5%) to low light (6 to 11%) decreased needle mass and increased root

Table III. Analyses of variance by species for the effects of trenching and canopy openness on the mean values of the following variables: (a) relative main stem height, (b) ln-total plant height, (c) ln-total plant mass, (d) ln-total needle mass, (e) ln-total stem mass, (f) ln-total root mass, (g) ln-total plant leaf area, (h) specific leaf area (SLA) and (i) leaf area ratio (LAR). Species are listed left to right in order of observed shade tolerance in the field. Degrees of freedom for trenching, canopy openness and error term were 1, 1 and 19, respectively. The interaction term is trenching \times canopy openness. Only *P* values < 0.10 are shown. Mean square values of the interaction term are shown only when significant.

Species	High ----- Shade Tolerance -----> Low									
	Abies balsamea	Picea glauca		Pinus strobus		Pinus resinosa		Pinus banksiana		
Variable	Mean sq.	<i>P</i>	Mean sq.	<i>P</i>	Mean sq.	<i>P</i>	Mean sq.	<i>P</i>	Mean sq.	<i>P</i>
(a) Relative main stem height (cm cm ⁻¹ year ⁻¹)										
Trenching	0.019	0.011	0.012	< 0.001	0.009	0.014	0.004	0.036	0.013	0.039
Canopy openness	0.001		< 0.001		< 0.001		< 0.001		< 0.001	
Interaction							0.003	0.044		
Error	0.002		0.001		0.001		0.001		0.002	
(b) ln Plant height (cm)										
Trenching	0.086	0.012	0.085	0.001	0.138	< 0.001	0.8223	0.018	0.189	0.003
Canopy openness	0.001		0.080	0.002	0.003		0.230	< 0.001	0.152	0.006
Interaction							0.121	0.005		
Error	0.013		0.006		0.006		0.012		0.016	
(c) ln Plant mass (g)										
Trenching	0.479	0.004	0.460	0.048	0.449	0.006	0.172		0.571	0.038
Canopy openness	0.005		0.970	0.006	0.034		0.000		0.248	
Interaction										
Error	0.044		0.103		0.047		0.067		0.114	
(d) ln Needle mass (g)										
Trenching	0.490	0.025	0.461	0.071	0.707	0.007	0.216		1.663	0.072
Canopy openness	0.007		0.849	0.018	0.037		0.323		0.308	
Interaction										
Error	0.083		0.127		0.078		0.169		0.459	
(e) ln Stem mass (g)										
Trenching	0.696	0.003	0.526	0.037	0.98	< 0.001	0.123		0.738	0.004
Canopy openness	0.032		1.091	0.004	0.009		0.414	0.034	0.392	0.025
Interaction							0.281	0.074		
Error	0.059		0.10		0.044		0.078		0.066	
(f) ln Roots mass (g)										
Trenching	0.598	0.004	0.23	0.054	0.085		0.072		0.138	
Canopy openness	0.002		1.31	< 0.001	0.037		0.149	0.050	0.042	
Interaction							10.71	0.091		
Error	0.056		0.06		0.043		0.034		0.141	
(g) ln Total leaf area (cm ²)										
Trenching	40446.7	0.017	47967.4	0.017	20655.5	0.010	2178.9		1613.9	0.040
Canopy openness	3160.4		31198.8	0.049	5363.4		11070.1	0.090	35.2	
Interaction										
Error	5941.6		7072.6		2561.0		3450.6		333.0	
(h) SLA (cm ² g ⁻¹)										
Trenching	8.1		24.7		93.3	0.052	42.7	0.055	210.0	
Canopy openness	304.6	0.090	174.4	0.036	17.0		31.5	0.095	164.0	
Interaction					81.1	0.068				
Error	95.3		34.1		21.6		10.2		102.0	
(i) LAR (cm ² g ⁻¹ plant)										
Trenching	46.3	0.050	3.6		8.7		1.6		40.3	
Canopy openness	57.5	0.031	60.6	0.020	110.0	0.001	200.2	0.001	28.7	
Interaction	49.9	0.043								
Error	10.5		9.4		5.9		14.1		0.192	

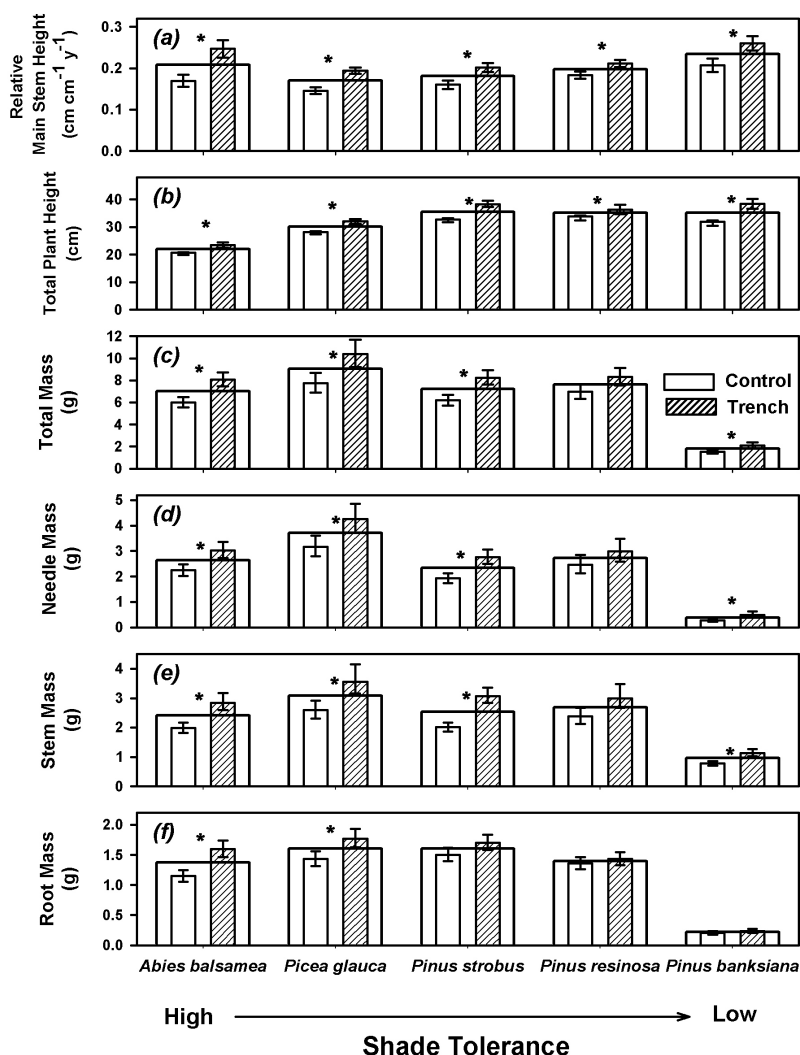


Figure 1. Effect of trenching on relative main stem height (panel *a*), total plant height (panel *b*), total seedling biomass (panel *c*), total needle mass (panel *d*), total stem mass (panel *e*) and total root mass (panel *f*) for five conifer species listed left to right in order of observed shade tolerance in the field (see Tab. III for ANOVA results). Values are least square adjusted means (\pm SE) compared at common light environment (6.6 percent canopy openness). The background bar represents the pooled mean between trench and control plots. Asterisks illustrate significant differences between trenched and control plots (see Tab. III for ANOVA results).

mass independent of plant mass for shade tolerant species *Abies balsamea* and *Picea glauca* (Tab. IV, Fig. 4).

3.3. Seedling survival

Percent survival after four years varied in relation with the species' reported shade tolerance rankings (Fig. 5). Mean seedling survival was 86% for *Abies balsamea*, 92% for *Picea glauca*, 87% for *Pinus strobus*, 77% for *Pinus resinosa* and 67% for *Pinus banksiana*. Trenching had a significant effect on seedling survival only for very shade intolerant *Pinus banksiana* (Likelihood ratio = 5.6, $P > \chi^2 = 0.02$), which had higher survival in trenched (mean = 38.5%, standard error = 1.8) compared to control (mean = 32.0%, standard error = 1.5) plots. Percent survival increased significantly (Likelihood ratio = 5.0, $P > \chi^2 = 0.03$) with greater light availability in *Picea glauca* from 87.5% (standard error = 3.52) in very low light to 95.2% (standard error = 2.9) in low light. Two other species, *Abies balsamea* (Likelihood ratio = 3.3, $P > \chi^2 = 0.07$) and *Pinus strobus* (Likelihood ratio = 3.0, $P > \chi^2 = 0.08$) showed trends towards altered survival when comparing the

two light classes. We did not find any significant trenching \times canopy openness interactions.

4. DISCUSSION

4.1. Growth responses to trenching and light in deeply shaded environments

In the deeply shaded understories of northern Wisconsin's temperate forests, trenching increased seedling mass and height independent of light level for both shade tolerant and intolerant species, supporting our hypothesis that increased soil resources will have a positive effect on whole-plant growth. For all species, mass increases due to trenching were the result of proportionally similar increases in roots, stems and needles. Thus, biomass distribution was not altered by increased soil resources, refuting our hypothesis that trenching will increase the proportional distribution towards leaves and stems and away from roots. Moreover, growth increased similarly as a result of trenching for all species regardless of their

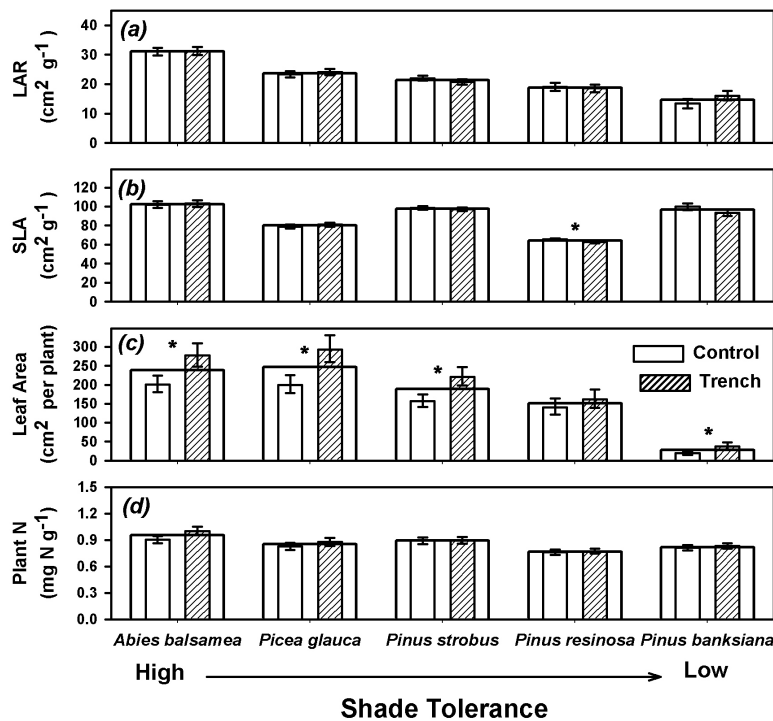


Figure 2. Effect of trenching on leaf area ratio (LAR, panel *a*), specific leaf area (SLA, panel *b*), total leaf area (panel *c*) and whole-plant nitrogen concentration (panel *d*) for five conifer species listed left to right in order of observed shade tolerance in the field (see Tab. III for ANOVA results). Values are least square adjusted means (\pm SE) compared at common light environments (6.6% canopy openness). The background bar represents the pooled mean between trench and control plots. Asterisks illustrate significant differences between trenched and control plots (see Tab. III for ANOVA results).

shade tolerance rankings, refuting the hypothesis that variation in shade tolerance will influence responses to trenching in the low light conditions of this study. Our results do not help to reconcile the current conflicting data. Some studies have shown that shade tolerant species tend to have greater growth rates in very low-light than intolerant species [23, 46] while, other studies have found that shade intolerant species grown in low-light environments have shown greater plasticity in biomass distribution to variation in soil resource availability (i.e., nitrogen, water) than for shade tolerant species [9, 29, 49, 50]. Thus, more plastic, shade intolerant species have shown greater growth responses to increased availability of soil resources than less plastic shade tolerant species.

Our results contradict previous experiments that have shown little or no variation in above-ground growth under low-light conditions in response to variation in soil resource availability (Dylis and Utkin in [45], [4, 9, 19, 20, 29, 46]). In contrast, positive growth responses to changes of soil fertility in deep shade have also been found in the trees *Piceetum myrtillosum* (Karpov in [46]), *Liriodendron tulipifera* growing in 3% daylight [29], *Acer saccharum* growing in 1.5% to 4% daylight [47] and the herb *Impatiens parviflora* growing in 5% daylight [34]. One study found positive responses in deep shade to variation in nutrient supply for shade tolerant but not intolerant species [50]. The variability of observed response to increased soil resources under deep shade could be in part the result of differences among studies in soil fertility [10], and/or result from incomplete data, i.e., no observations of below-ground biomass [9, 35]. Notably, our study was conducted on relatively low fertility sandy glacial outwash soils, which are the kind of sites that Coomes and Grubb (2000) predict would likely have severe below-ground limitations to seedling growth, even in low-light.

Increased light stimulated biomass growth only in the shade tolerant *Picea glauca*. Our results might either indicate that (1) the variation in light environments was not sufficient to cause detectable growth increases, although this range of light levels (3 to 11% canopy openness) has been previously reported to cause strong growth responses for many species both in field and in shade house experiments [24, 29, 46]; but see [4] or that (2) other sources of variation in this field study were large enough to mask any such response. However, height-to-mass ratios in the relative low-light conditions were different across species after averaging all light levels. Shade intolerant species were taller at a common mass than shade tolerant species, indicating that intolerant species etiolated in response to deep shade. Similar responses have been reported by Shirley (1945) working with the same species in northern Minnesota. Low-light did increase leaf area ratio (LAR) in four out of the five species studied as has been reported for some of the same species in a greenhouse experiment [38] and in both studies plasticity in LAR did not vary among species as a function of variation in shade tolerance. Overall, our findings suggest that whole-plant growth of shade tolerant and intolerant species growing in low fertility conditions is limited by below-ground competition for resources at light levels that have been widely reported to be strongly limiting to growth [4, 24, 29, 38, 46].

4.2. Biomass fraction in leaves, stems and roots: responses to trenching and light

Increased soil resources (both water and nitrogen availability) as a result of trenching increased growth roughly similarly for all species while it had no effect on biomass distribution. This finding is contrary to the suggestion discussed by several authors that changes in biomass distribution to above-ground

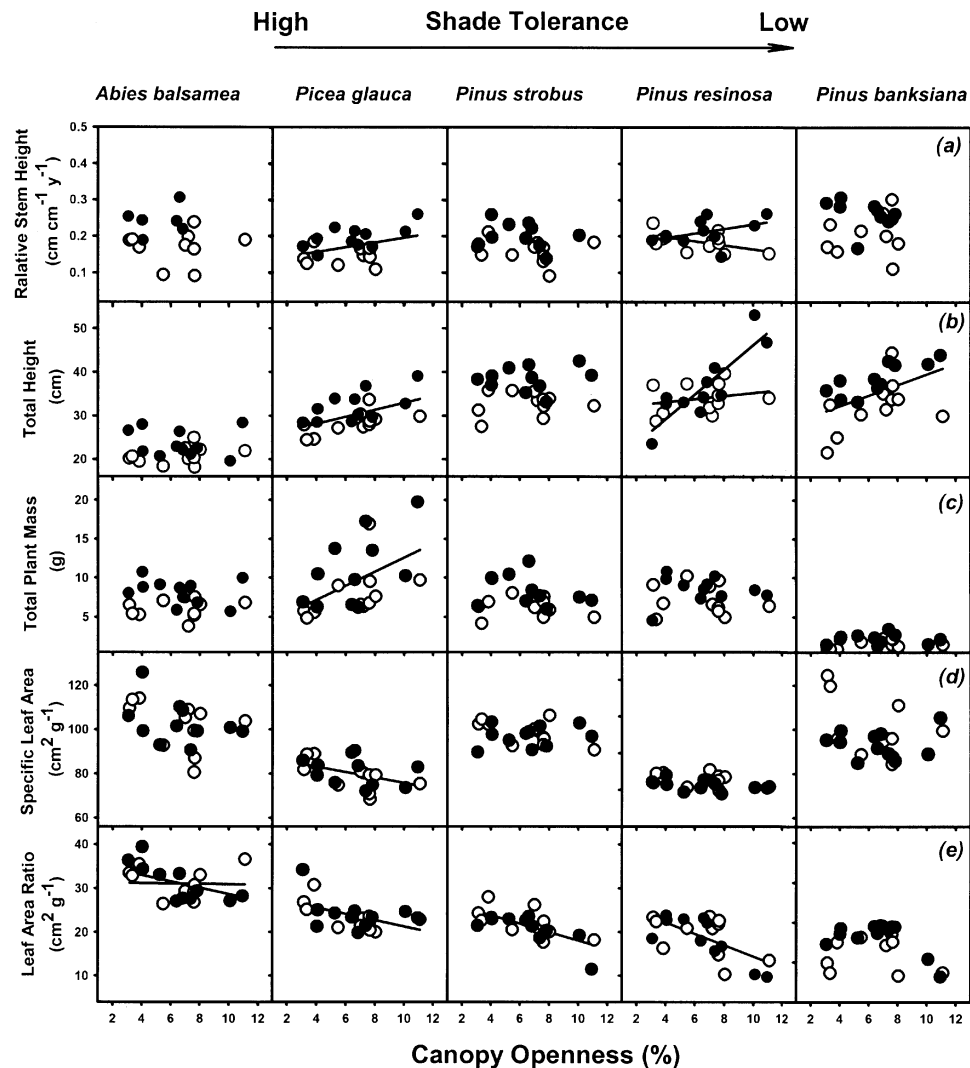


Figure 3. Effect of percent canopy openness on growth variables for seedlings in control (open circle) and trenched plots (closed circle). Growth variables are relative main stem height (panel *a*), total plant height (panel *b*), total plant mass (panel *c*), specific leaf area (SLA, panel *d*), and leaf area ratio (LAR, panel *e*), for five conifer species listed left to right in order of observed shade tolerance in the field. One line indicates that the response changes significant with variation in percent canopy openness. Two lines indicate the presence of canopy openness \times trenching interaction (see Tab. III for ANOVA results). Values are means of either control or trench plots.

biomass are a primary effect of trenching (Karpov in [45], [9, 29, 34–36]). However, some authors have proposed that if plants are to increase their ability to acquire limiting resources then changes in biomass distribution are of little adaptive significance compared to morphological changes such as surface area or length of tissues [1, 28, 37]. Moreover, it is possible that trenching increases growth by increasing physiological activity (i.e., photosynthesis) rather than by altering biomass distribution and that the increase in physiological activity is similar for all species.

4.3. Seedling survival

Our hypothesis about differential survival responses to increased soil resources of tolerant and intolerant species was only weakly supported. The very intolerant *Pinus banksiana*

showed a significant increase in survival as a result of trenching, as predicted, but the other intolerant pine species did not. Some other, but not all [46], studies have also shown that survival in low-light environments may increase with increases in soil fertility in some species or cases [25, 50]. Given their increased growth, we cannot reconcile the overall (all species) lack of survival response to increased soil resources, contrary to our prediction that trenching will have a positive effect on survival.

In general, all of the species in our study showed high levels of survival after four growing seasons (over 60%) regardless of light environment and trenching treatment. Mean seedling survival followed the species reported shade tolerance rankings, suggesting that survival was more closely linked to the overall level of light than soil resources.

Table IV. Analyses of covariance by species for the effects of trenching and low light environments on biomass distribution using ln-whole-plant mass as a covariate on the following variables: (a) relative main stem height, (b) ln-total plant height, (c) ln-total needle mass, (d) ln-total stem mass, (e) ln-total root mass and (f) ln-whole-plant nitrogen. Degrees of freedom for trenching, canopy openness and error term were 1, 1 and 80, respectively. Seedlings were group into two categories of percent canopy openness: low (3.1 to 5.5%) and high (6.4 to 11.1%). Species are listed left to right in order of observed shade tolerance in the field. The interaction term is trenching \times canopy openness. Only *P* values < 0.10 are shown. Mean square values of the interaction term are shown only when significant.

Species	High -----> Shade Tolerance -----> Low									
	Abies balsamea		Picea glauca		Pinus strobus		Pinus resinosa		Pinus banksiana	
Variable	mean sq.	<i>P</i>	mean sq.	<i>P</i>	mean sq.	<i>P</i>	Mean sq.	<i>P</i>	mean sq.	<i>P</i>
(a) Relative main stem height (cm cm ⁻¹ year ⁻¹)										
ln plant mass	0.014	0.0652	0.118	< 0.0001	< 0.001		0.008	0.0134	0.038	0.0013
Trenching	0.001		0.131	< 0.0001	0.002		0.009	0.0089	0.001	
Canopy openness	< 0.001		0.001		< 0.001		0.003	0.1014	< 0.001	
Interaction					0.006	0.0984				
Error										
(b) ln Plant height (cm)										
ln Plant mass (g)	0.816	< 0.001	0.955	< 0.001	0.806	< 0.001	0.824	< 0.001	1.05	< 0.001
Trenching	0.146	0.01	0.094	0.032	0.002		0.003		0.046	
Canopy openness	0.002		0.065	0.076	0.001		0.239	0.001	0.235	0.004
Interaction										
Error	0.021		0.020		0.011		0.02		0.026	
(c) ln Needle mass (g)										
ln Plant mass (g)	11.70	< 0.001	24.71	< 0.001	9.276	< 0.001	11.01	< 0.001	30.82	< 0.001
Trenching	0.047	0.056	0.001		0.001		0.009		0.081	
Canopy openness	0.15	< 0.001	0.083	0.001	0.011		0.941	0.001	0.025	
Interaction										
Error	0.013		0.007		0.021		0.082		0.091	
(d) ln Stem mass (g)										
ln Plant mass (g)	11.759	< 0.001	25.55	< 0.001	8.677	< 0.001	8.934	< 0.001	10.544	< 0.001
Trenching	0.014		0.001		0.014		0.002		0.011	
Canopy openness	0.033	0.022	0.00		0.012		0.323	0.001	0.046	
Interaction	0.036	0.018	0.043	0.044						
Error	0.006		0.01		0.012		0.0294		0.028	
(e) ln Roots mass (g)										
ln Plant mass (g)	8.786	< 0.001	12.796	< 0.001	4.532	< 0.001	5.602	< 0.001	9.784	< 0.001
Trenching	0.061		0.028		0.046		0.041		0.168	
Canopy openness	0.188		0.411	0.011	0.043		0.164	0.098	1.141	0.004
Interaction										
Error	0.066		0.061		0.045		0.056		0.127	
(f) ln N (mg plant ⁻¹)										
ln Plant mass (g)	9.91	< 0.001	16.589	< 0.001	7.528	< 0.001	9.316	< 0.001	14.189	< 0.001
Trenching	0.153	0.001	0.089	0.021	0.003		0.003		0.001	
Canopy openness	0.093	0.008	0.001		0.009		0.001		0.000	
Interaction	0.131	0.002					0.085	0.004	0.047	0.058
Error	0.013		0.016		0.013		0.01		0.013	

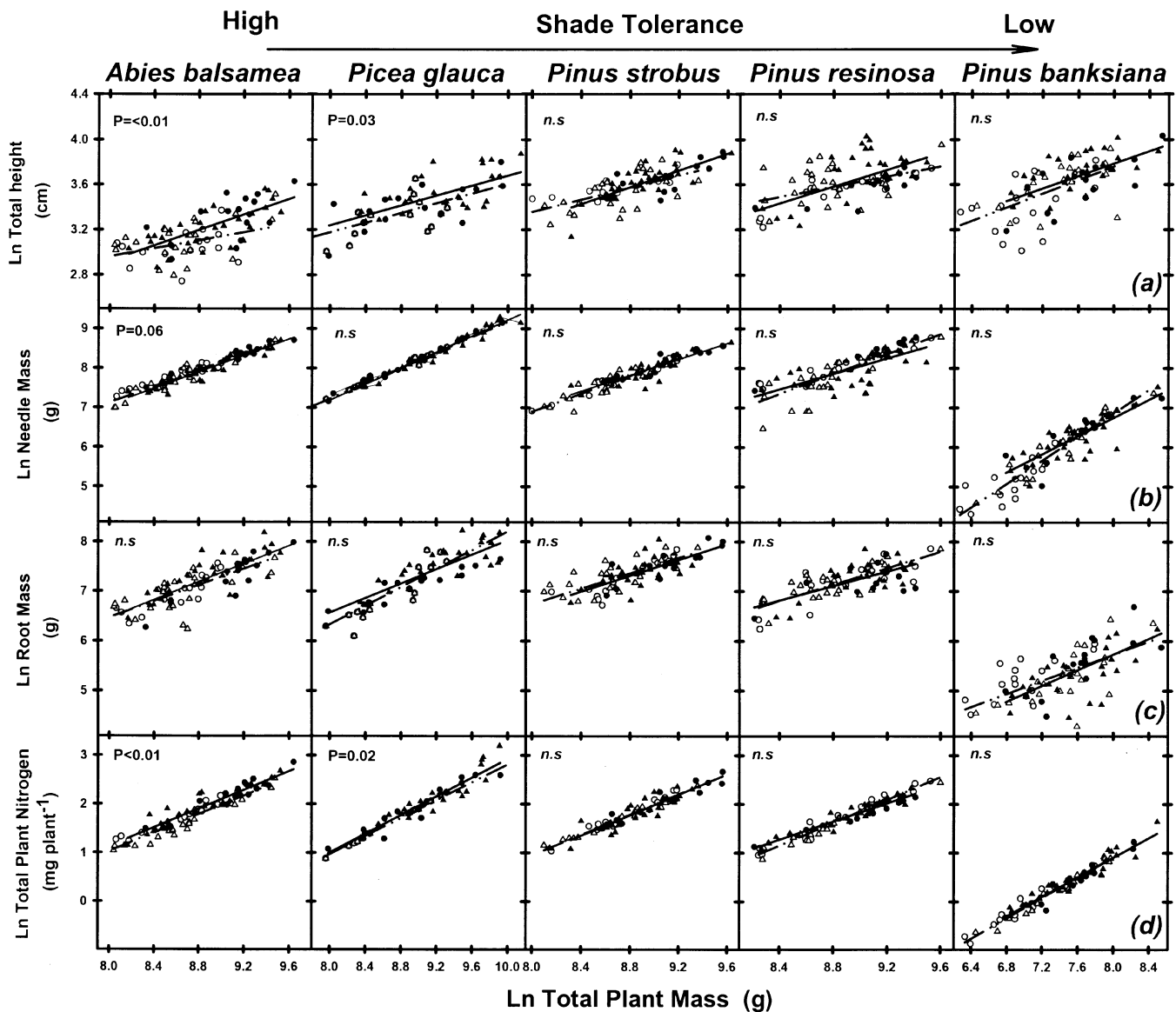


Figure 4. Relationship between total plant height (panel *a*), total needle mass (panel *b*), total root mass (panel *c*), total plant nitrogen (panel *d*) and total plant mass of seedlings grown in control (solid line) and trenched (dotted line) plots. Conifer species are arranged left to right in order of observed shade tolerance in the field. Light environments were pooled for the regression lines and were divided into very low (3.1 to 5.5) and low (6.4 to 11.1) percent canopy openness. Values are the means of control very low-light plots (open circle), control low-light plots (open triangle), trench very low-light plots (closed circle) and trench low-light plots (closed triangle). The full ANCOVA values are presented in Table IV.

4.4. Implications for community dynamics

Natural communities are composed of species that are assumed to be limited by different ranges of combinations of resources and these interspecific differences, could, in part, be driven by variation in biomass distribution patterns [8]. Consequently, interspecific variation in biomass distribution patterns and in the plasticity of these patterns to variation in resource availability may be important mechanisms underlying the pattern and dynamics of forested communities. These observations are among the pillars of the multiple resource

limitation theory, which suggests that plants adjust to situations of resource imbalance by allocating more biomass to the tissues that acquire the most strongly limiting resources [8, 16, 17, 42]. Although we found large differences among species in survival, and morphology (e.g., LAR was greater for shade tolerant than intolerant species), our study species differed little in their growth and biomass distribution responses to increased soil resource availability suggesting that variation in these responses is not an important component of adaptation to low-light forest understories, at least not across the range

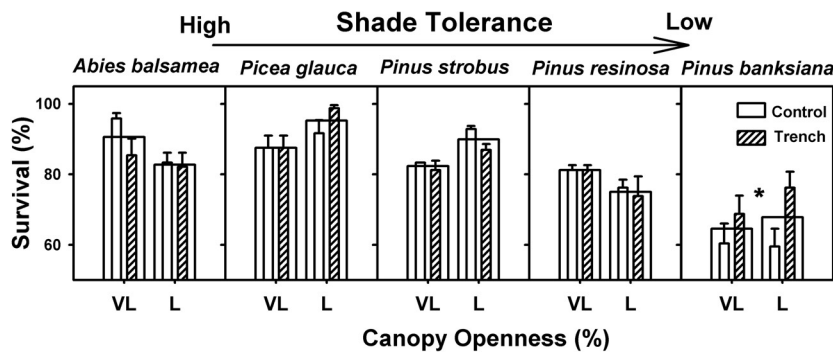


Figure 5. Trenching and canopy openness effects on percent seedling survival. Conifer species are arranged according to their shade tolerance rankings. Light environments were divided in very low (VL = 3.1 to 5.5) and low (L = 6.4 to 11.1) percent canopy openness. Percent survival was calculated based on the number of seedlings alive at the end of four growing seasons for each treatment combination. The background bar represents the pooled mean percent survival for all light environment classes within control and trench treatment. Asterisk illustrate significant differences between trenched and control plots.

of light and soil resource availability present in our study (consistent with [47], for *Acer saccharum*). Our study also shows that below-ground resources do matter to plant growth even for plants growing in deep shade, and regardless of their shade tolerance rankings.

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