Comparing the Importance of Seedbed and Canopy Type in the Restoration of Upland *Thuja occidentalis* Forests of Northeastern Minnesota

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Abstract

In cold-temperate ecosystems of the upper Great Lakes Region, evergreen conifer-dominated forests were once common. As a result of past management practices, early-successional deciduous forests now dominate the landscape. Embedded in this matrix are stands of shade-tolerant conifers, including *Thuja occidentalis*. For the past several decades, large-scale *T. occidentalis* regeneration in remnant *T. occidentalis* and adjacent *Betula papyrifera* forests has not occurred. Using a combination of restoration experiments and field surveys at three study sites on the Lake Superior Highlands, Minnesota, U.S.A., we examined safe sites for *T. occidentalis* regeneration under both *Thuja* and *Betula* canopy types. This study focused on the colonization and establishment phases of regeneration, differentiating among safe-site components for *T. occidentalis*. Seedbed type determined colonization success, with higher rates on conifer logs than on *B. papyrifera* logs, mounds, or pits. Mortality rates for seedlings on natural decayed wood seedbeds were higher under *Thuja* canopy than under *Betula* canopy, but the reverse was true for seedlings on manipulated seedbeds, suggesting that seedbed type was more important than the dominant canopy type. Growth rates for seedlings on moved log segments were greater under the *Betula* than the *Thuja* canopy type, but seedlings on natural decayed wood seedbeds did not exhibit this difference. Results indicated that *T. occidentalis* regeneration was more limited in *Betula* forest by seedbed availability, while in *Thuja* forest canopy conditions were more limiting.

Key words: ***Thuja occidentalis*, Minnesota, canopy type, seedbeds, safe sites, forests, restoration ecology, *Betula*.**

Introduction

Species with narrow regeneration niches (Grubb 1977) often require special safe sites for germination and establishment (sensu Harper et al. 1961). Numerous studies have explored the concept of safe sites required by late-successional canopy species in a variety of upland and lowland forest ecosystems. Some authors emphasize the importance of canopy dominance on the processes of tree regeneration and succession (Zinke 1962; Woods 1979, 1984; Frelich & Reich 1995; Evans et al. 1998). Others focus on the contribution of seedbed availability and seedbed specialization among late-successional species (Clements 1963; Beatty 1984; Beatty & Sholes 1988; Webb 1988; St. Hilaire & Leopold 1995; Chimner & Hart 1996; Hörnberg et al. 1997).

In most forested ecosystems, safe sites result from unique combinations of canopy dominance and seedbed conditions. These unique combinations are often influenced by a feedback loop, a divergent process in which each of two or more vegetation states makes its own environment more or less suitable for the other state(s) (sensu Wilson & Agnew 1992). Many authors have used feedback relationships to explain the diversity and distribution of seedlings of canopy species within forested ecosystems (Collins & Good 1987; Collins 1990; Takahashi 1994; Gray & Spies 1997; Simard et al. 1998). These relationships offer an opportunity to learn more about barriers to restoring the process of regeneration in forest ecosystems.

In the cold-temperate forests of the upper Great Lakes Region (Minnesota, Michigan, Wisconsin, and Ontario), conifer-dominated forests were once more common. Since the time of European settlement (circa 1850), the

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region's forests have been homogenized and today are dominated by early-successional deciduous forests of *Betula papyrifera* (paper birch) or *Populus tremuloides* (quaking aspen) (Mladenoff & Pastor 1993; Frelich 1995). Embedded within this early-successional matrix are occasional remnant stands of *Thuja occidentalis* (northern white cedar) and other mid-to-late successional conifers.

Historically, young deciduous forests in the southern boreal forest zone of this region have succeeded to late-successional forest types, including *T. occidentalis*, in the absence of catastrophic disturbances (Grigal & Ohmann 1975; Frelich & Reich 1995; Kneeshaw & Bergeron 1998). Over the last several decades, however, large-scale regeneration of *T. occidentalis* has not occurred. This lack of regeneration is attributed to several causes, including over-browsing by wildlife (Nelson 1951; Cornett et al. 2000*a*) and silvicultural practices (Heitzman et al. 1997). Cornett et al. (1997) have documented densities of small (<15 cm tall) *T. occidentalis* seedlings 10-fold higher within *Thuja* forest than in adjacent *Betula* forest due to higher seed availability. However, survival rates of *T. occidentalis* under heavy browsing pressure are lower beneath the low-light *Thuja* canopy type than the high-light *Betula* canopy type (Cornett et al. 2000*a*).

For successful regeneration, late-successional conifers, with *T. occidentalis* as an extreme example, require specialized safe sites for germination and establishment. Decayed wood seedbeds, frequently referred to as nurse logs, are a universally important component of the germination safe site for *T. occidentalis* and other late-successional conifers in forest ecosystems (McCullough 1948; Holcombe 1976; Christy & Mack 1984; Harmon & Franklin 1989; Cornett et al. 1997; Simard et al. 1998; but see Scott 1984). Among the critical attributes influenced by canopy conditions are adequate supplies of seed, appropriate seedbeds for regeneration, and light quantity and quality. These attributes create an intricate feedback loop between understory and overstory resources (Kneeshaw & Bergeron 1996; Gray & Spies 1997). In contrast, silvicultural recommendations for *T. occidentalis* regeneration include large-scale soil scarification after removal of the canopy (Johnston 1975; Johnston 1977; Verme & Johnston 1986), often with unsatisfactory results (Lanasa 1989). Simard et al. (1998) speculate that the traditional silvicultural practices that created predominantly younger deciduous forests have removed future nurse logs, thus contributing to the lack of recruitment of *T. occidentalis* and other conifers.

A number of barriers to *T. occidentalis* regeneration are poorly understood, despite being explored within a wide body of forestry and ecology literature. Understanding canopy-tree regeneration in increasingly human-dominated landscapes will contribute to restoring this process to remnant stands where it has been disrupted. To differentiate between the roles of canopy dominance and seedbeds, seedlings on both manipulated and natural seedbeds were examined beneath the late-successional conifer canopy type (*Thuja*) and the early-successional deciduous canopy type (*Betula*). The following questions were addressed: (a) Do canopy-seedbed relationships affect the ability of *T. occidentalis* to colonize natural and manipulated seedbeds in *Thuja-Betula* forests? And (b) Are survival and growth of *T. occidentalis* on natural and manipulated seedbeds influenced by canopy-seedbed relationships?

Study Sites and Methods

The study was part of a larger project investigating a number of barriers to regeneration of *T. occidentalis* in upland *Thuja* (Fig. 1) and *Betula* forests along a portion of the Lake Superior Highlands, running southwest (lat

Figure 1. Upland *Thuja occidentalis* forest at Tettegouche State Park, Lake County, Minnesota, U.S.A.

47°08′ N, long91°30′ W) to northeast (lat 47°58′ N, long 90°04′ W) in northeastern Minnesota. Restoration experiments and surveys were conducted on six 1 to 3 ha study plots within 3 sites, including Gooseberry Falls (GB1, GB2), Split Rock Lighthouse (SR1, SR2), and Tettegouche (TE1, TE2) State Parks.

The climate is continental with a mean annual temperature of 4.7°C and mean annual precipitation of 739 mm (Midwestern Climate Center, Illinois State Water Survey, Champaign, IL). Mean winter temperature within 2.5 km of Lake Superior is −5.5°C (Eichenlaub 1979). Elevation is about 250 m, with surface elevation of Lake Superior at approximately 184 m. Topography is gently rolling to steep, and soils are shallow Boralfs (<0.5 m to bedrock in places) (Anderson et al. 1984). Forests throughout the area are cold temperate, with conifer stands embedded in a matrix of early successional deciduous forest.

The study plots represented conditions commonly found within the *Thuja-Betula* forest type. SR2, TE1, and TE2 had dense canopy cover (≥90% cover). SR1, GB1, and GB2 had moderately open canopy conditions within the *Thuja* canopy type (70–90% cover) and a more open canopy within the *Betula* canopy type (55–75% cover). All plots were in the understory reinitiation phase of regeneration (sensu Oliver & Larson 1996). Dominant canopy species at the study plots included *B. papyrifera*, *P. tremuloides*, and *T. occidentalis.* Other common tree species included *Picea glauca* (white spruce), *Abies balsamea* (balsam fir), *Populus balsamifera* (balsam poplar), and *Fraxinus nigra* (black ash). At Split Rock, the mean age of canopy trees was 94.8 (± 3.8 years, SE) for *T. occidentalis* and 58.6 (± 2.2 years, SE) for *B. papyrifera* (Cornett et al. 1998). The prevalence of old stumps suggested a history of timber harvesting near all or at all study sites.

Colonization

Colonization potential was assessed by *Thuja* seed input, densities of *T. occidentalis* emergents (seedlings <1 year old), and seedbed availability.

Seed Dispersal. Seed traps were used to determine seed dispersal patterns under the *Thuja* canopy type and into the adjacent *Betula* canopy type. Traps were constructed of a circular wire hoop (area = 1,268 cm^2) with three pairs of legs. The corner of a cattle feed sack was suspended from each hoop (Ferrari 1993). The traps were placed along transects running from conifer patches into deciduous patches at SR1 and SR2. The Split Rock plots were selected because they were centrally located between the Gooseberry and Tettegouche plots, and reflected seed input within closed-canopy conditions. In 1994, six transects were oriented at six azimuths at SR2 (i.e., 45°, 105°, 165°, 225°, 285°, and 345°). Ten traps were spaced at 10-m intervals along each transect, for a total of 60 traps. Three traps on each transect were under *Thuja* canopy, 1 at the border between canopy types, and 6 under *Betula* canopy. Two transects were placed at SR1 in 1996. The small size (about 0.5 ha) and configuration of SR1 limited the placement of the traps. Each transect at SR1 consisted of nine traps, running from *Thuja* into *Betula* forest at 50°. Samples were collected from all traps at SR2 in the fall of 1994, 1995, 1996, and 1997 and at SR1 in 1996 and 1997. In the laboratory, seeds of *T. occidentalis* were separated from each sample and counted.

Colonization Seedbed Groups. At SR1 and SR2 in 1995, and TE1, TE2, GB1, and GB2 in 1996, three 40-m transects centered on the *Thuja-Betula* interface were established, for a total of 18 transects. At the end of the growing season, prior to *Thuja* seed dispersal, a total of 90 seedbed groups was created (hereafter called colonization seedbed groups), with five groups spaced at 10-m intervals along each transect.

Seedbed groups consisted of a decaying *B. papyrifera* and conifer log of spongy texture, a shallow pit, and a small mound of scarified soil. The surface area of each created seedbed was approximately 0.25 m^2. Decaying, downed conifer logs between 20 and 30 cm in diameter were selected at each of the study plots, and lengths of 85 to 125 cm were cut from them. Vascular plants, litter, and seeds were removed from each of the log segments. Bark was partially stripped from *B. papyrifera* logs because intact birch bark, even for logs in the advanced stages of decay, is impenetrable to the radicle of germinating *T. occidentalis* seeds. Conifer logs used in this experiment were sufficiently decomposed that bark was no longer present. Cedar was the prevailing species of log used, but some logs of spruce and balsam fir may have been included as it was difficult to distinguish among species when the logs were severely decomposed. Pits and mounds were created with a garden shovel. Newly emerged *T. occidentalis* seedlings were counted on each seedbed at the end of each growing season, and plots were cleared of seedlings and other vegetation in preparation for the next growing season.

Seedbed Availability. At TE1, TE2, GB1, and GB2, percent cover of decayed wood seedbeds was estimated using the line-intersect sampling method (van Wagner 1968). Seedbed cover at SR1 and SR2 was determined similarly in an earlier study (Cornett et al. 1997).

The age of each decaying wood seedbed was estimated using the criteria developed by Franklin et al. (1981) adapted for the Itasca region of Minnesota by Webb (1988): 0 = recent (about 1–5 years since formation), 1 = moderately old (about 6–50 years since formation), 2 = old (about 51–100 years since formation), and 3 = very old (about 100–300 years since formation). Decayed wood seedbeds were identified by species where possible, and were later lumped into two classes: "deciduous," (including *B. papyrifera* and other deciduous logs), or "conifer." Making this distinction was possible for 77% of all woody seedbeds. Canopy type was also recorded for all segments of each transect. If over 50% of stems of canopy trees within 10 m of the transect were coniferous, canopy type was labeled conifer. Otherwise, canopy type was labeled deciduous.

Survival and Growth

The influence of canopy and seedbed on the survival and growth of *T. occidentalis* was evaluated by examining densities of *T. occidentalis* seedlings ($\geq$1 year old) on manipulated logs. Experiments with manipulated logs were informed by and compared to background levels of natural regeneration on different types of seedbeds.

Natural Seedlings. A network of 100 circular subplots was established at SR1 and SR2 in 1994, and TE1, TE2, GB1, and GB2 in 1996 for a total of 600 subplots (see Cornett et al. 1997). Half the subplots were positioned under the *Thuja* canopy type and half under the *Betula* canopy type. Subplots under each canopy type were distributed at each site so that 20% were on each of the following naturally occurring seedbed types: pits, mounds, rotting logs, rotting stumps, and level ground. Newly germinated seedlings (emergents) of *T. occidentalis* were marked with plastic markers. At SR1 and SR2 up to 10 *T. occidentalis* seedlings closest to each subplot center were marked with a numbered tag, and their survival and growth were monitored over the course of the study.

Manipulated Logs. The manipulated log experiment tested the growth and survival response of established *T. occidentalis* seedlings when they were moved from the low-light environment beneath the *Thuja* canopy type to the high-light environment beneath the *Betula* canopy type. Decaying conifer logs (predominantly cedar) between 20 and 30 cm in diameter and containing abundant *T. occidentalis* seedlings were selected and cut as for the colonization seedbed groups, but vegetation was left intact. One hundred eighty log segments were placed at random locations under the *Thuja* (control) and the *Betula* canopies at SR1 and SR2 in 1995, and at GB1, GB2, TE1, and TE2 in 1996. All seedlings of *T. occidentalis* on manipulated logs were given a numbered tag, and their growth and survival were monitored throughout the study period.

Data Analyses

Nominal logistic regression models were used to analyze the presence of *T. occidentalis* emergents on colonization seedbed groups and seedling survival on manipulated and natural decaying log seedbeds (Sokal & Rohlf 1995). In the case of colonization seedbed groups, the influences of site (SITE), canopy type (CANOPY), seedbed (SEEDBED), and their interactions on whether a particular point was colonized at least once between 1996 and 1998 were evaluated. Patterns of seedling survival were explored for SR1 and SR2 in terms of manipulation status (MANIPULATION), plot (PLOT), canopy type (CANOPY), and their interactions. Logistic regressions were followed by likelihood ratio tests, calculated as twice the difference of the negative log likelihoods between a full model and a model without the effect being tested (JMP 3.0.2, SAS Institute Inc., Cary, NC; e.g., Cornett et al. 1998). Goodness-of-fit tests were used for pairwise comparisons separating categories within significant effects.

Wilcoxon nonparametric tests were used for a number of analyses for which the assumptions of parametric tests were violated (JMP 3.0.2, SAS Institute Inc., Cary, NC). Differences in seed rain and colonization rates between years and sites, as well as differences in seedling densities between sites and seedbeds were examined with Wilcoxon tests. Colonization of natural seedbeds and colonization seedbed groups by *T. occidentalis* were also compared with Wilcoxon tests. Percent cover of decayed wood seedbeds, comparable among the six plots and thus combined, was calculated for each of 98 transects. Wilcoxon tests were used to evaluate differences in percent cover of *B. papyrifera* seedbeds and woody seedbeds of other species (lumped) under each canopy type, as well as differences in percent cover between deciduous and conifer logs.

Effects of seedbed manipulation status (MANIPULATION), plot (PLOT) canopy type (CANOPY), and interactions (as shown above) on seedling height growth were evaluated with ANOVA models. Analyses were performed on log segment averages, as the fates of seedlings on individual log segments were not independent. Square-root transformations were used to normalize height growth distributions (Sokal & Rohlf 1995).

Results

Canopy-Seedbed Feedbacks and Colonization

Thuja seed input varied by year, site, and location relative to the *Thuja-Betula* canopy interface. Interannual variability in seed production was dramatic at Split Rock, with input nearly 15 times higher in 1994 and 1995 than in 1996 and 1997 ($p < 0.0001$, Wilcoxon) (Fig. 2). The highest seed input occurred closest to the *Thuja-Betula* interface and dropped dramatically with increased distance from the interface (Figs. 2 & 3).

Densities of *T. occidentalis* emergents were low overall on colonization seedbed groups. The ratio of number of emergents (m^2)/numbers of seeds (m^2) was $0.9 \times 10^{-3} \pm 0.2 \times 10^{-3}$ (SE). In zones with highest seed availability, SEEDBED was the most critical component of colonization success on colonization seedbed groups (Fig. 3). Within colonization seedbed groups, conifer logs were colonized twice as frequently as *B. papyrifera* logs, 4 times as frequently as mounds, and 20 times more frequently than pits (Fig. 3). Similarly natural decayed wood seedbeds were colonized more frequently than either pits or mounds (data not shown), but the ratio of number of emergents (m^2)/numbers of seeds (m^2) ($7 \times 10^{-3} \pm 1 \times 10^{-3}$ [SE]) was more than 7 times higher than on colonization seedbed groups ($X^2_{[1]} = 18.5$; Fig. 3; $p < 0.0001$ [Wilcoxon]). The trend of high colonization rates for *T. occidentalis* on natural decayed wood seedbeds persisted through all years for established seedlings at all three sites (Fig. 4). Across all sites densities of *T. occidentalis* emergents and seedlings were 2.8 and 2.5 times greater beneath the *Thuja* canopy type than the *Betula* canopy type, respectively ($p < 0.03$; Wilcoxon).

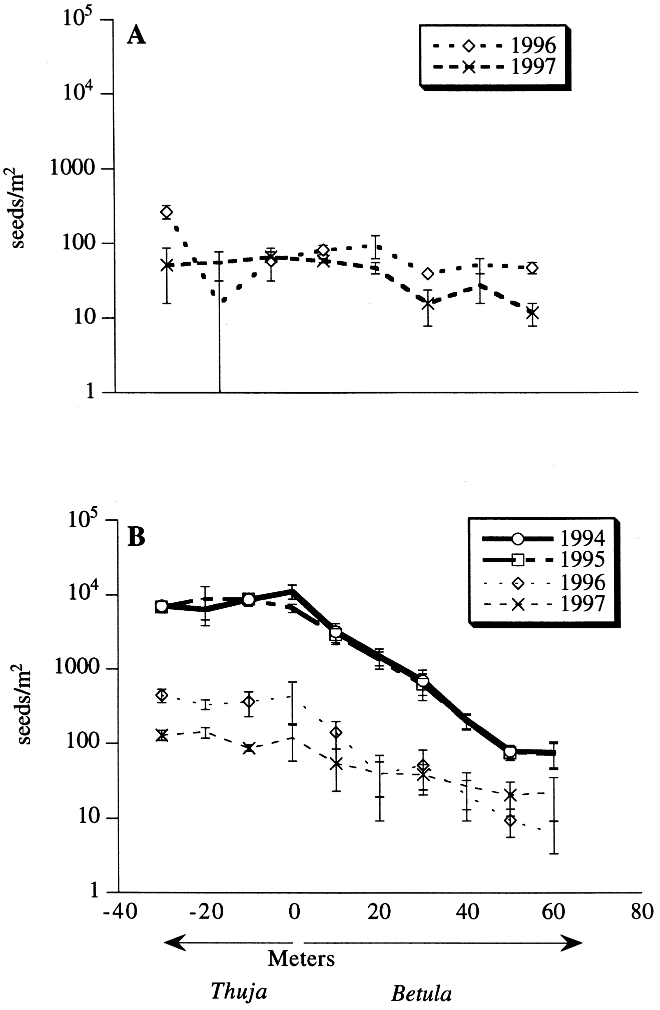

Figure 2. *Thuja* seed input at two Split Rock plots in the fall of (A) 2 years at SR1 and (B) 4 years at SR2. Distance (meters) is relative to the *Thuja-Betula* transition border, with negative numbers indicating locations beneath the *Thuja* canopy type. Points represent mean number of seeds/m^2 (± 1 SE) at 10-m intervals ($n = 2$ at SR1; $n = 6$ at SR2). Note log scale.

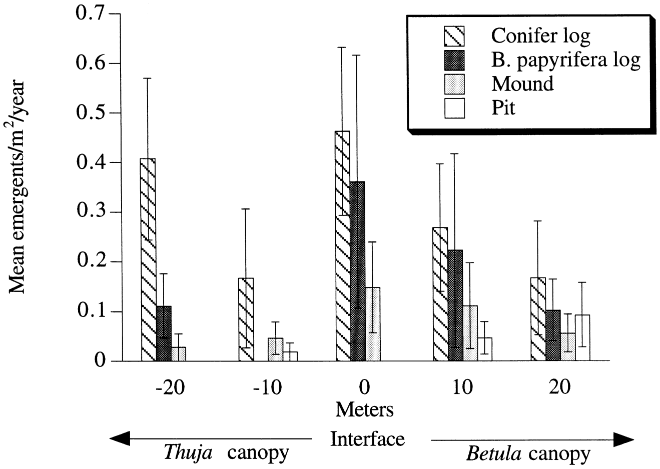

Figure 3. Mean number of new *T. occidentalis* emergents/year (± 1 SE) on colonization seedbed groups for 6 plots, 2 at each of 3 sites, over 3 growing seasons (1995 to 1998). Sample size = 42 for each bar, including 18 replicates for all three sites, and an additional 6 replicates for Split Rock in 1995. A separate logistic regression of the frequency with which each seedbed type was colonized by at least one *T. occidentalis* seedling/year showed that colonization of conifer logs over the 3-year period was greater than for the other seedbed types ($p < 0.02$) and that colonization of *B. papyrifera* logs was greater than for pits ($p = 0.08$).

The overall availability of decayed wood seedbeds did not differ beneath the *Thuja* and *Betula* canopy types in any of the decay classes (Table 1). When decay classes were combined, the species composition of logs differed beneath the two canopy types. The availability of conifer logs was higher beneath the *Thuja* than the *Betula* canopy type (8% vs. 5%; $X^2_{[1]} = 4.2$; $p = 0.04$, Wilcoxon).

Survival

Mortality rates of established *T. occidentalis* seedlings were generally high on both manipulated log segments and natural decayed wood seedbeds. Mortality rates on manipulated seedbeds were nearly twice as high as on natural seedbeds at SR1 ($p < 0.0001$), but this difference was not observed at SR2 ($p = 0.3$) (Table 2; Fig. 5).

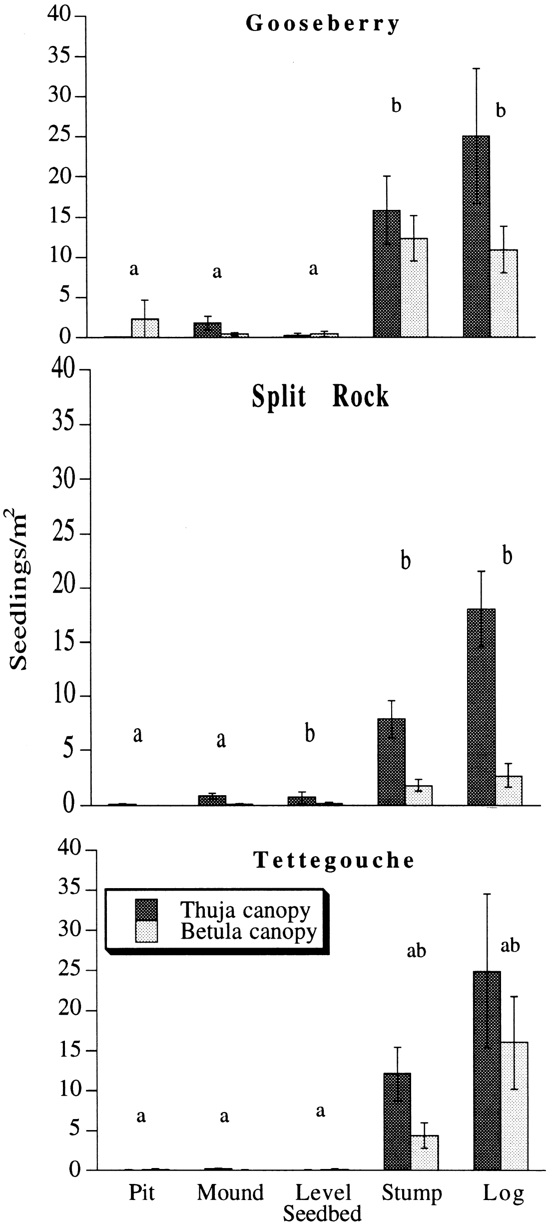

Figure 4. Mean number of naturally occurring *T. occidentalis* seedlings /m^2 (± 1 SE) on 5 seedbeds and under 2 canopy types at 3 sites over 1 (Gooseberry), 2 (Tettegouche), and 4 (Split Rock) growing seasons between 1994 and 1997. For the purposes of this figure, seedlings are defined as more than 1 year old (i.e., not new emergents). Non-overlapping letters indicate differences among seedbed types ($p \leq 0.008$, Wilcoxon) within each site.

Table 1. Mean percent cover of wood seedbeds, including logs and stumps, in four decay classes (see text for descriptions of decay classes) beneath *Thuja* and *Betula* canopy types (results combined for six plots at three sites, Split Rock, Gooseberry, and Tettegouche). Standard errors of the mean are in parentheses.

	Canopy Type	
Decay Class	Thuja	Betula
0	1.9 (0.7)	0.9 (0.4)
1	1.5 (0.3)	1.3 (0.3)
2	5.7 (1.6)	4.2 (0.4)
3	6.6 (0.9)	5.1 (0.4)

MANIPULATION, PLOT, and several interactions were good predictors of seedling mortality on manipulated seedbeds (Table 2). At SR1, mortality rates were slightly higher for log segments moved from beneath the *Thuja* canopy type to the *Betula* canopy type than for those moved from one location to another within the *Thuja* canopy type ($p = 0.03$; Fig. 5). This difference in mortality rates beneath the two canopy types was not observed at SR2 (Fig. 5). In contrast, for seedlings on natural decayed wood seedbeds, overall percent mortality was somewhat higher under the *Thuja* than the *Betula* canopy type at SR2 ($p = 0.0005$), but not at SR1 ($p = 0.5$) (Fig. 5). Seedlings that survived were larger on average at the beginning of the study (3.8 ± 0.1 cm tall) than seedlings that perished (2.7 ± 0.04 cm) ($X^2_{[1]} = 96.3$; $p < 0.0001$).

Growth

Seedlings that survived to the end of the study on manipulated logs grew more than those on natural decayed wood seedbeds (Fig. 6). MANIPULATION, CANOPY, and their interaction affected growth of established seedlings of *T. occidentalis* (Fig. 6). On manipulated log segments, seedlings increased in height on average 47% more under the *Betula* canopy type than under the *Thuja* canopy type across all plots (Fig. 7). On natural decayed wood seedbeds at Split Rock, growth between 1995 and 1997 did not differ beneath the two canopy types (Fig. 6).

Table 2. Results from logistic regression of seedbed manipulation status, plot, canopy type and interactions on mortality of *T. occidentalis* seedlings at two Split Rock plots (1995 to 1997).

Effect	X^2	p
MANIPULATION[a]	34.6	<0.0001
PLOT[b]	6.4	0.01
CANOPY[c]	1.2	0.3
MANIPULATION × PLOT	7.6	0.006
MANIPULATION × CANOPY	8.1	0.004
PLOT × CANOPY	9.4	0.002
MANIPULATION × PLOT × CANOPY	0.1	0.73

[a] Moved log segments versus natural decayed wood seedbeds.
[b] SR1 versus SR2.
[c] *Thuja* versus *Betula*.

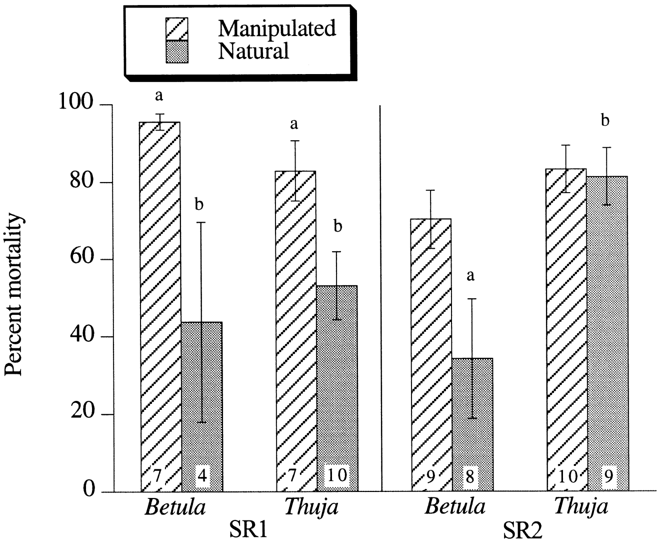

Figure 5. Comparison of percent mortality, based on log segment means (± 1 SE), on manipulated moved log segments and natural decayed wood seedbeds at SR1 and SR2 between 1995 and 1998. Sample sizes (n) are shown within each bar. Non-overlapping letters represent differences in mortality rates between manipulated and natural seedbeds within SR1 ($p < 0.07$) and differences between mortality rates of natural *T. occidentalis* seedlings beneath the two canopy types at SR2. Mortality rates for seedlings on manipulated seedbeds at SR2 did not differ between the two canopy types. Refer to Table 2 for more detail on the interactions among variables affecting mortality.

Discussion

Higher densities of natural emergents and seedlings of *T. occidentalis* beneath the *Thuja* canopy type resulted from higher seed and seedbed availability, and were coupled with lower survival rates than those that occurred for seedlings beneath the *Betula* canopy type. Creating suitable seedbeds for colonization and establishment of *T. occidentalis* beneath the higher light environment of the *Betula* canopy type was predicted to be advantageous for regeneration. In central Oregon conifer forests, shade-tolerant conifer seedlings emerge, survive, and grow best in relatively high light environments (e.g., large canopy gaps) (Gray & Spies 1996). In the present study, however, presence of decayed log seedbeds appeared to be universally beneficial for regeneration, while advantages and disadvantages were associated with each of the two canopy types.

Manipulation of canopy-seedbed relationships assisted in identifying regeneration barriers for canopy species. However, this technique is impractical for large-scale restorations, emphasizing the importance of conserving the natural process of seedbed deposition.

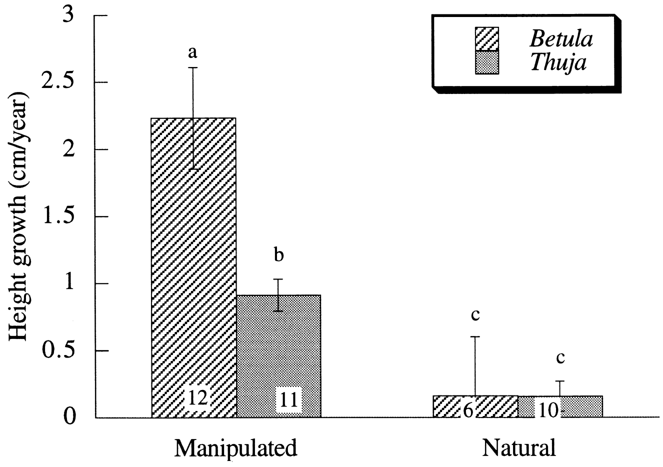

Figure 6. Comparison of mean height growth/year (± 1 SE) for *T. occidentalis* on manipulated moved log segments and natural decayed wood seedbeds between 1995 and 1998. Data from SR1 and SR2 were pooled. Sample sizes (n) are shown within each bar. Non-overlapping letters represent differences among manipulation status (moved log segments vs. natural decayed wood seedbeds, $p < 0.0001$), canopy type ($p = 0.02$), and the interaction of manipulation status and canopy type ($p < 0.0001$) as detected by a larger ANOVA.

Colonization

The low densities of emergents on colonization seedbed groups in 1997 and 1998 were likely related to the low seed input in 1996 and 1997. Within each year, logs

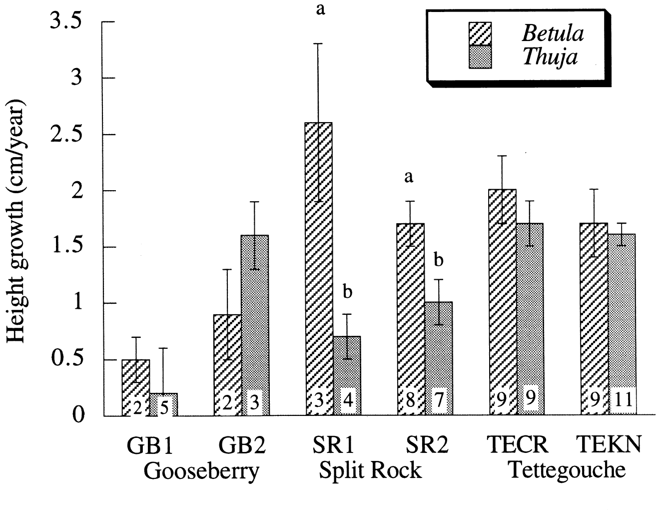

Figure 7. Mean percent height growth (± 1 SE) of *T. occidentalis* seedlings on manipulated log segments between 1995 (SR1, SR2), 1996 (GB1, GB2, TE1, TE2), and 1998 by canopy type. Sample sizes are shown within each bar. Combining all plots, growth rates were higher overall under the *Betula* canopy than under the *Thuja* canopy ($p = 0.02$, Wilcoxon). Letters indicate individual plots within which growth rates beneath the two canopy types differed ($p < 0.03$, Wilcoxon).

appeared to be "safer" seedbeds than either pits or mounds. Among the possible benefits conveyed by nurse logs compared with the pit and mound seedbeds are accumulation of bacterially fixed nitrogen (Sharp & Millbank 1973; Maser & Trappe 1984; Jurgensen et al. 1989), high concentrations of ectomycorrhiza (Harvey et al. 1976, 1979), and higher light availability (Kuuluvainen & Juntunen 1998). Cornett et al. (1997, 2000*b*) have demonstrated that higher emergence of *T. occidentalis* on decaying wood may be linked to higher temperatures, higher moisture retention, and lower accumulation of leaf litter in comparison with other types of seedbeds.

Cornett et al. (1997) determined that even where safe sites for germination occur under the *Betula* canopy, seed availability limited *T. occidentalis* colonization. The seed input results of the present study were consistent with this conclusion. In part because of its relatively short dispersal distances (Kneeshaw & Bergeron 1996; Cornett et al. 1997), the ability of *T. occidentalis* to colonize safe sites beneath the *Betula* canopy type is limited. However, colonization results of the present study suggested that safe site creation beneath the *Betula* canopy type within the zone of seed supply might not replicate natural safe site availability. For example, the log segments used may have been too short and narrow to maintain the moist micro-environment required for germination.

The comparatively low availability of appropriate seedbeds beneath the *Betula* canopy type was consistent with Simard et al. (1998), who suggest that nurse-log species occurring later in succession may be better for *T. occidentalis* establishment than those occurring earlier in succession. However, seedbed deposition and *Thuja* seed availability within the landscape examined in the present study have been impacted by the region's logging history. Whether the current conditions can result in successful *T. occidentalis* regeneration through natural succession alone is questionable.

Manipulation of seedbeds for colonization within the seed supply zone has the potential to result in a net increase in colonization by *T. occidentalis* beneath the *Betula* canopy type. The present study has demonstrated, however, that the success of artificially creating these seedbeds is limited, at least in years with low seed input.

Survival

Mortality of *T. occidentalis* in the understory of conifer-dominated forests has been linked to light availability. Scott and Murphy (1987) reported that seedlings of *T. occidentalis* in a Michigan old-growth forest were generally restricted to decayed-log seedbeds, and that surviving seedlings taller than 25 cm were associated 76% of the time with higher light conditions of a canopy gap. Similarly Simard et al. (1998) found that many conifers in boreal forests persist on decayed wood seedbeds with higher than average light availability. The results of manipulated seedbed-canopy relationships supported the work of other authors and revealed new complexities.

We assumed there would be an advantage for seedlings on log segments moved from a low-light (*Thuja*) to a high-light (*Betula*) environment. However, the high mortality rates observed at some plots on manipulated regeneration logs in general, and under the *Betula* canopy type in particular, suggested that a "cookbook" approach to manipulating canopy-seedbed relationships is not appropriate. For example, under the relatively exposed conditions at SR1, seedlings moved from beneath *Thuja* to *Betula* canopy likely perished as a result of the higher transpiration rates and desiccation that resulted from exposure to higher light and temperatures (Cornett et al. 1997). As with the colonization seedbed groups, log manipulation did not replicate the conditions created by natural processes.

Although mortality rates were lower overall for seedlings on natural decayed wood seedbeds, higher mortality rates beneath the *Thuja* than the *Betula* canopy type on natural seedbeds suggested that low light levels may ultimately limit recruitment. This trend was most apparent at SR2, where light availability beneath the *Thuja* canopy type was half that of the *Betula* canopy type (Cornett et al. 2000*a*). At SR1, the difference between the light environments beneath the two canopy types was less distinct (Cornett et al. 2000*a*), possibly explaining the similarity of mortality rates beneath the two canopy types.

Growth

Although seedlings on moved logs experienced higher mortality rates overall than those on natural decayed wood seedbeds, survivors also had greater growth, particularly under the *Betula* canopy type. For SR1, results were comparable to those of Gray and Spies (1996), who found that groups of conifer seedlings with highest survival rates had low growth rates.

The fact that movement of logs in general, even within the same canopy type, boosted growth rates of *T. occidentalis* seedlings relative to that of natural logs, suggests that some quality of the micro-environment was changed just by the act of moving the log. Simard et al. (1998) found that seedlings of late-successional conifers in a boreal forest generally grow in microsites with higher light availability than that which occurs on average in the understory. Although these differences were not quantified in the present study, it is possible that the moving of logs inadvertently created higher light environments, even within the *Thuja* canopy. New locations were selected randomly in advance, but the logs may have been unintentionally placed in spots with less undergrowth to enhance the ease of placement. Yet another possible explanation for enhanced growth rates on moved logs was the comparatively high mortality rate of small seedlings, which may have reduced competition among remaining seedlings.

Reasons were less clear for similarity of growth rates of seedlings on natural decayed log seedbeds beneath the *Thuja* and *Betula* canopy types. Naturally established seedlings under the *Betula* canopy are generally within the 20-m seed input zone. In such close proximity to the *Thuja-Betula* canopy interface, the light environment for seedlings on segments moved within the *Thuja* canopy type may be less distinct than for seedlings on manipulated logs, which were always moved more than 20 m from the interface. Additionally, other stressors (sensu Hobbs & Norton 1996) may affect seedlings that naturally establish under the *Betula* canopy type. For example, there may be a higher likelihood of germination on a lower-nutrient deciduous log, prolonged exposure to birch leaf litter, or greater competition with surrounding vegetation.

Restoration Implications

This study has several implications for restoring regeneration of *T. occidentalis* and other late-successional tree species. Under current conditions, seed and seedbed availability are greatest beneath the *Thuja* canopy type, but seedling mortality rates are lower under the *Betula* canopy type. Although experimental seedbed manipulation revealed insights about safe sites for *T. occidentalis*, attempts to mimic the process of safe site creation beneath the *Betula* canopy type produced mixed results and may be impractical on a large scale. Given the critical role played by decaying conifer logs in the regeneration of *T. occidentalis*, conservation of the natural process of seedbed deposition therefore, should take priority. However, in areas where this process has been disrupted, seedbed manipulation may be tested further. Focusing seedbed manipulation on areas within 30 m of a *Thuja* seed source is advisable to take advantage of natural seed rain. Investigating a range of log lengths and diameters larger than those used in the present study may prove worthwhile.

Choosing longer segments of large-diameter logs with larger established seedlings (>4.0 cm) may also be attempted to allow seedlings to take advantage of higher light conditions beneath the *Betula* canopy type. Further testing this method is recommended only at mesic sites with continuous deciduous canopy cover, because mortality rates at hotter, drier sites were unacceptably high.

Mixed results from the present study may be compared with more standard restoration strategies such as direct underplanting of seedlings (e.g., Cornett et al. 2000*a*). The present study examined only the early components of safe sites for *T. occidentalis* regeneration. Other factors, such as protection from herbivory, will also contribute to ultimate recruitment success, the topic of other papers by the same authors (Cornett et al. 2000*a*).

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