American Journal of Botany 87(12): 1807–1814. 2000.

SEEDBED AND MOISTURE AVAILABILITY DETERMINE SAFE SITES FOR EARLY *THUJA OCCIDENTALIS* (CUPRESSACEAE) REGENERATION[1]

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Regeneration of many late-successional tree species depends on specialized safe sites. The primary objective was to investigate the roles of seedbed and moisture retention as dimensions of safe sites for the early regeneration of drought-sensitive northern white cedar (*Thuja occidentalis*). We hypothesized that rates of germination, survival, and growth of *T. occidentalis* are unlikely to differ among seedbed types under conditions of abundant water, but that differences are likely to emerge as water becomes more limited. In a 67-d greenhouse experiment, cedar seeds were sown on logs, leaf litter, and soil of cedar and paper birch (*Betula papyrifera*) canopy origin. Seedbeds were subjected to three water treatments. Among the water treatments, highest germination rates occurred within the high water treatment, although germination on cedar litter was comparable to that of the low water treatment. Higher germination and survival rates occurred on decayed logs than other natural seedbeds for medium ($P = 0.001$) and low ($P < 0.0001$) water treatments. Germination on birch logs occurred at higher rates than on cedar logs within the low water treatment ($P = 0.04$). Seedling growth for the medium water treatment was lower on leaf litter than any other type of seedbed ($P < 0.01$). Results generally demonstrated that the interplay between seedbed and moisture retention is a component of safe sites for *T. occidentalis* regeneration.

Key words: Cupressaceae; decayed logs; leaf litter; mineral soil; Minnesota; moisture; safe sites; seedbeds.

The concept of ‘‘safe site’’ (sensu Harper et al., 1961) is a useful framework for examining the regeneration potential of many plant species. Fowler (1988) explored the notion that several variables interactively constitute the safe site for any given species, concluding that safe sites occur along a continuum of safety. The circumstances that enable individual species to persist in an ecosystem are often most critical during the early stages of germination and seedling establishment (Grubb, 1977). These early stages may be especially important for the conservation of certain shade-tolerant conifers with a recent history of poor regeneration. Late-successional conifers in general require specialized safe sites for germination and early establishment. *Thuja occidentalis* is an example of a species that has declined throughout much of its range, a trend attributed by some authors to a land use history that has resulted in inadequate availability of safe sites (e.g., Waller and Alverson, 1997; Simard, Bergeron, and Sirois, 1998).

Many authors have demonstrated the importance of decaying wood as a seedbed for conifers, including *T. occidentalis*, in both lowland and upland forest communities (McCullough, 1948; Nelson, 1951; Curtis, 1946; Holcombe, 1976; Christy and Mack, 1984; Scott and Murphy, 1987; Anderson and Winterton, 1996; Cornett, Reich, and Puettmann, 1997). Several characteristics of decayed wood may contribute to safe sites for the germination and establishment of many late-successional species. Among these characteristics are higher water retention by decaying logs than other substrates (e.g., Place, 1950; Harvey, Larsen, and Jurgensen, 1979); less buildup of leaf litter (Christy and Mack, 1984; but see Minore, 1972); presence of nitrogen-fixing microorganisms (Sharp and Millbank, 1973); earlier warming to temperatures sufficiently high for germination (Nelson, 1951); and a greater number of mycorrhizal associations (Maser and Trappe, 1984). Although many studies have speculated about the relationships between these characteristics and early germination and establishment of tree species, few have explored these links experimentally.

Although important for *T. occidentalis* regeneration, decaying logs are fairly rare in forests (Scott, 1984; Cornett, Reich, and Puettmann, 1997; Cornett, 2000). Leaf litter is generally the most abundant seedbed available, but is not considered favorable for the germination and establishment of *T. occidentalis* (Nelson, 1951; Caulkins, 1967). On disturbed, post-harvest sites, silvicultural treatments for *T. occidentalis* regeneration often include mechanical scarification or prescribed burns to create mineral soil seedbeds (Johnston, 1975, 1977; Verme and Johnston, 1986). The success of these silvicultural practices presumably results from better access to soil moisture (Scott, 1984; Davis, Puettmann, and Perala, 1998).

In addition to gross differences among litter, log, and mineral soil seedbeds, species origin of each of these seedbed types may also contribute to their relative safety. Canopy tree species directly influence the character of available seedbeds through deposition of leaf litter and logs, the decomposition of which shapes soil characteristics such as organic matter content and chemistry (e.g., Beatty, 1984; Cornett, Puettmann, and Reich, 1998; Evans, Miller, and Friedland, 1998). Decay rates also differ among leaf litter and logs of different species, which may partially determine seedbed safety (Sydes and

[1] Manuscript received 11 August 1999; revision accepted 29 February 2000.

The authors thank E. Perry and two anonymous reviewers for critiquing the manuscript, and C. Buschena for providing invaluable technical assistance in the greenhouse, and J. Murra, K. Walker, and J. Bobrowski for laboratory work. Financial support was provided by the Minnesota Department of Natural Resources, NSF Grant DEB-9623458, the Wilderness Research Foundation, and Fellowships from the Dayton-Wilkie, Anderson and Anderson, T. Schantz-Hansen, and Carolyn M. Crosby Funds from the University of Minnesota. Additional support was provided by the Gilchrest Potter Fund from Oberlin College.

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TABLE 1. Mean percentage seedbed moisture and water content by mass per cubic centimetre of substrate (±1 SE) for three water treatments.

Seedbed	High % dry mass	High Water (mg/cm³)	Medium % dry mass	Medium Water (mg/cm³)	Low % dry mass	Low Water (mg/cm³)
Birch log	751 (60)	505 (45)	429 (74)	404 (84)	171 (53)	132 (40)
Cedar log	516 (41)	421 (47)	167 (30)	194 (42)	45 (1)	31 (8)
Birch litter	154 (21)	108 (14)	37 (4)	23 (3)	53 (9)	23 (4)
Cedar litter	157 (15)	198 (17)	41 (4)	68 (10)	45 (7)	49 (7)
Cedar soil	122 (9)	370 (33)	64 (9)	168 (27)	21 (4)	55 (11)
Control	62 (6)	380 (51)	32 (10)	124 (28)	27 (14)	52 (14)

Grime, 1981; Hale and Pastor, 1999). Many of these interspecific differences may also interact with moisture availability.

A constant moisture supply is considered critical for the early development and survival of *T. occidentalis* (Curtis, 1946; Caulkins, 1967). Moisture availability results from an interaction between precipitation and the differential ability of seedbeds to retain moisture. Although decaying wood provides a good seedbed for *T. occidentalis* germination, some authors have questioned whether logs continue to function as safe sites during periods of prolonged drought (Caulkins, 1967; Scott, 1984). The degree to which decayed wood functions as a safe site for *T. occidentalis* may vary substantially with amount of precipitation. For example, in *T. occidentalis* forests on the Lake Superior Highlands in northeastern Minnesota, USA, rainfall during the growing season has ranged from 20 cm/yr to 43 cm/yr between 1989 and 1997 (Wolf Ridge Environmental Learning Center, Finland, Minnesota, USA). The present study addresses this variation in ''safety,'' which has not been adequately described previously.

Most of the existing information about safe sites for *T. occidentalis* seedlings has been generated by field surveys (e.g., Nelson, 1951; Scott, 1984; Scott and Murphy, 1987). However, some experimental work has compared *T. occidentalis* germination on different seedbeds. In a greenhouse experiment, St. Hilaire and Leopold (1995) found that *T. occidentalis* germinates better on seedbeds below shorter than taller mosses from a New York forested minerotrophic peatland. Work from upland *T. occidentalis* ecosystems is scarce, although a seeding experiment in a cliff escarpment ecosystem determined that *T. occidentalis* germinates and grows beneath deciduous canopy types provided leaf litter is removed before sowing (Bartlett, Reader, and Larson, 1991). A better understanding of safe sites for *T. occidentalis* germination and establishment is needed to understand fully the tremendous decline in its regeneration rates over the last several decades.

The objective of the study was to examine the combined influence of seedbed and moisture retention on the germination, survival, and growth of *T. occidentalis* seedlings under different levels of moisture availability. Although this experiment was conducted in a greenhouse, a general understanding of safe site complexity was sought within the context of a human-dominated landscape in northeastern Minnesota, USA. Experimental seedbeds were obtained from stands of upland *T. occidentalis* forest embedded within a matrix of early-successional deciduous forest (*Betula papryifera*—*Populus* sp.) to refine the definition of safe sites available beneath each of these canopy types for early *T. occidentalis* regeneration. We predicted that no differences among germination, survival, or growth responses will arise among different seedbeds as long as water is constantly abundant. When water is limiting, however, we hypothesized that germination, survival, and growth of *T. occidentalis* seedlings will be higher on seedbeds with higher moisture retention. Finally, we predicted that germination, survival, and growth of *T. occidentalis* on litter, log, and soil seedbeds may differ on seedbeds of different canopy origin (deciduous or conifer) under different watering regimes.

MATERIALS AND METHODS

The experiment was conducted from early January through mid-March 1997 in the East Greenhouse at the University of Minnesota's Department of Forest Resources. Greenhouse temperature was maintained at 21°C, fluctuating at a maximum of ±2.2°C during the course of the study. The temperature regime reflected mean high temperatures (22°C) that occur in the field during the germination and growing season for *T. occidentalis* germination (May through August). Extended day lighting was used such that seedlings received between 9 and 10 h of light each day, also to mimic field conditions during the growing season.

The experimental design consisted of six replicates (pots) of seven seedbeds subjected to three water treatments, for a total of 126 pots. In each pot, 50 seeds of *T. occidentalis* were sown. Seeds and seedbeds were collected in the fall of 1996 within the natural range of *T. occidentalis* from a *Thuja-Betula* stand at Tettegouche State Park in northeastern Minnesota.

Seeded pots were arranged in a stratified-random design. The 126 seeded pots were placed on a central greenhouse bench, 18 pots long and seven pots wide. Another block of 36 unseeded pots served as reference pots for water content. Although each row of pots received the same water treatment, the arrangement of seedbeds within a row was random, as were the water treatments assigned to each row. To compensate for the heterogeneity that occurs even within a controlled greenhouse environment, rows of pots were rotated every 7 d.

Water treatments—High, medium, and low treatments consisted of water applied in different frequencies and amounts to simulate natural patterns, which range from 1.29 cm/mo to 26.4 cm/mo in the field during the growing season. A fine-mist nozzle was used to water the pots. The rate of water flow was calibrated with a beaker and timer before each watering session to determine watering rate in millilitres per second, generally 10 mL/s. All pots received 500 mL (0.38 cm) of water on the day of sowing. High water treatment pots received 200 mL (0.15 cm) on a daily basis thereafter. Medium water treatment pots received 500 mL water every 7 d, and were given 125 mL (0.1 cm) of water in the middle of the week. Low water treatment pots received 500 mL of water every 14 d and were given 125 mL of water on the 7th d.

A 2 cm³ core of seedbed material was extracted from each unseeded reference flat once a week prior to watering. Gravimetric water content (e.g., Pratt, 1986) was determined for each core by weighing immediately after extraction, drying at 80°C for 3 d, and weighing cores again. Reference water retention levels were determined for six of the seven seedbed materials within each water regime, with insufficient soil from beneath the birch canopy to use for reference pots (Table 1).

Seedbeds—Three types of seedbeds were used, originating from white cedar and paper birch canopy types. Samples of each type of seedbed were gathered from two to three locations beneath each canopy type. Samples of the same type from different locations were pooled. Cedar litter, soil, and decaying cedar log were collected beneath the cedar canopy type. Birch litter, soil, and decaying birch log (bark removed) were collected beneath the birch canopy type. A control consisted of a 50/50 peat/sand mixture.

Pots (11.5 × 11.5 × 5.5 cm) were filled with a 2-cm layer of 50/50 peat/sand mixture. A 2-cm layer of seedbed material was placed on top of the peat/sand mixture. In the case of leaf litter and soil, the seedbed material was spread over the peat/sand mixture. For decayed logs, small chunks were placed over the peat/sand mixture.

New germinants were counted for each pot twice a week over 67 d. Each germinant was marked with a colored toothpick. Successful germination was defined as the point at which radical elongation surpassed the length of the seedcoat. At the end of the study, seedling mortality was recorded for each flat. To test the germinative energy of the *T. occidentalis* seeds, 50 seeds were sown in each of five petri plates kept continuously moist. Each day, new germinants were recorded and removed.

At the end of the study period, all seedlings in each flat were counted and washed. For each pot, one seedling of average size was selected at random. Total root length was measured using AgVision®, a monochrome system for root and leaf analysis (Decagon Devices, Inc., Pullman, Washington, USA).

To determine whether seedling size, in addition to water and substrate treatments, influenced root:shoot ratios, a small, medium, and large seedling were selected from each pot. Each of these seedlings was divided into root and shoot, dried at 80°C for 4 d, and weighed. The remaining seedlings from each pot were divided into roots and shoots. The separate portions were combined, and dried and weighed similarly. From this group of seedlings, mean biomass/seedling, mean root mass/seedling, mean shoot mass/seedling, and root mass/shoot mass were calculated within each pot. When sufficient numbers of seedlings for the above measurements were unavailable, (i.e., within the low water treatment), the biomass of the randomly selected seedling of average size was also determined.

Data analyses—Data presented are based on effective, rather than absolute, seedling emergence. Percentage effective emergence (%EE) was determined by dividing the number of emerged seedlings by the mean number of viable seeds, calculated from the five petri plates, and converting to percentage.

Logistic regression models were used to examine the importance of seedbed, water treatment, and their interaction for %EE and survival. Logistic regressions were followed by likelihood ratio tests, calculated as twice the difference of the negative log likelihoods between a saturated model and a model without a particular effect or interaction (JMP 3.0.2; SAS Institute Inc., Cary, North Carolina, USA). Differences among seedbed and water treatments were further explored with nonparametric Wilcoxon tests. Pairs of seedbeds within each water treatment were compared, as well as pairs of water treatments with seedbeds pooled.

Seedling growth data were analyzed in different ways. For each of the five growth variables, an initial ANOVA was conducted examining the importance of seedbed, water treatment, and their interaction as predictors. Response variables were normalized with square root or natural log transformations where appropriate. Means separation tests for important predictors of growth response were conducted with a Tukey-Kramer test where the assumptions of normality and homoscedasticity were met, or by a nonparametric Wilcoxon test if this was not the case. To determine whether differences in allocation resulted from experimental treatments or differences in seedling size, an analysis of covariance was conducted for each seedbed, with water treatment, ln(seedling biomass), and their interactions as predictors of ln(root mass).

RESULTS

Effective emergence (%EE)—Seedbed, water treatment, and the interaction of seedbed and water treatment were important predictors of %EE (Table 2). Final %EE was 21 and 85% higher for the high than the medium and low water treatments, respectively (Fig. 1). Differences in %EE occurred among the seedbed types with constantly abundant water (i.e., the high water treatment). Final %EE was highest on controls and lowest on cedar litter seedbeds (Table 3, Fig. 1). Patterns of %EE within the medium water treatment were similar to those of the high water treatment, but more pronounced (Table 3, Fig. 1). As with the high water treatment, final %EE was highest on controls and lowest on cedar litter seedbeds (Table 3, Fig. 1). Among the seedbed types within the low water treatment, patterns of %EE resembled somewhat those of the high and medium water treatments (Fig. 1). On the log and birch litter seedbeds, %EE was two to four times higher than on either soil seedbed, cedar litter, or the control (Table 3, Fig. 1C).

TABLE 2. Likelihood ratios[a] and $P > \chi^2$ (in parentheses) for emergence and mortality of *T. occidentalis*.

Dependent variable	Water treatment (df = 2)	Seedbed (df = 6)	Water treatment × seedbed (df = 12)
Emergence	650.4 (<0.0001)	137.8 (<0.0001)	98.9 (<0.0001)
Mortality	1.1 (0.57)	176.9 (<0.0001)	730.7 (<0.0001)

[a] From logistic regression.

Only a few minor differences in %EE emerged in comparing like seedbed types of different canopy origin (Table 3, Fig. 1). The most consistent difference was that, across all three water treatments, %EE was higher on fall-collected birch litter than on cedar litter. However, %EE on cedar litter was lower than on all other substrates, not just birch litter. Under the low water treatment only, %EE on birch logs was higher than on cedar logs (Table 3, Fig. 1C).

Survival—Seedbed and the interaction of seedbed and water treatment were important predictors of survival, but water treatment alone had little effect (Table 2). Under the high water treatment, 95% of an average of 16.5 initial germinants per flat survived until the end of the experiment. No differences in survival occurred among seedbed types within the high water treatment (Table 4, Fig. 2A). For seedlings receiving the medium water treatment, survival was slightly lower than for those receiving the high water treatment. Ninety percent survived of an average of 13 initial germinants per flat (Fig. 2B). Differences in percent survival among the seven seedbed types within the medium water treatment were modest in magnitude (Fig. 2B). Cedar litter and the control had survival rates of 100%, with rates on birch log and birch soil seedbeds low by comparison (Table 4).

Survival of seedlings receiving the low water treatment was variable, ranging from 38 to 100%. However, survival rates were calculated from an average of only 2.4 initial germinants per flat (Table 4, Fig. 2C). Although initial numbers of germinants were low on birch litter, cedar litter and cedar soil, survival on these substrates was 100% over the 67-d study period (Table 4, Fig. 2C). Survival on birch logs was 38%, out of a total of 35 seedlings, while neither of the two seedlings that germinated on birch soil survived.

Survival was similar on seedbeds of the same type but of different canopy origin under the high and medium water treatments. Under the low water treatment, survival rates for seedlings growing on birch soil (0%) were lower than on cedar soil (100%), but for a sample size of only two seedlings each (Table 4, Fig. 2).

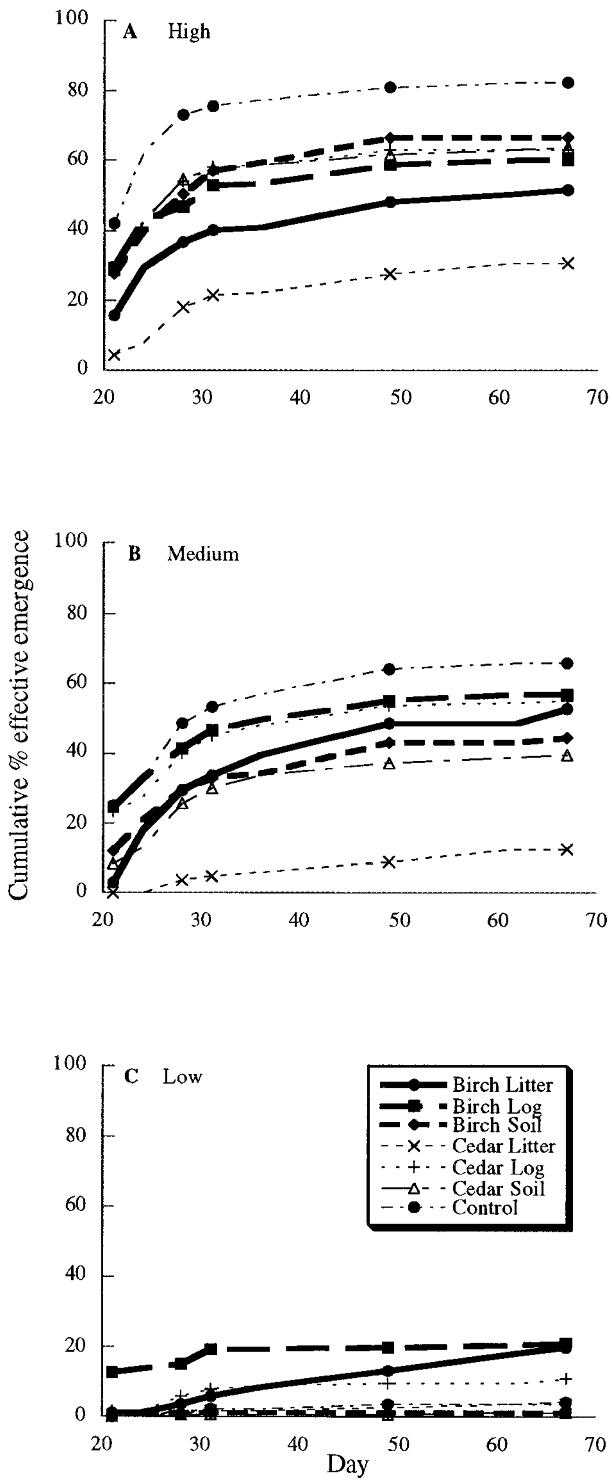

Fig. 1. Cumulative % effective emergence (%EE) of *T. occidentalis* on seven seedbeds over the 67-d greenhouse study for (A) high, (B) medium, and (C) low water treatments. Each point represents %EE for six replicates of each seedbed type.

Growth—Among most of the seedbeds within the high water treatment, seedling growth responses did not differ (Table 5). However, seedlings growing on birch litter had shorter roots than those growing on birch logs (Table 5). The trend of larger roots on logs than on litter seedbeds was observed even after adjusting for seedling size (P = 0.03, Wilcoxon) (Table 6). Additionally, root : shoot ratios were highest for seedlings on birch logs relative to seedlings rooted in soil and litter seedbeds regardless of canopy origin (Table 5).

Within the medium water treatment, some differences in

TABLE 3. Results (P values) from pairwise comparisons of *T. occidentalis* percentage effective emergence between each seedbed within each water treatment using nonparametric Wilcoxon tests.[a]

	Birch litter	Birch log	Birch soil	Cedar litter	Cedar log	Cedar soil	Control
High water treatment							
Birch litter	—						
Birch log	0.25	—					
Birch soil	0.17	0.37	—				
Cedar litter	0.05	0.004	0.01	—			
Cedar log	0.29	0.47	0.57	0.02	—		
Cedar soil	0.34	0.37	0.94	0.04	0.81	—	
Control	0.02	0.008	0.17	0.04	0.09	0.17	—
Medium water treatment							
Birch litter	—						
Birch log	0.05	—					
Birch soil	0.93	0.15	—				
Cedar litter	0.08	0.004	0.008	—			
Cedar log	0.41	1.0	0.33	0.006	—		
Cedar soil	0.47	0.19	0.52	0.01	0.11	—	
Control	0.05	0.26	0.04	0.004	0.38	0.05	—
Low water treatment							
Birch litter	—						
Birch log	0.61	—					
Birch soil	0.003	0.003	—				
Cedar litter	0.007	0.005	0.46	—			
Cedar log	0.19	0.08	0.01	0.06	—		
Cedar soil	0.003	0.003	0.67	0.70	0.01	–	
Control	0.007	0.006	0.15	0.54	0.09	0.05	—

[a] See Fig. 1 for direction and magnitude of differences.

TABLE 4. Results (P values) from pairwise comparisons of *T. occidentalis* percentage survival between each seedbed within each water treatment using nonparametric Wilcoxon tests.[a]

	Birch litter	Birch log	Birch soil	Cedar litter	Cedar log	Cedar soil	Control
High water treatment							
Birch litter	—						
Birch log	0.22	—					
Birch soil	0.15	0.90	—				
Cedar litter	0.22	0.90	0.90	—			
Cedar log	0.20	0.90	0.90	0.90	—		
Cedar soil	0.59	0.52	0.52	0.52	0.52	—	
Control	0.86	0.29	0.15	0.29	0.21	0.59	—
Medium water treatment							
Birch litter	—						
Birch log	0.21	—					
Birch soil	0.07	0.51	—				
Cedar litter	0.32	0.02	0.02	—			
Cedar log	0.09	0.51	1.0	0.02	—		
Cedar soil	0.40	0.73	0.61	0.14	0.49	—	
Control	0.32	0.02	0.02	1.0	0.02	0.14	—
Low water treatment							
Birch litter	—						
Birch log	0.007	—					
Birch soil	0.01	0.30	—				
Cedar litter	1.0	0.08	0.15	—			
Cedar log	0.06	0.45	0.24	0.25	—		
Cedar soil	1.0	0.08	1.0	1.0	0.25	—	
Control	0.07	0.27	0.27	0.27	0.81	0.27	—

[a] See Fig. 2 for direction and magnitude of differences.

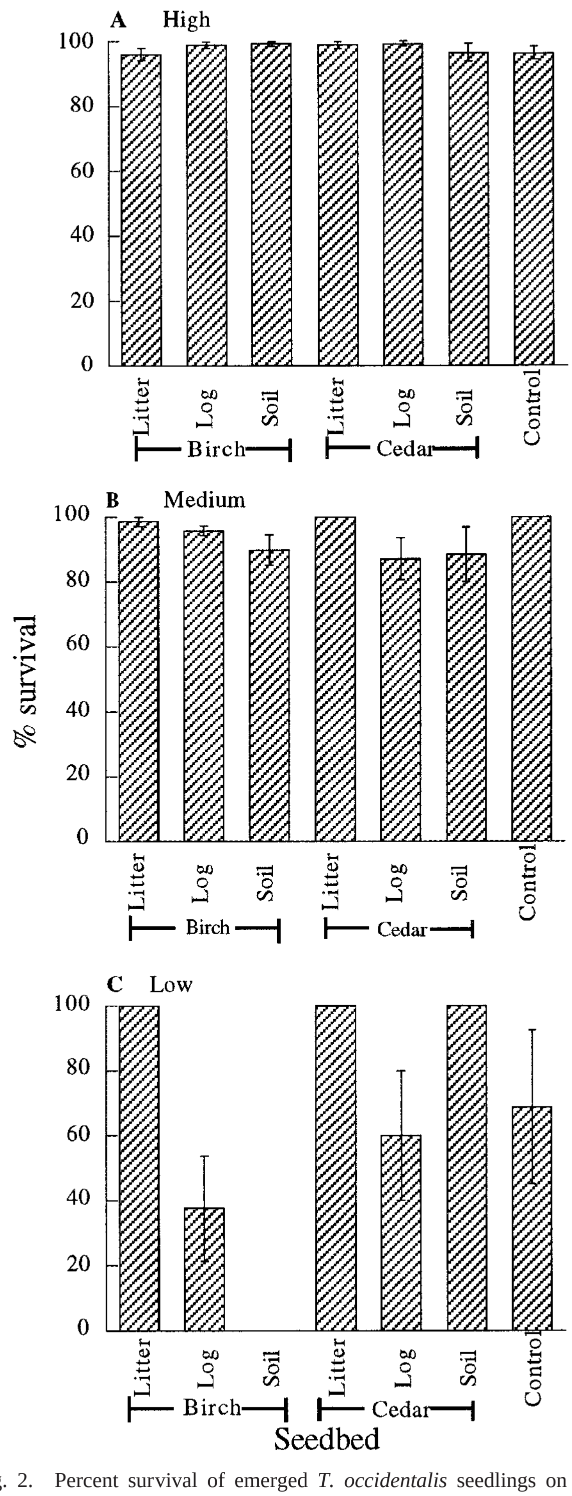

Fig. 2. Percent survival of emerged *T. occidentalis* seedlings on seven seedbeds by the end of the 67-d study period for (A) high, (B) medium, and (C) low water treatments. Each bar represents mean % survival for six replicates of each seedbed type. Error bars are ±1 SE.

seedling growth patterns were also observed. Root mass, root length, and root : shoot ratio were lower for seedlings growing on cedar litter than for seedlings on other seedbed types (Tables 5, 6), a pattern that paralleled %EE. Unadjusted, but not adjusted, root : shoot ratios were higher overall for seedlings subjected to the medium water treatment than the high water

TABLE 5. Seedling growth on seven seedbeds under high (H), medium (M), and low (L) water treatments* ± (1 SE). ND = No data.

Growth parameter	Water treatment	Litter		Log		Soil		Control
		Birch	Cedar	Birch	Cedar	Birch	Cedar	
Mean[1] biomass/seedling (mg)	^{A}H	0.7 (0.1)	0.6 (0.6)	0.7 (0.06)	0.9 (0.1)	1.0 (0.1)	0.9 (0.1)	0.9 (0.1)
	^{AB}M	0.5 (0.1)	0.4 (0.1)	0.7 (0.04)	0.6 (0.2)	0.8 (0.2)	0.7 (0.1)	0.8 (0.1)
	^{B}L	0.9 (0.3)	0.7 (0.2)	0.5 (0.2)	0.5 (0.1)	ND	0.01 (–)	0.3 (0.1)
Mean[1] root mass (mg)	^{A}H	0.17 (0.03)	0.16 (0.02)	0.25 (0.02)	0.27 (0.03)	0.26 (0.02)	0.26 (0.04)	0.25 (0.01)
	^{A}M	0.12 (0.03)^{ab}	0.0008 (0.03)^{a}	0.28 (0.01)^{ab}	0.22 (0.05)^{ab}	0.27 (0.05)^{b}	0.26 (0.03)^{b}	0.26 (0.03)^{ab}
	^{B}L	0.11 (0.03)	0.0017 (0.06)	0.18 (0.06)	0.21 (0.04)	ND	0.04 (0.01)	0.1 (0.03)
Mean[2] root length (cm)	^{A}H	12.6 (2.4)^{a}	13.7 (1.5)^{ab}	18.4 (0.6)^{b}	21.6 (2.8)^{ab}	13.5 (1.1)^{ab}	14.1 (2.4)^{ab}	13.5 (1.4)^{ab}
	^{AB}M	7.5 (0.7)^{a}	6.8 (0.9)^{a}	14.6 (1.6)^{ab}	16.1 (1.9)^{b}	16.4 (1.7)^{b}	15.5 (1.4)^{ab}	17.2 (2.2)^{b}
	^{B}L	7.8 (1.6)	7.6 (1.1)	10.1 (2.6)	11.8 (2.3)	ND	4.0 (–)	10.1 (2.1)
Mean[1] shoot mass (mg)	H	0.6 (0.1)	0.4 (0.04)	0.6 (0.1)	0.6 (0.08)	0.7 (0.1)	0.6 (0.1)	0.7 (0.1)
	M	0.4 (0.2)	0.7 (0.4)	0.4 (0.05)	0.4 (0.1)	0.8 (0.2)	1.0 (0.3)	0.5 (0.1)
	L	0.8 (0.3)	0.5 (0.1)	0.3 (0.1)	0.4 (0.06)	ND	1.0 (–)	0.2 (0.1)
Root mass/shoot mass (mg)[1]	H	0.31 (0.02)^{a}	0.38 (0.03)^{ab}	0.54 (0.02)^{c}	0.43 (0.01)^{bcdef}	0.37 (0.01)^{ad}	0.41 (0.004)^{egh}	0.40 (0.03)^{agh}
	M	2.68 (2.3)^{a}	0.43 (0.20)^{b}	0.79 (0.17)^{c}	1.73 (1.09)^{cde}	0.86 (0.46)^{df}	1.28 (0.91)^{cd}	1.05 (0.57)^{eg}
	L	0.22 (0.7)^{a}	0.31 (0.05)^{ab}	0.49 (0.18)^{cd}	0.46 (0.04)^{bc}	ND	0.04 (–)^{a}	0.42 (0.01)^{ad}

* Different lowercase letters indicate responses that differed within a water regime (row) ($P < 0.05$; Tukey-Kramer means separation test), and different uppercase letters indicate differences among water treatments within a given growth response.
[1] Calculated per pot.
[2] Calculated for one randomly selected individual per pot.

TABLE 6. Mean root mass (mg) ± (1 SE) for high and medium water treatments of three individual seedlings/pot adjusted for seedling size[a].

Seedbed	High water	Medium water	P
Birch litter	0.16 (0.02)	0.13 (0.03)	0.2
Birch log	0.27 (0.03)	0.25 (0.03)	0.7
Birch soil	0.25 (0.04)	0.35 (0.04)	0.09
Cedar litter	0.20 (0.02)	0.08 (0.03)	0.001
Cedar log	0.26 (0.03)	0.23 (0.03)	0.5
Cedar soil	0.22 (0.02)	0.26 (0.02)	0.3
Control	0.26 (0.03)	0.26 (0.03)	0.9

[a] Values presented are for a small, medium, and large seedling from each pot and accompany results from an analysis of covariance of seedbed, water treatment, and ln(biomass) on ln(rootmass) (see Fig. 3). Results for the low water regime are not shown because there were not enough replicates. *P* values are the results of *T* tests.

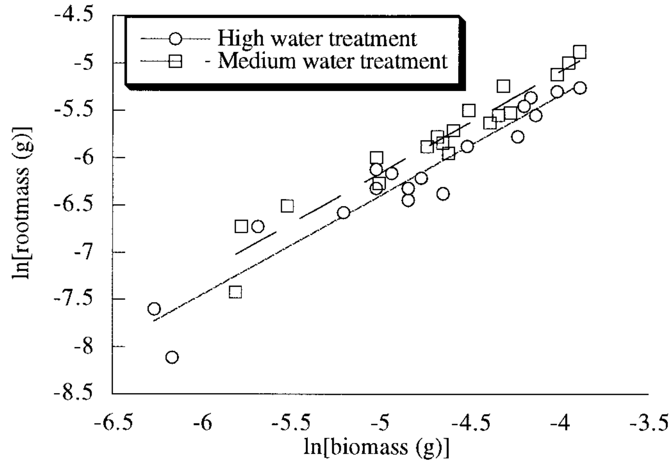

Fig. 3. Relationship between seedling and root biomass of *T. occidentalis* growing on birch soil for high [ln(root mass) = −1.16 + 1.05 × ln(total seedling mass), r^2 = 0.91] and medium [ln(root mass) = −0.84 + 1.06 × ln(total seedling mass), r^2 = 0.93] water treatments.

treatment (Tables 5, 6). The analysis of covariance indicated that for most seedbeds the proportion of biomass allocated to roots was strongly related to seedling size, although differences in allocation could also be partially explained by the water treatments (Fig. 3). However, when seedbeds were pooled, seedling biomass did not differ between high and medium water treatments (Table 5), and water treatment ($F_{1,6}$ = 23; $P <$ 0.0001), ln(seedling biomass) ($F_{1,6}$ = 880; $P <$ 0.0001), and their interaction ($F_{1,6}$ = 21; $P <$ 0.0001) all contributed to differences in allocation to roots.

Also consistent with patterns of %EE within the low water treatment, seedlings growing on log seedbeds had the highest root : shoot ratios (Table 5). Mean root mass/seedling was lower overall for low water treatments than for high and medium water treatments. Mean biomass/seedling was similarly lower overall for the low water treatment, but variable with lowest biomass/seedling on the control and cedar soil.

A few differences in growth and allocation were apparent among seedlings growing on seedbeds of the same type but of different canopy origin under the high and medium water treatments. Under the high water treatment, slightly higher root : shoot ratios occurred on cedar than on birch soil (Table 5). Under the medium water treatment, slightly higher root : shoot ratios occurred on birch litter than cedar litter (Table 5). Despite comparable seedling growth on birch and cedar logs, seedlings on birch logs had lighter foliage and a chlorotic appearance. Insufficient sample sizes obscured any differences in growth variables on like seedbeds of different canopy origin within the low water treatment.

DISCUSSION

Abundant water—Seedbeds receiving abundant water generally proved safest for germination of *T. occidentalis*. However, the prediction that %EE would not differ among different seedbeds receiving abundant water was not upheld. Instead, variability in safety was observed, even within the highest water was not upheld. Instead, variability in safety was observed, even within the highest water treatment. The much lower %EE on cedar litter and higher %EE on the control indicated either that water availability to seedlings differs among seedbeds even when the supply is equal or that qualities not addressed by the present study distinguish these seedbeds from the others. Many authors have implicated leaf litter as a physical barrier to germination (e.g., Place, 1955; Ahlgren and Ahlgren, 1981; Sydes and Grime, 1981; Knapp and Smith, 1982; Bartlett, Reader, and Larson, 1991; Cornett, Puettmann, and Reich, 1998; but see Williams et al., 1990), possibly the result of blocked access to otherwise available soil moisture. Control seedbeds may have produced the highest %EE by providing the easiest access to soil moisture. The pure sand/peat mixture was probably also relatively pathogen-free compared with some of the field-collected seedbeds.

In terms of survival, water treatment was also the most important component of the *T. occidentalis* safe site. Survival patterns within the high water treatment generally supported the prediction that few differences occur among seedbeds receiving abundant water. Although birch and cedar logs absorbed several times their mass in water, abundant moisture did not affect survival on these seedbeds. Conversely, early survival of *T. occidentalis* depends on unsaturated soil conditions (Chimner and Hart, 1996). The similarity of survival rates among seedbeds with different water contents indicated that saturation was not reached under the high water treatment.

Limited water—Conditions of abundant water as described above are unlikely to persist under typical field conditions. Although water treatment was the strongest component of the *T. occidentalis* safe site, continua of safety for germination, survival, and growth became more prominent within treatments for which water was limited, upholding the second hypothesis. Many of these differences coincided with the capacity of seedbeds to retain water.

Higher %EE on logs than on cedar soil in the low water treatment suggested that greater water retention by these seedbeds conferred an advantage for %EE. Under field conditions, decayed wood maintains consistently higher moisture levels than other seedbeds (Place, 1950; Harvey, Larsen, and Jurgensen, 1976). Anderson and Winterton (1996) suggest that for some conifers, such as *Picea engelmannii*, better germination on logs than other types of seedbeds is linked to higher moisture retention. Within the low water treatment, although the maximum %EE was achieved on log seedbeds, the low response overall suggested that no seedbed is unequivocally safe for germination under severe drought conditions.

The highest root : shoot ratios overall occurred for the medium water treatment, suggesting that moisture availability as a safe site component produces different effects at different life stages. An increase in root : shoot ratio is both a consequence of and coping strategy for water stress. During times of moderate water stress, shoot growth is reduced while photosynthesis remains relatively stable, resulting in increased allocation of photosynthates to roots (Kozlowski, Kramer, and Pallardy, 1991).

Similar continua of safety observed for germination and survival on different seedbeds also occurred for early growth. The smaller root length, root mass, and root : shoot ratios for seedlings grown on leaf litter in comparison with log seedbeds under all three water treatments was consistent with Nelson (1951) and may have additional explanations beyond access to moisture, such as more mycorrhizal associations on logs (Harvey, Larsen, and Jurgensen, 1976, 1979) or physical barriers to root elongation posed by leaf litter (e.g., Ahlgren and Ahlgren, 1981; Sydes and Grime, 1981). Although seedlings on cedar litter had good survival rates over the study period, the less vigorous roots could result in higher rates of seedling mortality in the field.

Comparing like seedbeds of different canopy origin—The differences between %EE on like seedbeds of different canopy origin supported the third hypothesis under conditions of limited water (i.e., birch vs. cedar logs within the low water treatment). The differences observed may have been linked to the higher rate of moisture retention of birch logs compared with cedar logs. It is possible that decomposition of birch logs was more advanced than that of cedar logs in the present study, leading to higher moisture retention. This result contrasted with data from a field experiment in upland *Thuja-Betula* forests, in which germination rates were higher on average on cedar than on birch logs (Cornett, 2000). Cornett (2000) used numerous logs for the field study, while seedbeds in the present study were obtained from only a few birch and conifer logs, not allowing for the diversity of conditions in a natural setting. Other artifacts of the present study may also have resulted from the controlled environment of the greenhouse or timing of seedbed collection.

Although %EE differed between cedar and birch litter for all water treatments, consideration of these differences related to canopy origin was limited to log seedbeds. In a forest setting, birch litter is thought to hinder *T. occidentalis* germination even more than cedar litter (Ahlgren and Ahlgren, 1981; Scott, 1984). In the present study, however, the timing of seedbed collection caused the birch litter to curl and function as less of a barrier than the compacted, partially decomposed leaf litter typically present during spring germination of *T. occidentalis*.

Differences in growth response on like seedbeds of different canopy origin did not appear to be related to water retention. The higher root : shoot ratios on cedar soil than on birch soil within the high water treatment supported Noble (1972), who found that even small differences in soil chemistry can cause clear differences in seedling survival and root elongation for *Picea engelmannii* seedlings in their first year of growth under the same water treatment.

Chlorosis of *T. occidentalis* seedlings growing on birch logs indicated that continued survival over a longer period might be higher on cedar logs. Jurgensen et al. (1989) found that higher rates of bacterial nitrogen fixation occur in deciduous logs hosting white rot than in conifer logs hosting brown rot fungi. Decay induced by white rot fungi happens more rapidly than that of brown rot, possibly resulting in more rapid immobilization of nitrogen in deciduous than conifer logs. Lower nitrogen availability may have contributed to the chlorosis observed in *T. occidentalis* seedlings. Thus, although birch logs retained moisture better than cedar logs in the present study, cedar logs may be safer for long-term survival on the basis of nutrient availability. This question could be addressed by examining plant nitrogen content over a longer experimental period.

The broad patterns that emerged during the present study were generally linked to the water treatments, with some exceptions. Much of the variation in %EE, survival, and growth within the water treatments also appeared to correspond to differences in gravimetric water content among the seedbeds. Gravimetric water content was used as a comparative index among seedbeds in this study, but water availability to the plant may differ among seedbeds of different texture with similar water content (Rundel and Jarrell, 1991). Comparing the water content of substrates in the present study with those of other studies suggested that within the high water treatment, water availability was similar between log and soil substrates, but was much lower for litter. Within the high water treatment, the water potential of the two litter types was likely quite negative, given that Dix (1985) reported a potential of -2.8 MPa for undecomposed leaf litter at a similar water content (Table 1). Dix (1985) also reported a water potential of -2 MPa for decayed birch logs with a water content of 125 mg H_2O/cm^3, similar to the value for decayed birch logs in the low water treatment of the current study (132 mg H_2O/cm^3). Hence, the much higher water contents of decayed birch logs in the medium and high water treatments may represent much less negative water potentials.

Safe sites for *T. occidentalis* occurred along a continuum of moisture availability and seedbed type. With a few exceptions, the extremely divergent water treatments were the strongest dimension of safe site in this study, but within water treatments seedbed type and canopy origin also contributed to early regeneration success. Among field-collected seedbeds, maximum %EE and survival occurred under higher moisture and nonlitter seedbed conditions. When moisture was moderately limiting, the safest seedbed for *T. occidentalis* (i.e., logs) had high moisture content relative to other seedbeds. However, under conditions of extreme drought as frequently occur in the field, decayed wood may be no safer than other types of seedbed for *T. occidentalis* regeneration.

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