Factors limiting the early survivorship of *Thuja plicata* on northern Vancouver Island, British Columbia

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Abstract: Western redcedar (*Thuja plicata* Donn ex D. Don), a late successional species on northern Vancouver Island, has a low seedling survival in mature hemlock (*Tsuga heterophylla* (Raf.) Sarg.) – amabilis fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes) (HA) stands. Shade, moss competition, and substrate were tested as causes of low cedar establishment. Cedar seeds were sown on reference and local soils isolated from surrounding soil, on nonisolated local soil, and on forest floor with moss removed. Western hemlock, amabilis fir, and cedar seeded on forest floor acted as controls. Treatments were implemented in the HA interior and the HA–clearcut edge, with soil treatments also implemented in clearcuts. Germinants and very young seedlings of cedar have a low leaf area of needle-like primary foliage. Cedar development of secondary foliage (the scale foliage normally associated with this species) was correlated with greater vigour and growth. Secondary foliage developed in the rankings forest edge and clearcut > forest interior, and reference isolated soil > local isolated soil > nonisolated local soil. Seedling survival rankings were edge > interior, and amabilis fir > hemlock > cedar on soil and with moss removed > cedar on forest floor. Cedar and amabilis fir showed a smaller growth response to light than hemlock. The results indicate that cedar, normally considered a late successional species, needs disturbance for early seedling establishment and survival and thus has some characteristics of an early seral species.

Résumé : Les semis de thuya (*Thuja plicata* Donn ex D. Don), une espèce de fin de succession dans le Nord de l'île de Vancouver, ont un faible taux de survie dans les peuplements murs de pruche (*Tsuga heterophylla* (Raf.) Sarg.) et de sapin gracieux (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes) (PS). L'ombrage, la compétition de la mousse et le type de substrat ont été testés comme causes de la difficulté d'implantation du thuya. Des graines de thuya ont été semées dans un sol de référence, des sols locaux isolés, des sols locaux non isolés et sur le sol forestier après enlèvement de la mousse. La pruche de l'Ouest, le sapin gracieux et le thuya semés à même le sol forestier ont servi de témoins. Les traitements ont été implantés à l'intérieur des PS et à la limite entre des PS et une coupe totale; les traitements impliquant le sol ont également été implantés dans des coupes totales. Les graines ayant germé ainsi que les très jeunes semis de thuya ont une faible surface de feuillage juvénile aciculaire. Le développement du feuillage adulte du thuya (le feuillage squamiforme normalement associé à cette espèce) est corrélé à une vigueur et une croissance plus forte. Les différentes situations testées ont influencé le développement du feuillage adulte dans l'ordre suivant : lisière forestière et coupe à blanc > intérieur forestier et sol isolé de référence > sol local isolé > sol local non isolé et la survie des semis dans l'ordre suivant : lisière > intérieur et sapin gracieux > pruche > thuya sur le sol et mousse enlevée > cèdre à même le sol forestier. Le thuya et le sapin gracieux ont montré une réponse de croissance moins forte à la lumière que la pruche. Les résultats indiquent que le thuya, normalement considéré comme une espèce de fin de succession, nécessite une perturbation pour l'établissement précoce et la survie de ses semis et que ce dernier possède quelques caractères d'une espèce de début de succession.

[Traduit par la Rédaction]

Introduction

Interspecific differences in shade tolerance are widely believed to drive forest successional dynamics (Spurr and Barnes 1980; Shugart 1984; Kobe et al. 1995; Walters and Reich 1996). Light gradient partitioning theory, which suggests that species have specific ranges of light within which they outgrow and outsurvive others, is often cited as the mechanism for species replacement in succession (Latham 1992; Kobe et al. 1995; Kobe 1999; Messier et al. 1999). More detailed studies have attempted to relate the relative shade tolerance of species to varied habitats, both in the field (Carter and Klinka 1992; Wright et al. 1998*a*) and in greenhouse studies, often with controlled nutrient levels (Latham 1992; Walters and Reich 1997; Finzi and Canham 2000). While much research has attempted to determine physiological variables that dictate a species' shade tolerance (e.g., Niinemets 1997; Khan et al. 2000), very little attention has been paid to the diverse factors in ecosystems

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that may determine a species' ability to survive, such as the interactive effects of canopy cover with predation, substrate, and root competition (but see Wright et al. 1998*b*; Coomes and Grubb 2000).

The western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) – amabilis fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes) (HA) forest type is common on mesic sites on northern Vancouver Island. Most recent HA stands were initiated by large windstorms in the early 1900s, with the most damaging one blowing down approximately 16 000 ha in 1906. It is expected that in the absence of large-scale disturbance, western redcedar (*Thuja plicata* Donn ex D. Don) will establish in the HA understory, eventually creating a cedar-dominated ecosystem (Lewis, cited in Prescott and Weetman 1994).

Cedar has two distinct foliage morphologies at a young age. Primary needle leaves, with a low surface area, are formed almost immediately after cotyledon emergence, and these tend to grow only on the leader. Secondary foliage is produced after primary foliage and has the scale-like form characteristic of cedar. Previous sampling revealed that cedar seeds and germinants are fairly common in mature HA stands, but very few cedar seedlings survive to a secondary foliage stage (B. Gilbert, unpublished data). In contrast, hemlock seedlings and saplings are common (Keenan 1993), suggesting that these stands are beginning to undergo understory reinitiation of the existing species rather than cedar (sensu Oliver and Larson 1996). These observations are inconsistent with the literature on cedar, which consistently ranks cedar as one of the most shade-tolerant tree species in coastal British Columbia (Carter and Klinka 1992; Kobe and Coates 1997; Khan et al. 2000). Our study was designed to explore why cedar is not establishing in this habitat.

We tested several hypotheses concerning the factors limiting cedar establishment in HA stands: (*i*) cedar is light limited in the HA, (*ii*) factors specific to the HA humus or soil substrate are limiting cedar establishment, and (*iii*) competition from the moss layer is limiting cedar establishment.

Materials and methods

Study area

The nine sites used in this study were randomly selected from HA stands bordering recent clearcuts. HA sites are classified as poor to medium in nutrient regime and fresh to moist in moisture regime (T. Lewis, unpublished data, using the system of Pojar et al. 1987). Slope was minimal on all sites (<10%), and aspect was not controlled. All sites were within the Port McNeill forest area of Tree Farm License 6 on northern Vancouver Island and within the Coastal Western Hemlock very moist subzone and variant 1 (Krajina 1965, modified by Pojar et al. 1987). Meteorological data from the Port Hardy airport (approximately 15 km from the study area) had a mean annual precipitation of 1700 mm, with most of this occurring in the winter months (from Keenan et al. 1993). Mean daily temperatures range from 2.4°C in January to 13.8°C in August. Mean hours of sunshine vary from 1.5 h/day in December to 6.4 h/day in July due to summer fog and frontal clouds in the winter. Soils are typically Humo-Ferric Podzols with 0.1- to 1-m-deep mor humus overlying surficial unconsolidated morainal and fluvial outwash material (Lewis 1982). The interior of the HA stands had mounds 30–100 cm high and 2–6 m apart. The mounds likely resulted from windthrow events and result in variable depths of forest floor over mineral soil. Much of the forest floor is woody material in various stages of decay (Keenan et al. 1993).

The forest interior contained a sparse (0–3% cover) understory of salal (*Gaultheria shallon* (Pursh), deer fern (*Blechnum spicant* ((L.) Roth)), blueberry (*Vaccinium ovalifolium* (Sm.)), and salmonberry (*Rubus spectabilis* (Pursh)) (nomenclature from Qian and Klinka 1998). The forest edge had a more vigorous herb and shrub layer (0–15% cover), with the same species plus occasional fireweed (*Epilobium angustifolium* (L.)). Both the interior and edge had a consistent cover (70–100%) of mosses, mainly *Hylocomium splendens* (Hedw.) and *Rhytidiadelphus loreus* (Hedw.) with lesser amounts of *Plagiothecium undulatum* (Hedw.). Clearcuts had almost no moss cover but 50–80% cover of herbs, shrubs, and young (7- to 12-year-old) trees. The main plant species in the clearcuts were fireweed, salal, and salmonberry.

Experimental design

Two experiments were conducted between May 1997 and June 2000. The first examined the effects of substrate, nutrients, and root competition on cedar development in the HA forest interior, at the forest edge, and in a clearcut. The second examined the effects of substrate and immediate aboveground vegetation on cedar development in the HA stand interior and edge and also contrasted cedar, hemlock, and amabilis fir development on undisturbed forest floor.

Experiment 1

The primary hypothesis for the first experiment was that light and a factor related to the substrate (either mineral soil, forest floor, or root interactions) were working singly or in conjunction to limit cedar survival and development of secondary foliage. Cedar survival and development of secondary foliage were monitored under the following conditions: (*i*) undisturbed forest floor, (*ii*) exposed local mineral soil (area with the forest floor scraped off), (*iii*) isolated local mineral soil (mineral soil from within the forest and isolated from the surrounding soil by a plastic barrier), (*iv*) isolated clearcut soil (mineral soil from the clearcut, isolated from the surrounding soil by a plastic barrier), and (*v*) isolated reference soil (a sandy soil taken from a riverside location, fertilized with ammonium nitrate pellets and isolated from the surrounding soil by a plastic barrier).

Each treatment was applied at each of three locations: stand interior (50 m in from the clearcut edge), stand edge (under the drip-line of the outermost trees), and clearcut (50 m from the stand edge). The experiment was laid out in a blocked, incomplete split-plot design with a total of four sites that acted as blocks, the locations acting as main treatments, and substrate treatments acting as split treatments. All future mention of "location" refers to the location within the HA stand (interior, edge, or clearcut) and "treatment" refers to manipulation of substrate, fertilizer, etc., within a location. "Experimental unit" refers to an individual treatment within a location.

To test mineral soil as it occurs in the HA, randomization of the exposed mineral soil treatment was limited to areas where it was naturally close to the surface of the forest floor (i.e., on the top or side of mounds). Our decision to use existing microsites in the forest violates standard randomization practices for experimental design, but we feel that it is justified in that it represents a random sample of the mineral soil microsites that exist.

All substrates that were isolated from the surrounding soil (isolated local mineral soil, clearcut soil, and reference soil) were placed into holes approximately 30 cm in diameter, with a plastic barrier around the circumference extending to about 30 cm depth. Slow-release ammonium nitrate pellets were applied to the surface of the reference soil treatment, and nitrogen addition was believed to occur over much of the 2-year period of sampling, as small remnants of the pellets were observed during the final measurements. Although the level of fertilization was not quantified, the inference that we drew from the treatment is simply for a nitrogen-rich "reference soil".

All locations had at least one replicate of all treatments, and some experimental units were replicated several times within locations to compensate for the high mortality that was expected. Experimental units were positioned on relatively flat, homogenous microsites that were large enough (approximately 2 × 3 m) to house all substrate treatments. No discrimination was made between microtopographic features, except that wood was avoided as were nonmesic patches (creek beds, etc.). Each experimental unit was seeded with 30 cedar seeds between April 30 and May 3, 1997. Seeds were obtained from the British Columbia Ministry of Forests Tree Seed Centre in Surrey, B.C. Seedling survival and development of secondary foliage were recorded every 1–4 months until September 1998.

Experiment 2

The second experiment was designed to test the effects of light, moss competition, and substrate on cedar survival and development and to test the relative abilities of cedar, hemlock, and amabilis fir to survive and develop on the forest floor. The substrate and species treatments were as follows: (*i*) cedar on undisturbed forest floor, (*ii*) cedar with moss removed (forest floor with mosses, small herbs, and seedlings cut away), (*iii*) cedar on exposed mineral soil (plots with the forest floor scraped off), (*iv*) hemlock on undisturbed forest floor, and (*v*) amabilis fir on undisturbed forest floor.

This experiment was a blocked split-plot design with within-site replicates. There were 10 replicates of each treatment at each of two locations: the forest interior (50 m from the stand edge) and the forest edge, with replicates established within each location in conditions similar to those of experiment 1. Experimental units were seeded between September 3 and 6, 1997, with 30 cedar, hemlock, or amabilis fir seeds. Hemlock and amabilis fir seeds were stratified prior to sowing. Survival, development of mature leaves (cedar only), vigour (cedar only), height, and length of longest leaf or branch of each seedling were recorded every 1–4 months until May 29, 2000.

Measurements

There is no single measure that accurately represents shade tolerance of a species. Growth on its own is not necessarily a good predictor of shade tolerance, as various studies have shown that shade-tolerant species may grow more in the shade (Kobe et al. 1995; Walters and Reich 1996), less in the shade (Walters et al. 1993; Reich et al. 1998), or approximately the same in the shade as shade-intolerant species (Lee et al. 1996; Coates 2000). However, growth is considered a good indicator of survival within a species (Carter and Klinka 1992; Kobe et al. 1995; Walters and Reich 2000). We have used growth in combination with survival to assess shade tolerance for all species (Kobe 1999) and have included a measure of vigour to provide a more complete picture of cedar's performance within each treatment.

Percent germination and survival from seed could not be determined, as some seeds germinated outside of their original experimental units in both experiments. As a result, survival data are based on ratios of the final number of seedlings observed to the initial number that germinated within an experimental unit. Likewise, development of secondary foliage was measured as the ratio of the final number of cedar seedlings with secondary foliage to the initial number that germinated.

The vigour of cedar germinants was measured in experiment 2. Many cedar seedlings showed a characteristic colour change before dying, turning from a dark green to a rusty red colour. On this basis, we ranked all live seedlings using the following scale: vigour score = Σ(colour score × % of leaf area that was each colour), with red having a colour score of 0, pale green a colour score of 0.5, and green a colour score of 1. Thus, all living cedar plants in the treatment units were assigned a score between 0 and 100. All colour scores were assigned by one person.

Height and lateral growth (millimetres) were measured in experiment 2. Height was defined as the length of the stem from the root collar to the tip of the leader. Lateral growth was defined as the length of the longest branch (or leaf) on each plant.

Light was measured in both experiments on overcast days between May 11 and June 6, 2000, using the instantaneous, one-point technique described by Parent and Messier (1996). Point estimates provide accurate estimates for total seasonal photosynthetic photon flux density (PPFD) in forest interiors (Parent and Messier 1996; Messier and Parent 1997; Comeau et al. 1998). Two calibrated Decagon sunfleck ceptometers were used to simultaneously measure the PPFD at the height of the seedlings within experimental units and in the open, with two measurements taken at 90° to each other over each experimental unit. Percent PPFD at each experimental unit was then recorded as (average PPFD at the experimental unit/PPFD in the open) × 100.

Statistical analyses

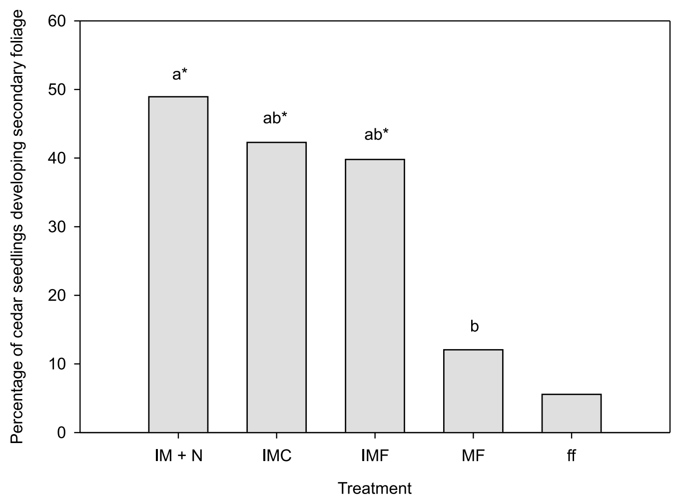
Both experiments were analysed using a blocked, split-plot ANOVA using SAS version 6.1 (SAS Institute Inc. 1996), with locations and treatments considered fixed. The block by location interaction term was used to test the effect of the location and block (Hicks 1993). Within-site replicates were averaged. The residual variance was used to test the effect of treatments and the treatment by location interaction. Survival data were transformed as needed using an arcsine transformation to meet assumptions of normality and homogeneity of variance (Neter et al. 1996). All means are presented in their original units.

Post hoc comparisons were performed using Tukey's multiple comparison procedure ($\alpha = 0.05$) when the number of observations was equal in all treatments. Otherwise, post hoc comparisons were made using the least square mean, in which case Bonferroni's adjustment was used so that the adjusted α = 0.05/number of comparisons (Neter et al. 1996).

Height growth in experiment 2 was analysed with one outlier removed to meet model assumptions. Removal of the outlier lowered the mean value for hemlock seedlings on the edge, but this difference did not change the statistical significance of the results. Means for height data were compared within treatments between the edge and interior to test the location by treatment interaction.

Vigour, height, and lateral growth were compared between cedar seedlings that had developed secondary foliage and all other cedar seedlings on the forest edge, as only edge seedlings developed secondary foliage. Mean values were calculated for each on a per site basis, and a paired *t* test was used to test the hypothesis that those with secondary foliage had greater growth and vigour than the others. Each site comparison acted as a paired observation.

Fig. 1. Mean percentage of western redcedar seedlings developing secondary foliage at the edge and clearcut. Soil type: M, mineral soil; ff, forest floor; N, nitrogen added; place of soil origin: C, clearcut; F; forest. Treatments with the same letter are not significantly different ($\alpha = 0.05$). The forest floor treatment could not be compared with other treatments due to the unbalanced experimental design. An asterisk indicates that values are significantly different from zero ($\alpha = 0.05$).



Results

Variables measured in both experiments were compared to test for differences caused by year to year variation in growing conditions. Mean survival and development of secondary leaves showed no significant difference in similar treatments between experiments 1 and 2 (analysis not shown), indicating no significant annual variation in cedar survival during the 3 years of our study.

Experiment 1

PPFD was measured at the top of the seedlings and therefore represents light available to the uppermost leaves of seedlings. PPFD varied from 3.7 to 32% full sunlight in the interior and edge locations, respectively, and increased to 77.6% in the clearcut.

Substrate treatments had no significant effect on survival in experiment 1 ($p > 0.05$), but location did ($p = 0.003$). Cedar survival was significantly lower in the interior (9.3%) than in the edge (54.3%) and the clearcut (59.5%).

No seedlings developed secondary foliage in the interior, and the difference between the edge and clearcut in developing secondary leaves was not significant ($p > 0.05$). However, there was a significant ($p = 0.03$) difference among substrate treatments (Fig. 1). In the reference soil, a significantly greater percentage of plants developed secondary leaves than in the exposed mineral soil (48.9 and 12.1%, respectively). Secondary foliage development in the isolated clearcut soil and the isolated mineral soil from the forest interior was not significantly different from that in any of the other treatments. Comparisons with the forest floor treatment could not be made due to the unbalanced design of the experiment.

Overall, development of mature foliage in cedar declined in the order clearcut and edge > interior, and reference isolated soil > isolated mineral soil > exposed mineral soil > forest floor. Thus, cedar seedling development was greatest on the isolated mineral soils in the edge and clear-cut locations.

Experiment 2

The transition from the forest interior to edge in experiment 2 was accompanied by an increase in PPFD from 3.5 to 37.2%. Only seedlings at the edge locations developed secondary foliage, but this difference in secondary foliage development was not statistically significant. Seedlings with secondary foliage had significantly greater vigour scores and greater height and lateral growth than those without (Table 1). Development of secondary foliage is likely a good indicator of future survival of cedar seedlings, as it is correlated with increased vigour, height growth, and lateral growth.

There was a significant effect of both location ($p = 0.01$) and treatment ($p = 0.0001$) on survival of seedlings. Survival at the edge was 23.5% greater than in the interior (Fig. 2). Cedar survival on the forest floor was significantly lower than that of hemlock and amabilis fir in both locations. Survival rankings for all seedlings were edge > interior, and amabilis fir (forest floor) > hemlock (forest floor) > cedar (mineral soil and moss removed) > cedar (forest floor).

Vigour of cedar seedlings was significantly ($p = 0.0003$) greater in the forest interior than at the edge, with mean scores of 59 and 18, respectively. The greater vigour in the interior appears to contradict the survival results presented above.

There was a significant ($p = 0.009$) location by treatment interaction in height measurements (Fig. 3). There were no significant differences in cedar height growth between interior and edge locations; mean height growth was 23 mm in all treatments. Amabilis fir had greater average growth (38 mm) than cedar, but there was no significant growth difference between interior and edge locations. Hemlock height growth was significantly greater at the edge (35 mm) than in

Table 1. Differences in vigour, lateral growth, and height growth between western redcedar seedlings with and without secondary foliage.

Variable	Mean of seedlings with secondary foliage	Mean of seedlings without secondary foliage
Vigour	63.7*	21.7
Lateral growth (mm)	15*	5
Height (mm)	38*	23

*Mean difference greater than zero at $\alpha = 0.05$.

Fig. 2. Percentage of seedlings surviving in the forest interior and edge locations. Substrate: ff, undisturbed forest floor; veg, minor vegetation removed; min, exposed mineral soil. Mean values for treatments with the same letter are not significantly different ($\alpha = 0.05$). Interior and edge treatments are significantly different for all treatments ($p = 0.01$).

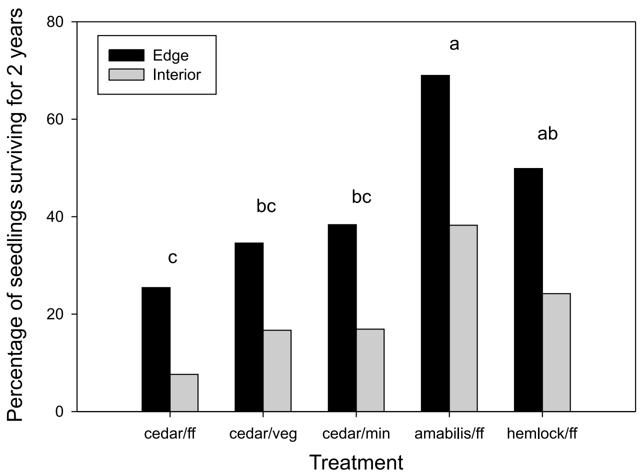
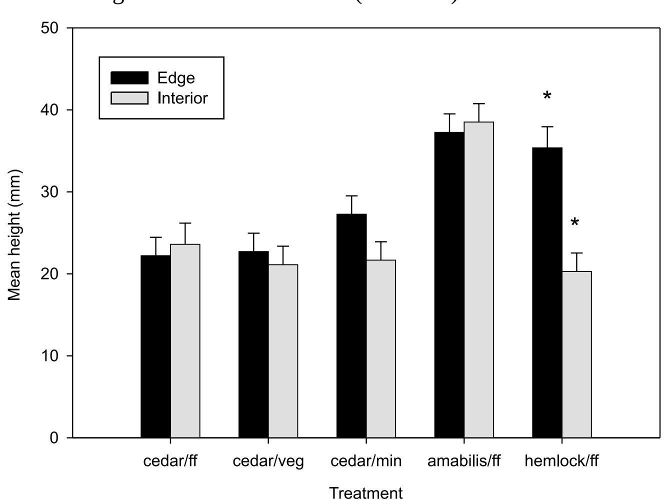


Fig. 3. Mean heights (and SEM) of species in each treatment at the edge and interior locations. Substrate: ff, undisturbed forest floor; veg, minor vegetation removed; min, exposed mineral soil. An asterisk indicates a significant difference between edge and interior heights within a treatment ($\alpha = 0.05$).



the interior (20 mm). The greater change in hemlock growth in the edge conditions indicates that it is more responsive to light than cedar and amabilis fir.

Lateral growth differed significantly between species ($p = 0.0001$), but there was no difference within any of the species. Only within-species differences in growth provide a good indication of likelihood of survival; therefore, treatment means are not illustrated.

Discussion

Stand position effects

Results from both experiments show a strong effect of light on cedar establishment across all treatments. Lower survival in the forest interior could be due to greater amounts of inhibitory leaf exudates (Whittaker 1970), higher levels of pathogen infection (Augspurger 1984), or low carbon fixation resulting from low light levels (Kobe 1997). The increase in survival with decreased forest overstory is consistent with other field studies on cedar (Wang et al. 1994; Feller and Klinka 1998). However, cedar is considered to be more shade tolerant than hemlock (Carter and Klinka 1992; Kobe and Coates 1997; Khan et al. 2000), and its lower survival than hemlock in the understory is surprising. Light is clearly cedar's most limiting factor in the HA, as shown by the large increase in survival and secondary foliage development in the edge and clear-cut locations, but the vigour and growth results suggest that light does not fully explain cedar's lack of establishment in the HA. The lack of difference in development of secondary foliage between the forest edge and clear-cut locations indicates that cedar's ability to develop secondary leaves in 2 years is not light limited beyond 32% PPFD.

Cedar's lower vigour on the edge appears to contradict survival results. However, the scale for the vigour scoring was based on colour, with lower scores recorded for plants that were predominantly red and pale green. Weger et al. (1993) showed that cedar turns a red colour when under cold stress because of an increase in rhodoxanthin levels. This increase in rhodoxanthin is correlated with a decrease in chlorophyll content and is believed to aid in photoinhibition, thus protecting the plant's photosynthetic apparatus (Weger et al. 1993). Ida (1981) found that several members of the Taxodiaceae showed similar responses to cold and water stress but that colour changes did not occur in shaded leaves. It is likely that cedar would accumulate rhodoxanthin as a response to any stress that would impact the photosynthetic apparatus (R. Guy, The University of British Columbia, personal communication). Cedar seedlings in the HA slowly turned a rusty red colour, with only the new growth emerging green. It appears that greater discolouration in the edge indicates higher exposure to light, not a lower probability of survival. However, the low vigour scores in both locations indicate that cedar in the HA are continually stressed at the edge and in the interior.

Unlike cedar and amabilis fir, hemlock height growth significantly increased from the interior to the edge. Increased growth within a species is considered a good estimator of future survival (Carter and Klinka 1992; Kobe et al. 1995; Walters and Reich 2000). The lack of response in amabilis fir growth is consistent with Klinka et al. (1992) finding that amabilis fir had a fairly flat growth curve at the light levels included in our study. Coates and Burton (1999) reported that cedar showed a larger growth response than hemlock to increasing light at low light levels (<20%). A large height growth response to increasing light at low light levels was also reported for cedar by Carter and Klinka (1992), Wang et al. (1994), and Khan et al. (2000). The differences between our study and previous studies indicate that light is not the only limiting factor in cedar height growth in HA forests. The greater survival of hemlock on the forest floor of both the interior and the edge and its greater response in height growth to stand edge conditions appear to make it a superior competitor relative to cedar in both conditions. This superior competitive ability of hemlock relative to cedar across the range of locations that we examined is contrary to what much of the ecological literature on coexisting species suggests; plants that take advantage of high-resource situations by growing quickly tend to die in low-resource situations (e.g., Tilman 1988).

Soil substrate effects

Soil substrate had a significant effect on cedar survival, with cedar responding positively to increased disturbance. The increase in cedar survival in both exposed mineral soil and moss-removed treatments may be due to a decrease in aboveground vegetation, allowing for higher access to light, or to the resulting change in belowground resource availability (for water and (or) nutrients). Although several studies have shown the inhibitory effects of phenolics from the forest floor on plants (Whittaker 1970; Perry and Choquette 1987), the similar response of cedar to mineral soil and moss removal treatments suggests that the effects of phenolics and other attributes of the HA forest floor, such as pH, do not play an important role in cedar survival. The survival of hemlock and amabilis fir on mineral soil and on the forest floor with moss removed was not tested, but Wright et al. (1998*b*) have shown that hemlock has a higher survival rate on forest floor with the moss layer removed.

Cedar development of secondary foliage was likewise greatest in the most disturbed treatments: soils isolated from the surrounding soil. The reference soil, which showed higher levels of secondary foliage development than the exposed mineral soil, was mixed and isolated from surrounding roots. Soils disturbed to this degree often show higher levels of nutrient availability in experimental conditions (Johnson et al. 1995) and in nature (Vitousek and Melilo 1979; Vitousek et al. 1979; Silver and Vogt 1993; Feller and Kimmins 1984). Adams and Mahoney (1991) demonstrated a greater growth response of cedar to aboveground competition removal than to simply tying back competing herbs, presumably because of resulting changes in belowground dynamics. Studies on other plant species have shown root isolation and fertilization to increase height growth and leaf width (Cook and Ratcliff 1984; Callaway et al. 1991), and fertilization trials conducted with cedar have likewise resulted in increased height growth (Prescott and Brown 1998). The lack of difference between the isolated soil treatments (reference, forest mineral soil, and clearcut mineral soil) in our study indicates that soil disturbance and (or) root isolation are more important to cedar establishment than soil type. Additional factors related to the soil disturbance, such as nutrient availability and formation of mycorrhizal associations, may be important to cedar shade tolerance and warrant further study (Kough et al. 1985; Gehring and Whitham 1992; Latham 1992).

Although disturbed substrate is important to the establishment of cedar, it is secondary to high light levels. Secondary cedar foliage only developed at the forest edge and in the clearcut; a combination of high light and soil isolation is needed to produce high levels of cedar establishment in HA stands.

Size effects

Initial survival rates of seedlings may be related to seed size, although Hewitt (1998) showed that long-term shade tolerance and seed size are not related for North American conifers. A study by Walters and Reich (2000) showed that all species studied with a seed mass less than 3.2 mg showed mortality due to low light (0.5–7%) within 40 days of germination. At larger seed sizes (17–44.6 mg), trends were less clear, with variable mortality occurring within 80 days of germination. Cedar, hemlock, and amabilis fir have seed masses of 1.4, 2.4, and 40 mg, respectively. The findings of Walters and Reich (2000) suggest that seed size difference does not adequately explain the difference in cedar and hemlock survival over the time frame of our measurements, although it may be one factor contributing to high amabilis fir survival.

The comparison of seedlings with secondary foliage with those without demonstrates that the former had greater lateral growth, as was expected, but also greater vigour and height growth. This does not indicate whether the development of secondary foliage produces this advantage or if those seedlings that are performing better are simply more likely to develop secondary foliage. Development of secondary foliage does not guarantee future survival, but these findings suggest that it is a good indicator of the relative likelihood of cedar survival. Previous studies that have shown cedar to be more shade tolerant than hemlock have used cedar seedlings or saplings with secondary foliage (Carter and Klinka 1992; Kobe and Coates 1997; Khan et al. 2000), suggesting that survival rankings may change if cedar attains a certain size. A strong decline in mortality has been documented to occur with an increase in tree size (Clark and Clark 1992; Kobe 1999), supporting the hypothesis that shade tolerance of cedar increases as it ages. However, Givnish (1988) has modeled a negative relationship between tree size and shade tolerance based on energy allocation patterns and photosynthetic rate, which implies that the relationship between seedling size and shade tolerance is not well understood. The possibility that cedar's shade tolerance ranking relative to other species changes with seedling size merits further study.

Conclusion

It is impossible to make accurate predictions for cedar establishment in the long-term given that the conditions tested do not accurately represent the range of conditions existing after different disturbances in the forest. Nonetheless, given the results of this study, it appears that cedar is at a disadvantage on the forest floor at any light level so long it has equal numbers of germinants as hemlock and amabilis fir. The response of cedar to high light and soil disturbance indicates that cedar acts as a shade-intolerant species in its early establishment phase. Cedar's ability to reproduce vegetatively by layering and by rooting of fallen branches may be an important mechanism of self-replacement in mature cedar stands.

The hypothesis that cedar needs disturbances to establish and survive appears to contradict much of the literature stating that it is a shade-tolerant species. It is possible that cedar's ability to survive in shade is more strongly related to its size than for other species studied, such as hemlock. In this case, initial growth would play a large role in long-term establishment of the species on a site. This theory is supported by other studies that have found fire disturbances to best explain the cedar establishment trends observed in coastal forests of southern British Columbia (Daniels et al. 1995; Feller and Klinka 1998). Alternately, the low vigour in the seedlings studied may indicate that conditions specific to HA ecosystems are responsible for the low survival and growth rates of cedar. In this case, removal of the influence of HA species (as done with the soil isolation treatments in the edge and clearcut) would offer the greatest opportunity for cedar establishment. Both hypotheses are supported by our results, which indicate that cedar is most likely to establish on disturbed mineral soil in areas with little or no canopy influence.

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