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Survival and growth as measures of shade tolerance of planted western redcedar, western hemlock and amabilis fir seedlings in hemlock-fir forests of northern Vancouver Island

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ABSTRACT

We examined two measures of shade tolerance (survival and growth) of planted 1-year-old seedlings of western redcedar (*Thuja plicata* (Donn ex D. Don)), western hemlock (*Tsuga heterophylla* ([Raf.] Sarg.)) and amabilis fir (*Abies amabilis* ([Dougl. ex Loud] Dougl. ex Forbes)). Seedlings were planted at two different sites (forest interior: 4.5% mean above canopy photosynthetically active radiation [ACPAR], and forest edge: 41.5% mean ACPAR), in a 90-year-old, windthrow origin, unmanaged mesic western hemlock-amabilis fir stand. Seedlings were planted in 1997, and re-measured in 1998 and 2001 (after five growing seasons). To assess the effects of deer browsing on redcedar survival and growth, additional seedlings of this species were planted and protected with Vexar© tubes. To examine for nutrient-light interactions, half of these seedlings were fertilized with N-P-K and micronutrients at planting. Western redcedar had high levels of survival after 4 years (98% in edge plots and 93% in interior plots). Redcedar seedlings in edge plots were more vigorous but were browsed more heavily than in the interior plots. At edge sites, the negative effects of the Vexar© tubes may have been lower than their positive effects. Hemlock survival was about 50% in the stand interior but 80% in the edge plots. Amabilis fir in the interior plots had the lowest survival of the three species, with only 40% of initial seedlings surviving over the next four years, but had high survival in edge plots (95%). Height, biomass, and root collar diameter growth were significantly higher in edge plots for fir and hemlock. However, for redcedar, only biomass was significantly higher and no differences were detected for height and diameter. Our results show that shade tolerance cannot be assessed by simple measures of leaf/light relationships alone, but also requires consideration of light, nutrition, growth and browsing.

1. Introduction

An ongoing trend for the last decade is driving forest management away from clearcutting and planting towards partial and variable retention harvesting with natural regeneration (Gustafsson et al., 2012), based on concerns about biological diversity (Lindenmayer and Franklin, 2002; Fedrowtiz et al., 2014), hydrological issues (Hartman, 2004), ecosystem function (Lindenmayer et al., 2012), and public antipathy towards the aesthetics of clearcut harvesting (Sheppard and Harshaw, 2000). Partial harvesting systems inevitably increase the role of natural regeneration, but planting will likely be necessary for desired species with unreliable seed production, heavy seed predation, lack of a seed source or inadequate seedbed/germinant establishment conditions. Therefore, silvicultural systems with natural regeneration, augmented where needed by planting, have been promoted or suggested over the last two decades (Arnott and Beese, 1997; Serrouya and D'Eon, 2004; Nilsson et al., 2006; Bott et al., 2014; Bragg et al., 2015; Antos et al., 2016).

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Success of both natural regeneration and planting in partial harvesting and variable retention systems requires knowledge of shade tolerance (Wright et al., 1998b) and the associated belowground competition for soil resources. Shade tolerance is a multidimensional concept (Dean, 2012; Lienard et al., 2015), and simple photosynthetic light saturation curves do not adequately define it (Wright et al., 1998b; Valladares and Niinemets, 2008; Lienard et al., 2015). Prediction of successional pathways requires an understanding of what it means for one plant species to establish and grow in the shade of another (Weber et al., 2014). Basing such predictions only or even mainly on light, as is the case in many process-based forest models (see reviews by Lo et al., 2011, 2015, and references therein) can lead to erroneous conclusions, if other factors are not accounted for (Kimmins et al., 2008; Blanco et al., 2015; Dybzinski et al., 2015). Carbon allocation shifts in response to soil resource availability (Franklin et al., 2012; Farrios et al., 2013) can have significant effects on interspecific competition and successional pathways (Weber et al., 2014). Seedling establishment is a key process that involves multiple biotic and abiotic factors (Blanco et al., 2009). Therefore, ecosystem-level models are vital for the development of adaptive, flexible decision support tools for sustainable forest management (Messier et al., 2003; Kimmins et al., 2010). Credible mechanistic process models of ecosystem response to natural and management-induced disturbance (Perrera et al., 2004) at the stand and landscape scale (Seely et al., 2004) cannot be developed without this knowledge, as the minimum complexity needed to represent the main processes that affect tree growth is not reached (Kimmins et al., 2008).

Complex interactions between factors affecting seedling survival have been studied in forests on northeastern Vancouver Island. Weber et al. (2003) compared the relative performance of the three species studied in this paper in similar site conditions and light environments grown from seed. Also, a study of the role of mycorrhizae in determining germinant shade tolerance was carried out (Weber et al., 2005), as well as an assessment of what the results of all these studies mean for successional pathways in these forests (Weber et al., 2014). Other previous studies in the area have reported the growth of western hemlock and redcedar in different light environments (Carter and Klinka, 1992; Wang et al., 1994; Drever and Lertzman, 2001; Karakatsoulis, 2004). Klinka et al. (1992) reported the response of amabilis fir.

Recently, Lienard et al. (2015) have offered a review of the shade tolerance concept in which the tree species studied here are all ranked as "very tolerant", but on the other hand, McKenzie and Tinker (2013) have shown that at least western redcedar can behave as a pioneer species. Therefore, traditional forest management of these forests needs to be revisited and updated in view of the recent findings on forest ecology (Antos et al., 2016). Particularly, traditional management experience in these forests indicates that there are marked differences among the three species, assuming that the shade tolerance sequence follows the pattern: amabilis fir ⩾ western redcedar > western hemlock. In addition, our team's previous research has shown that shade tolerance of seedlings and adult trees can be different, at least for western redcedar (Weber et al., 2003, 2005), and that such inter-specific differences in shade tolerance can have important successional consequences (Weber et al., 2014). Bringing light to such issues has been highlighted as one of the main points for future research at these sites (Antos et al., 2016).

Therefore, our general objective was to test if a multi-variable response of the seedlings of these three species supports traditional light-related measures of shade tolerance for western redcedar (*Thuja plicata* [Donn ex D. Don]), western hemlock (*Tsuga heterophylla* [[Raf.] Sarg.]) and amabilis fir (*Abies amabilis* [Dougl. ex Loud] Dougl. ex Forbes)) seedlings planted in two contrasting light environments (forest edge and forest interior) in western hemlock-amabilis fir (HA) stands on northeastern Vancouver Island, British Columbia. To reach this goal, our specific objectives were to test: (1) if shade tolerant conifer species have different survival rates in the shade; (2) if shade tolerant conifer species show different height growth responses across a gradient of light conditions; and (3) if shade tolerant conifer species maintain or reduce their height:diameter ratios as light levels decline. The information provided by these tests allowed us to establish a ranking of shade tolerance for three major forest species in western Canada.

2. Materials and methods

This study was part of a larger study of the successional pathways on northeastern Vancouver Island (Weber et al., 2003, 2005, 2014). Succession in these ecosystems has generally been interpreted in terms of wind-related disturbance, light competition and relative shade tolerance. However, the SCHIRP study (Salal-Cedar-Hemlock Integrated Research Project; Prescott and Weetman, 1994), of which this study is a component, was undertaken to expand the scope of successional investigations in these forests to the ecosystem level, including nutrition and various biotic interactions. To address the objectives, nursery-stock seedlings were planted in interior and edge plots of western hemlock (*Tsuga heterophylla*) – Pacific silver fir (*Abies amabilis*) stands (HA) stands and their survival and growth were measured over five years. Secondarily, since we were interested in factors limiting redcedar recruitment in HA stands as detected by Weber et al. (2003), we tested whether redcedar seedling survival and growth was affected by nutrient availability or browsing damage. Such a test was done by including an additional factorial experiment on treatments of fertilizer and browsing protection for redcedar seedlings.

2.1. Research sites

In 1997, four sites were selected at random from the population of HA stands bordering recent clearcuts within the Port McNeill (50°35′25″N, 127°05′5″W) forest area of Tree Farm License 6, a 170,000 ha region on northeastern Vancouver Island. Elevation ranged from 300 to 600 m.a.s.l. Slope was minimal (<10%) on all stands, and consequently aspect was not controlled. Meteorological data from the Port Hardy airport (approximately 15 km north of the study area) showed a mean annual precipitation of 1700 mm, with most of this occurring in the winter months (Keenan, 1993). Mean daily temperatures range from 2.4 °C in January to 13.8 °C in August.

Selected sites were all in the Submontane Very Wet Maritime Variant (CWHvm1) of the Coastal Western Hemlock biogeoclimatic zone (Krajina, 1965, modified by Pojar et al., 1987). Selected stands were representative of zonal sites and were dispersed throughout the study area. HA sites are classified as poor-to-medium in nutrient regime and fresh-to-moist in moisture regime (Pojar et al., 1987). The average mass of forest floor in HA stands is 211 Mg ha^{-1} (Keenan, 1993). Soils are typically humo-ferric podzols with 0.25 m of mor humus (combined LFH layers) overlying surficial unconsolidated morainal and fluvial outwash material (Sajedi et al., 2012).

In early 1997, four sites were selected. The major disturbance that initiated the studied stands was a windstorm in 1908 that affected about 30,000 ha (Prescott et al., 1993). As a consequence, the stands selected were even-aged and about 90 years old at the start of the experiment in 1997. At each of the four sites, four plots were established at the stand edge (just inside the canopy, within the canopy dripline) and four in the interior of the forest (defined as 50 m from the stand edge). Each plot contained 24 seedlings, for a total of 768 seedlings per species used in the experiment. All