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Seedling Regeneration in the Alpine Treeline Ecotone: Comparison of Wood Microsites and Adjacent Soil Substrates

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Although climate warming is generally expected to facilitate upward advance of forests, conifer seedling regeneration and survival may be hindered by low substrate moisture, high radiation, and both low and high snow accumulation. To better understand substrate-related factors promoting regeneration in the alpine treeline ecotone, this study compared 2 substrates supporting conifer seedlings: rotten downed wood and adjacent soil. Study locations, each with 3 levels of incoming radiation, were randomly selected at forest line–alpine meadow borders in Pacific Northwest wilderness areas extending along an east–west precipitation gradient. Associations among substrate type, seedling density, radiation, site moisture, site temperature, plant water potential, and plant stomatal conductance were assessed. Wood microsites, flush with the ground and supporting *Abies* spp conifer seedlings, extended up to 20 m into alpine meadows from the forest line. Although wood

microsites thawed later in the spring and froze earlier in the fall, they had warmer summer temperatures, greater volumetric water content, and more growing degree hours, and seedlings growing on wood had higher water potentials than seedlings growing on adjacent soil. At drier eastern sites, there was a positive relationship between seedling density and volumetric water content. Further, there was a positive relationship between seedling stomatal conductance and volumetric water content. Our study indicates that in the Pacific Northwest, and likely elsewhere, seedlings benefit from wood microsites, which provide greater water content. Given predictions of increased summer drought in some locations globally, wood microsites at forest line–alpine meadows and forest line–grasslands borders may become increasingly important for successful conifer regeneration.

Keywords: Forest line; alpine treeline ecotone; plant water potential; moisture; temperature; conifer seedling regeneration; Pacific Northwest.

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Introduction

The theme “Dynamic Planet” highlighted at the Perth III Conference is exemplified by studies of upper forest limitation (Future Earth 2014). For example, with climate warming, there is a general expectation that forests will advance, but factors including low substrate moisture, low substrate temperatures, high radiation, fire, and both low and high snow accumulation may limit seedling regeneration and survival, restricting upward advance (Baig and Tranquillini 1980; Callaway 1995; Bansal and Germino 2008; Harsch et al 2009; Tranquillini 2012; Müller et al 2016). Upward advance of the alpine treeline ecotone (ATE), the zone ranging from the upper limit of subalpine forest (forest line) to the treeline, is dependent on successful germination and survival of seedlings. Transitions from forest line to treeline can be abrupt or diffuse and include alpine meadows, krummholz, and tree

islands—features associated with regeneration and upward advance potential (Harsch and Bader 2011).

Little is known about factors affecting the survival of seedlings during initial years of growth and establishment, the period of greatest mortality of all life stages within the ATE (Germino et al 2002; Maher and Germino 2006; Johnson et al 2011). Globally, soil temperature is associated with treeline dynamics (Körner and Paulsen 2004), but lack of moisture, considered the primary cause of seedling mortality (Germino et al 2002; Moles and Westoby 2004), may also restrict seedling regeneration and limit forest upward advance (Gieger and Leuschner 2004; Maher et al 2005; Harsch and Bader 2011; Moyes et al 2015; Müller et al 2016). Although microsites, ranging from millimeters to meters in size, are known to have a key role in promoting seedling regeneration (Rochefort et al 1994; Holtmeier and Broll 2012), examinations of functional relationships between seedling survival and

TABLE 1 Characteristics of the 6 study sites.

| Site | Elevation | Latitude | Longitude | Aspect | Slope | Mean annual values | | Mean summer values | |
|------|-----------|----------|-----------|--------|-------|--------------------|-------------|--------------------|-------------|
| | | | | | | Precipitation | Temperature | Precipitation | Temperature |
| 1 | 1585 m | 48.144°N | 21.385°W | 0° | 21° | 2370 mm | 4.0°C | 200 mm | 12.6°C |
| 2 | 1676 m | 48.475°N | 21.062°W | 250° | 35° | 1980 mm | 5.8°C | 142 mm | 15.4°C |
| 3 | 1768 m | 48.733°N | 20.882°W | 140° | 5° | 1800 mm | 4.1°C | 137 mm | 14.3°C |
| 4 | 1875 m | 48.509°N | 20.761°W | 160° | 14° | 1580 mm | 3.6°C | 106 mm | 14.2°C |
| 5 | 1910 m | 48.724°N | 20.664°W | 300° | 21° | 1510 mm | 2.4°C | 110 mm | 13.2°C |
| 6 | 1996 m | 48.738°N | 20.668°W | 85° | 23° | 1530 mm | 2.4°C | 112 mm | 13.1°C |

Source: Temperature and rainfall information was obtained from DAYMET (15-year averages).

topographically controlled ATE site conditions are still rare (Holtmeier and Broll 2007; Harsch and Bader 2011; Müller et al 2016). Studies linking abiotic factors (ie temperature, radiation, moisture, and nutrient availability) to physiologic factors (eg stomatal conductance, water potential, and foliar nitrogen content) for young seedlings growing on microsites above the forest line provide a clearer understanding of current climatic factors affecting potential expansion of the ATE (Rochefort et al 1994; Smith et al 2009).

Rotten downed-wood microsites (hereafter referred to simply as wood microsites) facilitate seedling growth by lessening the destructive influence of snow movement, known as snow glide, reducing species competition, increasing mycorrhizal populations, and having fewer pathogens than the adjacent soil (Zhong and van der Kamp 1999; Baier et al 2007). Wood microsites are key substrates in subalpine forests (Veblen 1989; Gratzner et al 1999; Zielonka and Niklossen 2001; Brang et al 2003; Narukawa et al 2003; Motta et al 2006; Baier et al 2007). A reconnaissance study of wood microsites in the Pacific Northwest found that mature trees, typically *Abies lasiocarpa*, which commonly fell directly into alpine meadows from the forest line via blow-down and wind snap, decayed and created warmer and moister conditions that produced greater seedling density and seedling survival than the adjacent soil substrates (6.85 seedlings per meter squared on wood versus 3.64 seedlings per meter squared on soil, $P = 0.026$; Johnson and Yeakley 2013). To gain a more mechanistic understanding of specific site conditions facilitating seedling regeneration, we initiated a study evaluating both site conditions and water use by seedlings growing out of wood microsites and out of adjacent soil substrates.

This research aimed to quantify substrate temperature, substrate moisture, and seedling water use, as influenced by various radiation levels, at multiple Pacific Northwest subalpine forest–alpine meadow borders along a regional moisture gradient. Measurements were made both annually and during the growing season with 2 main goals: (1) compare temperature and moisture conditions between

wood microsites and adjacent soil substrates supporting conifer seedlings, and (2) compare plant water use by seedlings growing on wood microsites with that of seedlings on adjacent soil substrates.

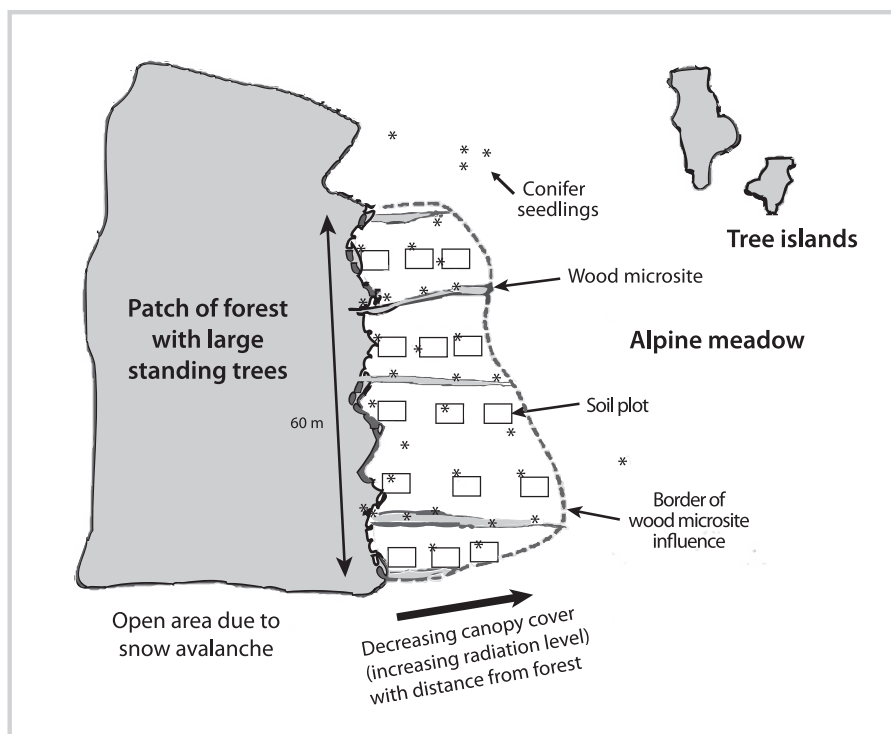
Study areas

Six forest line–alpine meadow sites were chosen based on an observed lack of snow avalanching, timber harvest, grazing by nonnative animals, or notable impacts of forest fire. The 6 sites extended from the western to the eastern side of the Cascade Mountains of Washington State. The sites were all chosen to be within 4 hours or less hiking distance from a road.

Of the 6 study sites, 3 were located within the *Tsuga mertensiana* zone on the western portion of the North Cascades (west of longitude 120.7°W) and 3 were located in the *Abies lasiocarpa* zone on the eastern side of the North Cascades (east of longitude 120.7°W); both zones included subzones of closed forest and upper parkland (Franklin and Dyrness 1979; Table 1). Treeline form, considered diffuse, was characterized by gradually declining tree height and density with proximity to the tree limit (Harsch and Bader 2011). All of the sites were managed as wilderness areas.

Each site had at least 4 pieces of large downed woody debris (>0.15 m in diameter), flush to the ground, extending up to 20 m from subalpine forest into alpine meadows. These wood pieces were very decayed (decay class 5; see Sollins et al 1987). Seedling height (ranging from 1 to 15 cm) and seedling density did not differ by distance into alpine meadow or by eastern or western location ($P > 0.1$, Johnson and Yeakley 2013). Although seedling species on nurse logs included *Tsuga mertensiana*, *Abies lasiocarpa*, *Abies amabilis*, *Chamaecyparis nootkatensis*, *Picea engelmannii*, and *Larix occidentalis*, at least 90% of the seedlings were *Abies lasiocarpa* and *Abies amabilis*. Mature subalpine fir trees may have been especially prone to wind snap due to weakening by internal wood decay and infestation with fir engraver beetles (Alexander et al 1984; Hennon 1995; McCarthy 2001). At our sites, the herbaceous families Poaceae,

FIGURE 1 Wood microsites extending into alpine meadows and stratified sampling used to evaluate seedling densities on the wood microsites and adjacent soil substrates. (Adapted from Johnson and Yeakley 2013)



Ericaceae, and species including *Vaccinium sp* and *Veratrum viride* were commonly found on soil substrates, whereas on wood microsites, plant occurrence consisted solely of conifer seedlings and/or moss.

The Cascades sites span a yearly precipitation gradient from 250 cm in the west to 150 cm in the east, with summer rainfall (June, July, and August) totaling 20 cm on the western sites and 10 cm on the eastern sites. Timberline elevations range from 1585 m on the western sites to 1996 m on the eastern sites. Mean annual summer temperatures are 14.1°C on the western sites and 13.5°C on the eastern sites (DAYMET 2016; Table 1). Snow typically covers alpine meadows from mid or late October to late June or early July, with depths exceeding 3.8 m on eastern sites and 3.3 m on western sites (USDA NRCS National Water and Climate Center 1971–2000).

In general, the geology is volcanic on the western sites and sedimentary on the eastern sites, with intrusive volcanics in the mid-range. Soils are well-drained Cryorthods, and have textures ranging from fine sandy loam to sandy gravelly loam. Organic horizon depths ranged from 0.5 to 1.0 cm at the study sites. Total depth of the soil to bedrock ranged from 0.2 m to 1.0 m with A-horizons ranging in depth from 0 to 0.2 m (USDA NRCS 2008).

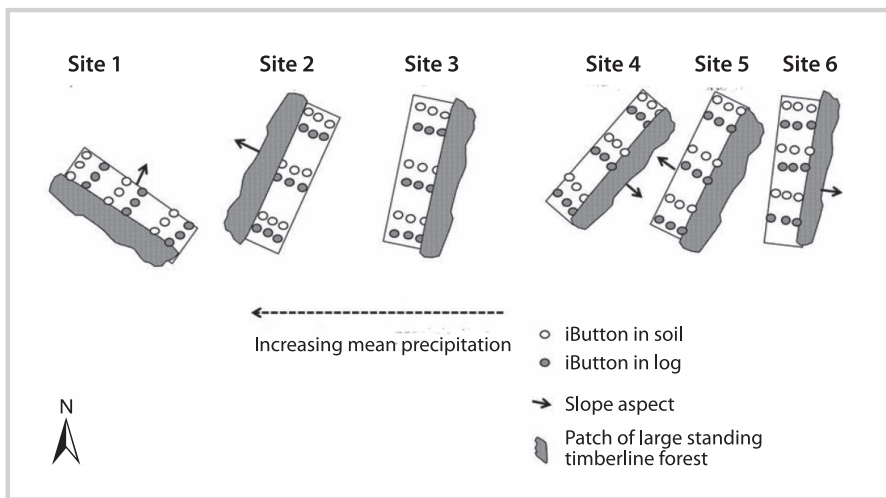
Methods

At each location, wood microsites and adjacent soil substrates at forest line–alpine meadow borders were

assessed under conditions of low, medium, and high percent transmitted radiation, areas initially described by 3 levels of overstory directly under forest-line trees, approximately 3–10 m beyond the forest line into alpine meadow, and open areas generally located 5–20 m beyond the forest line into alpine meadow (Figure 1). Measures of overstory were estimated with photographs taken skyward from the forest floor with a 180° hemispherical (fish-eye) lens mounted on a Nikon digital camera to produce circular images of forest overstory. Camera images were initially analyzed for percentage of open sky at each of the 6 sites using Gap Light Analyzer software (Frazer et al 1999).

To calculate the percentage of incoming radiation from overstory levels using Gap Light Analyzer, additional parameters were needed, including latitude, longitude, elevation, aspect, slope, growing season start and stop date, clear sky transmission (percentage of clear sky over extraterrestrial radiation), solar constant (amount of incoming solar electromagnetic radiation per unit area indicant on a plane perpendicular to the rays), and cloudiness index (percentage of the mean daily extraterrestrial radiation arriving at the ground as global solar radiation; Frazer et al 1999). Calculation of incoming percent radiation took into account tracking of the sun on the horizon through openings in overstory and area of open sky through canopy. Mean incoming radiation in the low, medium, and high categories was found to be significantly different (14.8%, 26%, and 54.8%,

FIGURE 2 Site aspect and iButton locations on wood microsites and soil substrates. The iButtons were used to measure soil temperature. VWC, plant stomatal conductance, and plant water potential measurements were made in the vicinity of iButton locations.



respectively; $P < 0.001$). We assumed clear sky transmission of 0.65 (Frazer et al 1999, used for Vancouver, Washington, in the summer), a solar constant of 1365 W/m^2 , and a cloudiness index of 0.5 for the western sites and 0.7 for the eastern sites. Considering that a snow-free period generally occurs between mid-June and mid-July (USDA NRCS National Water and Climate Center 2000–2011), we used a growing season of July 1 to September 30 for calculations.

Soil and wood temperatures were monitored with iButton data loggers (iButton-Link, LLC, East Troy, WI) for nearly 2 years for all 3 radiation categories at the 6 sites. Each of the 3 radiation categories had 3 replicates for each of the 2 substrate types (18 measurements per site, 108 iButtons total; Figure 2). The iButtons were installed directly in the wood microsites and adjacent soil substrates in the midst of seedlings at depths of 6 cm. A sample rate measurement interval of 4.25 hours was used; that produced 2048 possible sample points in 1 year.

Timing of fall freeze, spring thaw, and summer growing season temperature was evaluated for both soil substrates and wood microsites. Sites 1, 2, and 3 were considered western sites with wetter conditions, and sites 4, 5, and 6 were considered eastern sites with drier conditions. Fall freeze date was assumed to be the first >24 -hour period when substrate temperatures were $\leq 0^\circ\text{C}$, and spring thaw was assumed to be the first >24 -hour period with temperatures $>0^\circ\text{C}$.

Associations among conifer seedling regeneration, radiation, volumetric water content (VWC), plant stomatal conductance, plant water potential, and growing degree hours (GDHs, a measure of heat accumulation necessary for growth; Prentice et al 1992) were assessed on both wood microsites and adjacent soil substrates. Density of seedlings (<3 years old and <2 cm), assessed in an earlier study (Johnson and Yeakley 2013), was related to

associated wood microsites and soil substrates with low, medium, and high transmitted radiation.

Substrate VWC, stomatal conductance, and plant water potential were measured within each of the 3 radiation categories 3 times during the growing season: mid-July, mid-August, and mid-September. The VWC was measured with a Field Scout TDR Soil Moisture Meter (Spectrum Technologies, Plainfield, IL). The moisture meter was calibrated for wood microsites by adding known volumes of water; for soil substrates, it was calibrated for sand-silt loams. Stomatal conductance was quantified with a porometer (Decagon Devices, Pullman, WA). Newly growing clusters of needles extending from the apical meristem of 3- to 6-year-old seedlings (<4 cm) were placed in the stomatal conductance chamber. Once equilibrium of water content was reached, measurements were made. An effort was made to choose similar-aged seedlings with approximately the same number of needles (generally 3 or 4) for measurement. Plant water potential was measured for only 1 randomly selected seedling in each radiation category to minimize destructive sampling of the seedlings. Pre-dawn measurements were made with a Pump-up Pressure Chamber (Plant Moisture Stress Instruments, Albany, OR) by placing a seedling specimen in the pressure chamber with the cut stem sealed and protruding from the chamber to atmospheric pressure, sealing, pressurizing the vessel, and noting the pressure at which the sap first exuded from the xylem of the plant.

GDH, a measure of heat accumulation necessary for growth (Prentice et al 1992), was used:

$$\text{GDH} = \sum(\text{TA} - \text{TO})dt \quad (1)$$

GDH was adapted to our field application by using a base substrate temperature (TO) of 7°C , by temperature measurement intervals (dt) of 4.25 hours and by specific wood microsite and soil temperatures (TA), as opposed to measures of air temperature. For the period during which

TA > TO, temperature increments were accumulated for each day. For each substrate/radiation category, temperature and GDH were pooled and averaged. For the entire study period, when at least 1 substrate was >7°C, comparisons were made of mean daily GDH.

Statistical tests included separate one-way analysis of variance for multiple comparisons among radiation categories, temperature, VWC, plant stomatal conductance, plant water potential, and seedling density for wood microsites and soil substrates. Post hoc multiple comparison tests (Tukey's) were conducted when significant differences were detected. If comparisons were made between pooled data for wood microsites and soil substrates or mean freeze date and thaw date, a t-test was used. Linear regressions were used to assess significant differences of response variables, including substrate temperature, VWC, seedling density, and stomatal conductance. Statistical significance was assessed with $\alpha = 0.05$. All statistical analyses were performed using R 2.7 (R Core Development Team 2008).

Results

Although no differences were found in thaw and freeze dates between wood and soil at different radiation levels ($P > 0.2$), wood microsites and soil substrates combined had a significantly shorter period of nonfrozen ground on eastern sites than on western sites. Mean thaw date was June 27 for western sites and July 4 for eastern sites ($P = 0.017$); mean freeze date was November 10 for western sites and October 23 for eastern sites ($P = 0.009$). Later thaw dates and earlier freeze dates resulted in 25 fewer days of nonfrozen ground (wood and soil) at eastern locations.

Temperature, GDH, and VWC values are summarized in Figure 3.

For mean annual temperature, western wood microsites with low and medium radiation were cooler than their corresponding soil substrates; in high-radiation sites, substrate types were not significantly different (1.76°C versus 1.93°C, $P < 0.001$; 1.6°C versus 1.78°C, $P = 0.002$; and $P = 0.99$, respectively). At the eastern sites, wood was cooler than soil at low-radiation sites and warmer at high-radiation sites; at medium-radiation sites, substrate types were not significantly different (respectively, 0.87°C versus 1.24°C, $P < 0.001$; 1.78°C versus 1.48°C, $P < 0.001$; $P = 1.0$).

For mean summer temperature, western wood microsites with high radiation were warmer than their corresponding soil substrates; at low and medium radiation, there was no significant difference (respectively, 7.9°C versus 7.4°C, $P = 0.04$; $P = 0.99$; $P = 1.0$). Compared with their respective soil substrates, eastern wood microsites with low radiation were cooler and wood microsites with high radiation were warmer, but at medium radiation, there was no difference (respectively, 5.1°C versus 5.85°C, $P = 0.001$; 7.13°C versus 6.25°C, $P < 0.001$; $P = 0.058$).

GDH at western sites was similar for wood and soil at all radiation levels ($P = 0.9$ for low, $P = 0.99$ for medium, and $P = 0.8$ for high radiation). For eastern sites with medium radiation, wood microsites had more GDH than soil substrates (49.0 versus 35.0, $P < 0.001$), but at low and high radiation, they were not different ($P = 1.0$ and $P = 0.89$, respectively).

VWC of wood microsites was greater than that of soil substrates at both western and eastern locations (respectively, 28.3% versus 19.6%, $P < 0.001$; 21.9% versus 15.1%, $P < 0.001$). On western sites with medium or high radiation, wood had greater VWC than soil (respectively, 30.7% versus 20.9%, $P = 0.004$; 30.7% versus 14.2%, $P = 0.008$). At eastern locations with low radiation, wood had greater VWC than soil; VWC did not differ significantly at medium- and high-radiation sites (respectively, $P = 0.01$, 21.7% versus 15.0%; $P = 0.12$; and $P = 0.11$).

Density of seedlings growing on wood and soil (Figure 4) was not significantly different at different radiation levels or at western and eastern locations ($P = 0.17$ and $P = 0.05$, respectively). Density of seedlings on wood microsites at eastern locations was negatively associated with substrate temperature ($P = 0.047$, $r^2 = 0.38$). For wood microsites and soil substrates combined, a negative relationship existed between VWC and temperature ($P = 0.0002$, $r^2 = 0.32$). Density of seedlings was not related to VWC for wood or soil at western locations ($P > 0.09$), but density was positively related to VWC for both wood and soil at eastern locations (eastern wood $P = 0.03$, $r^2 = 0.42$; eastern soil $P = 0.01$, $r^2 = 0.51$; respectively).

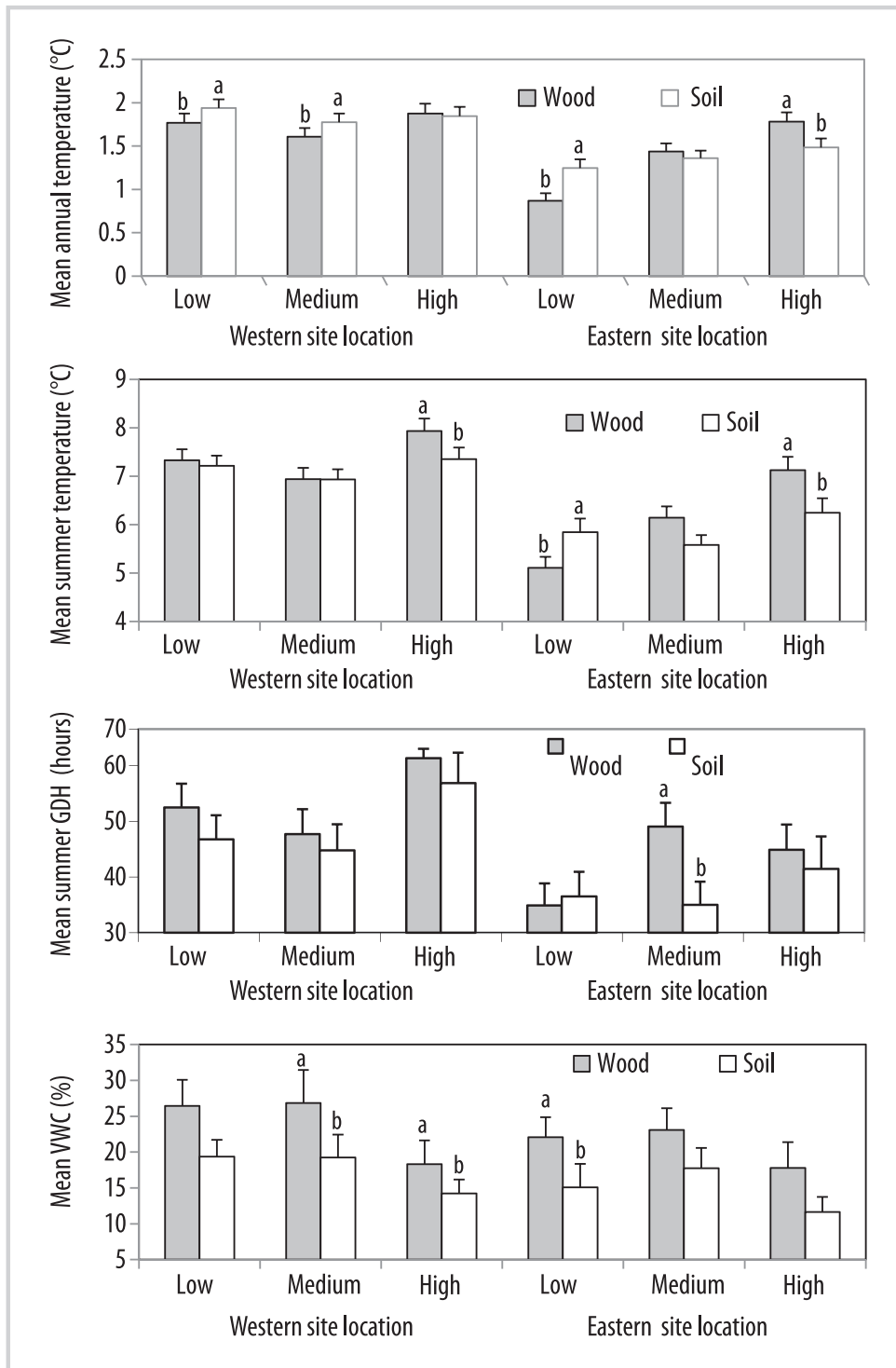
Water potential and stomatal conductance values are summarized in Figure 5.

Seedlings' early-morning water potential was less negative on wood microsites than on adjacent soil substrates ($P = 0.007$, -4.9 Ψ WP [Bar] and -6.1 Ψ WP [Bar], respectively); seedling water potential was less negative on wood than on soil in July, August, and September ($P \leq 0.02$ for all comparisons). Water potential decreased significantly over the sampling period for seedlings on both wood and soil ($P < 0.05$). Water potential was not significantly different for radiation categories of wood and soil ($P = 0.89$, $n = 14$ to 30 for wood and 18 to 24 for soil).

There was no significant relationship between water potential and VWC ($P > 0.05$).

No significant relationship was found between stomatal conductance and wood or soil temperature ($P = 0.7$). No differences were found in stomatal conductance for seedlings growing on wood versus soil or for seedlings (on wood and soil) under different radiation levels; but for wood and soil combined, significantly greater stomatal conductance occurred under medium radiation than under high radiation in August ($P = 0.30$ and $P = 0.008$, respectively). A positive relationship was found between stomatal conductance and VWC for seedlings growing on wood microsites with high radiation ($P = 0.03$, $r^2 = 0.24$; $P > 0.1$ for all other regressions).

FIGURE 3 Comparison of wood microsites and soil substrates at 3 different radiation levels at eastern and western locations. Bar plots indicate means and 95% confidence intervals for annual temperature, summer temperature, summer GDH, and VWC. Comparisons were only made between wood and soil substrates with similar radiation levels. For these pairs, significant differences are indicated by different letters.

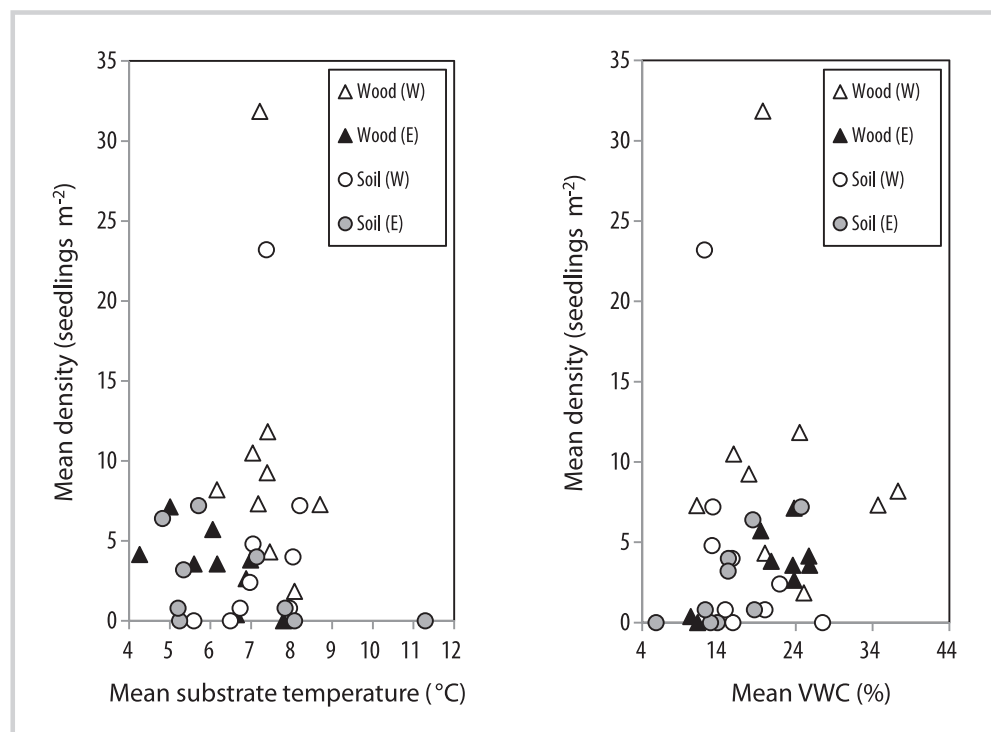


Discussion

Like others (Germino et al 2002; Maher et al 2005), we found that the benefits of different substrate and microsites types depended on radiation level, moisture

content, and temperature. Compared with adjacent soil substrates, wood microsites supporting greater *Abies* spp densities thawed later in the spring and froze earlier in the fall, had lower summer temperatures at low-radiation

FIGURE 4 Density of seedlings (<3 years old) by mean substrate temperature and VWC.



sites and higher summer temperatures at high-radiation sites, and had more GDH at medium-radiation sites. Evidence that local substrate moisture was more important than substrate temperature for regenerating seedlings (Gieger and Leuschner 2004; Müller et al 2016) was demonstrated particularly at drier eastern sites by a positive relationship between VWC and seedling density, a positive relationship between VWC and stomatal conductance, and a negative relationship between temperature and VWC.

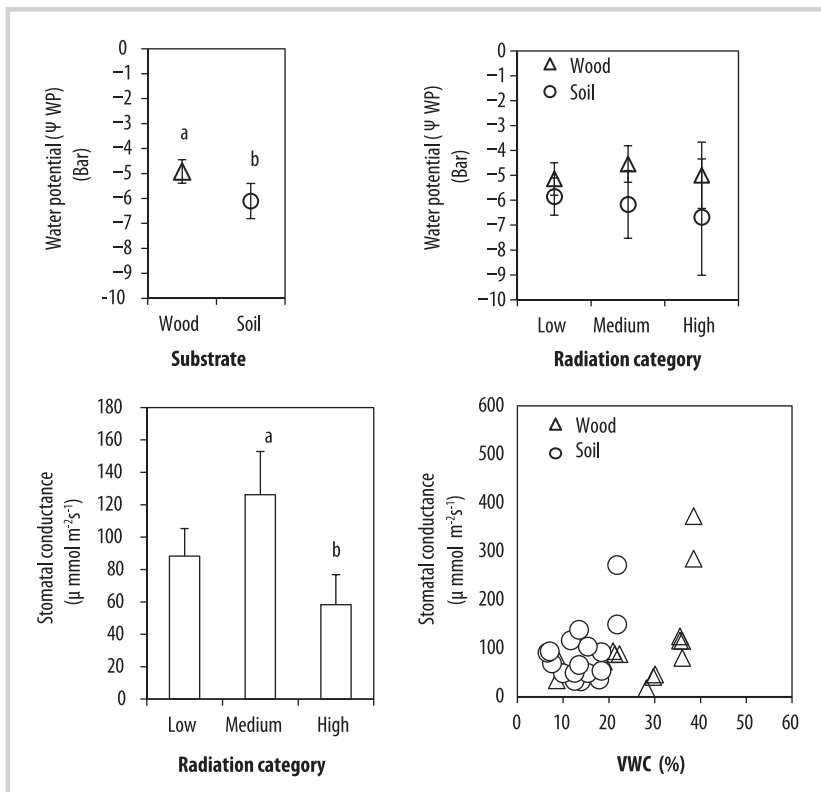
Similarly, in high-elevation subalpine forests of Dawadang Mountain, China, greater stomatal conductance for *Rhododendron calophytum* was attributed to the higher moisture and more abundant nutrients provided by wood microsites than by adjacent soil substrates (Ran et al 2010). In the Snowy Mountains of Wyoming, higher moisture contents, increased seedling density, and greater photosynthetic efficiency were associated with soil substrates having shade provided by herbs and trees (Maher et al 2005).

Presence of healthy *Abies* spp seedlings in high-radiation (high sky exposure) alpine meadow locations has 2 implications: successful seedling regeneration was not limited to shade-related sites as it is elsewhere (Ball et al. 1991), and photoinhibition was not a major cause of seedling death. Although our level of sky exposure for high-radiation sites was very similar to that of Rocky Mountain locations studied by Germino et al (2002)—66.9% versus 67.6% cover, respectively—we found healthy

seedlings at our sites, unlike that study. This suggests that photoinhibition, a notable cause of seedling death in ATEs of Australia (Ball et al 1991), Spain (Castro et al 2004), and the US Rocky Mountains (Germino and Smith 1999), is not as common in US Pacific Northwest ATE locations. Commonly damaging trees in open alpine areas, photoinhibition is associated with periods of night frost followed by clear-sky days (Ball et al 1991). Compared with 18 days of <0°C nighttime temperatures in the Rocky Mountains (Germino et al 2002), we found 8 or fewer days of <0°C temperatures during the growing season at eastern sites.

While available warmth is generally assumed to be the main limitation for forest upper expansion worldwide (Körner and Paulsen 2004; Hoch and Körner 2009), predictions of expected moderate drought associated with climate warming (Dirnböck et al 2003; Casalegno et al 2010; Mote and Salanthe 2010) indicate that seedling regeneration and potential for ATE advance may be moisture limited. Future patterns of snow accumulation and summer precipitation could be at least as important as rates of warming in determining the potential for tree establishment (Moyes et al 2015). Given enhanced VWC content, wood microsites likely compensated for moisture limitations, most apparent at our eastern, more continental, sites. Upward advance of the forest line, with resulting in-filling of the ATE facilitated by wood microsites, is dependent on cycles including tree growth to maturity, fall of mature trees into alpine meadows,

FIGURE 5 Early morning plant water potential and stomatal conductance for seedlings growing on wood microsites and soil substrates. For stomatal conductance radiation level comparisons, wood microsites and soil substrates were combined for the month of August. For stomatal conductance measurements versus VWC, only high radiation sites are compared. For water potential and stomatal conductance radiation comparisons, 95% confidence intervals are indicated. For these comparisons, significant differences are indicated by different letters.



decay of fallen trees, and subsequent seedling regeneration on wood microsites.

Conclusion

The aim of this research was to compare the roles of wood microsites and adjacent soil substrates within the ATE. Wood microsites, extending into alpine meadows from the forest line, had greater temperature and greater moisture and supported greater populations of *Abies* spp seedlings. Substrate moisture, rather than soil temperature or level of radiation, was most associated with increased density of seedlings, particularly at drier eastern sites. At our Pacific Northwest sites, mean

summer substrate temperatures $<8^{\circ}\text{C}$ and VWC $>12\%$ at 6 cm rooting depths appeared to be of primary importance to regeneration of young seedlings. Summer mean temperatures greater than about 8°C were associated with lower substrate moisture and lower seedling densities. Given climate warming and potential increase in drought, sites in both the Pacific Northwest and elsewhere that have more moisture and less radiation (cooler sites) will likely facilitate regeneration of conifers better than warmer, drier, higher-radiation sites. Given our results, it is suggested that the role of wood microsites is currently underrecognized given the likely presence of rotten downed wood at many forest-line locations globally.

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