Muscling into Meadows: A Preliminary Dendrochronological Analysis of Recent Conifer Encroachment in Mount Rainier’s Subalpine Meadows

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ABSTRACT

A dramatic reconfiguration of the subalpine ecotone is underway in many mountainous regions. One of the changes occurring in subalpine ecosystems is the shrinking and fragmentation of subalpine meadows. In July 2016, we investigated the encroachment of conifers into a subalpine meadow on the south side of Mount Rainier as part of the North American Dendroecological Fieldweek, a unique experiential learning program dedicated to training participants in the theories and techniques of dendrochronology. We collected increment cores and cross-section disks from conifers in a subalpine meadow to determine their dates of establishment. We compared these establishment dates with climatic and environmental variables to assess potential drivers of encroachment. Our results show that the establishment of conifer seedlings occurred in distinct pulses over the twentieth century coinciding with periods of low summer snowfall. We found that seedling establishment rates were much higher on locally convex micro-topographic settings and in areas with a dense cover of woody shrubs. The spatiotemporal patterns of seedling establish-
ment we observed appear to be the result of the complicated and highly scale-dependent interplay between climatic fluctuations and both biotic and abiotic microsite conditions. While our results should be considered a preliminary analysis, they reveal a compelling story of the spatiotemporal patterns of conifer encroachment and suggest potential causal mechanisms that warrant further investigation.

**Introduction**

Subalpine and alpine ecosystems are experiencing dramatic changes in response to the direct and indirect effects of climate change and land use practices (Parmesan 2006; Gottfried et al. 2012). Warming temperatures, decreasing snow pack, fire exclusion, and changes in grazing patterns all contribute to these changes. In addition to upward shifts in the elevation of local treeline (Parmesan 2006; Smith et al. 2009), changes in the spatial patterns of subalpine forests have been observed in many areas where conifers are encroaching into meadows and grasslands (Agee and Smith 1984; Rochefort et al. 1994; Klasner and Fagre 2002; Haugo et al. 2011). The subalpine ecotone, which forms a dynamic transitional zone between alpine herbaceous vegetation communities and subalpine forests, often contains parkland communities consisting of a patchwork landscape of closed-canopy tree clusters and open meadows. Over the past century, many mountainous areas’ subalpine ecotones have undergone both a change in location and a spatial reconfiguration of the plant communities within the ecotone.

Changes in the subalpine forest-meadow ecotone can be a strong indicator of shifts in climate due to the sensitivity of high-elevation species. High-elevation meadows have a short growing season with typically shallow soils, making them particularly sensitive to climatic changes. In the Cascade Mountains of western North America, the subalpine forest-alpine ecotone is often characterized by a mosaic of forest and meadow. These meadows are typically small, isolated habitat patches dominated by herbs and shrubs that act as islands in a matrix of forest (Rochefort et al. 1994). These meadows are critical habitat for many organisms and act as an important reservoir of biodiversity (Haugo and Halpern 2007). Subalpine meadows serve as important forage habitat for native ungulates such as elk (Huang et al. 2002) and habitat for pollinators (Macior 1973), and are one of the primary recreational attractions for visitors (Manni et al. 2013). Fragmentation and loss of meadows due to conifer encroachment can have serious negative implications for ecosystem functioning and biodiversity, and may be dif-
difficult to reverse even with intensive restoration efforts (Haugo and Halpern 2007). Determining patterns and drivers of tree establishment is therefore critical to developing site-specific management plans designed to sustain the valuable ecosystem services that subalpine meadows provide.

Subalpine meadow encroachment was chosen as a topic of study for the 2016 North American Dendroecological Fieldweek (NADEF). NADEF is a unique summer field school that takes an experiential learning approach to training participants in the theories, methods, and applications of dendrochronology for use in ecological and climatological analyses. The first NADEF was held in 1990, and since then it has moved to different locations each summer (Speer et al. 2006). Volunteer instructors lead group research projects in which participants design and implement an original field research project, including all steps from sample collection to sample processing in the lab to data analysis and interpretation. Participants include students, faculty, and professional foresters (Speer et al. 2006). Few universities offer dendrochronology courses, so this field school serves an important role in training new users of this methodology, as well as providing an opportunity for participants to network and share ideas. The collaborative research projects undertaken at NADEF are often used as the starting point for theses or as pilot projects for larger studies, or may be published on their own as peer-reviewed manuscripts (Speer et al. 2006). In July 2016, NADEF participants spent an intensive nine days completing research on the south side of Mount Rainier, Washington. Projects looked at old-growth forest ecology, paleoclimate reconstructions, and conifer encroachment. This paper presents the finding of the research group that focused on establishment of conifer seedlings in subalpine meadows.

In Mount Rainier National Park in Washington, conifer species including *Abies lasiocarpa* (subalpine fir), *Tsuga mertensiana* (mountain hemlock), and *Xanthocyparis nootkatensis* (Alaska yellow cedar) have been encroaching into subalpine meadows since around 1930 (Franklin et al. 1971). There are multiple controls on the temporal and spatial patterns of seedling establishment, reflecting a complex interplay between abiotic factors such as climate, soils, and geomorphic disturbances, and biotic factors including seed source availability, competition, and facilitation. Two previous studies analyzed conifer establishment on the south side of Mt. Rainier, but both focused exclusively on the east-southeast facing slopes with subalpine meadows directly upslope from the Paradise visitor center. As there is readily apparent spatial variability in the composition and structure of subalpine forest
patches in this area, we set out to update and expand the coverage of these previous studies by collecting samples approximately one km northeast of the previous studies on a south-southwest facing slope. We collected basal disks and increment cores to determine the establishment dates of conifers and compared these dates with climate records and detailed measurements of microsite characteristics. We used these data to answer the following research questions: (1) Has conifer encroachment been continuous or episodic? (2) How is conifer establishment associated with specific microtopographic settings, vegetation characteristics, and climatic conditions?

**Methods**

**Study Area**

Mount Rainier National Park is located southeast of Seattle, Washington, in the Cascade Range. The park area is 98,560 ha, and elevation ranges from 488 meters to 4,395 meters. The Paradise region is an area of mixed subalpine forest and subalpine meadows located at approximately 1,680 meters elevation at the base of the south-facing slope of Mount Rainier. Climate here is temperate, with cold, wet winters and mild, dry summers. Mount Rainier is one of the snowiest places on earth, with average annual snowfall of 16,332 mm from 1920 to 2016 in the Paradise region of the park (National Park Service).

The strata underlying Mount Rainier is a 3,000-meter-deep layer of coal, sandstone, and shale dating back 60 million years, called the Puget Group (Henderson 1974). The mountain itself is a volcano, the cone of which was gradually built up from lava flows and is composed of andesite, pumice, lahar deposits, and pyroclastic materials (Henderson 1974). Deposits of volcanic material over the parent bedrock comprise the dominant soil type on Mount Rainier and help to shape plant communities.

In late July 2016, we surveyed 165 individuals, collecting 65 samples of *A. lasiocarpa*, *T. mertensiana*, and *X. nootkatensis* along two 25- to 40-meter transects. The transects spanned opposite sides of a subalpine meadow in the Paradise region of the park (Figure 1). Transect sites were selected based on the presence of variable-height stands of *A. lasiocarpa*, *T. mertensiana*, and *X. nootkatensis* within subalpine meadows dominated by shrubs and herbs and the absence of recent disturbance indicators such as charred trees or cut stumps. Two transects, Fourth Crossing (FCR) and Skyline Trail (STM), were selected within the study area (Figure 2). The
primary shrubs and forbs along the transects were *Vaccinium deliciosum* (Cascade blueberry), *Phyllodoce empetriformis* (pink mountain-heath), *Valeriana sitchensis* (Sitka valerian), and *Erythronium grandiflorum* (glacier lily). The elevation at the start of the FCR transect was 1,640 meters, and the elevation of the STM transect was 1,669 meters. The transects followed topographic contours to remain at approximately the same elevation throughout their length.

### Field Methods

**FCR Site (Fourth Crossing Trail)**

We quantified tree age and detailed microsite characteristics along a 40-meter transect located approximately 85 meters downslope of the Skyline Trail at the edge of an island of mature trees (46.791907° N, -121.724619° W) and followed the contour across the slope at a 320° azimuth. Tree measurements and shrub cover were recorded within 40 consecutive 1 m² plots on both sides of the transect. Dendrochronological samples were collected from alternating square meters, beginning on the left (downslope) side of the transect. Trees larger than 1 cm in basal diameter were either cut with a handsaw or cored with an increment borer at the base of the tree for age determination. Trees less than 1 cm in diameter at the base were tallied as seedlings and...
their species recorded, but not measured or sampled. Variables collected for each sample included measurements for height, diameter at breast height, basal diameter, micro-topographic position (convex vs concave surfaces), and distance along the transect (Figure 3).

STM Site (Skyline Trail Meadow)
We quantified tree age along a 25-meter transect located within a group of trees near an unnamed creek (46.793041° N, -121.725945° W), 35 meters downslope from the Skyline Trail and followed along a 90° azimuth. This transect was used to increase our sample depth for tree establishment dates, but was not used in analyses of microsite conditions. Within 1 meter of the transect line, all trees that were tall enough to have a diameter at breast height greater than zero were identified and cored with an increment borer, if possible, or cut with a handsaw to collect a basal disk. Variables collected for each sample included measurements for diameter at breast height, basal diameter, and distance along the transect.
Figure 3.—Collecting data along our FCR transect. Transect tape is visible as the thin white line running west from a line of mature trees on the eastern side of the meadow. Recent encroachment is apparent as the cluster of young trees growing on a locally convex micro-topographic surface.

**Lab Methods**

All cores were mounted on grooved wooden blocks. Cores and disks were finely sanded and annual rings were counted under the dissecting microscope. Years containing narrow rings in each sample were recorded for use in visual crossdating, using the “list method” (Yamaguchi 1991). Years indicating narrow rings in over 50% of the samples were considered “marker” years, and were used to visually crossdate samples and identify general trends in growth conditions. Ring widths were measured under a microscope using a Velmex UniSlide and the software program Measure J2X (Voor Tech Consulting 2008). Raw ring-width data for all series were exported for subsequent comparisons and analyses.

Both statistical and visual methods were used to crossdate series based on ring-width measurements. The program COFECHA (Grissino-Mayer 2001) was used to statistically verify our visual crossdating of each series older than 50 years by checking them against all other measured samples.
and an existing chronology of low-elevation *A. lasiocarpa* within the Rainier area from the International Tree Ring Data Bank (Peterson and Peterson 1992). If we identified a potentially misdated series, we re-measured and, when appropriate, adjusted our measurements using the editing program EDRM. Series that were younger than approximately 50 years could not be reliably statistically crossdated due to the short record length, so they were visually crossdated using the list of narrow marker rings that had been previously established using longer samples whose crossdating was statistically verified using COFECHA.

**Climate Data**
Climate data were obtained from the Global Historical Climatology Network (Menne et al. 2012). Climate data were collected at the Paradise weather station, which is located 1.5 km southwest of our study site. We examined monthly records of 18 meteorological variables, including precipitation, temperature, and snowpack, from 1916 to 2016.

**Data Analysis**
Establishment years for all dated samples were grouped into five-year bins for further analysis. These bins were used instead of precise dates because exact establishment dates could not be reliably determined due to the difficulty of accessing the exact base of the tree and its root collar. Establishment years were then compared to climate data time series and tree characteristics such as height and radial growth rate, using Pearson’s correlation analysis. At the FCR transect we collected detailed micro-site information and compared establishment dates with micro-site variables, including stem density, basal area at the stem base, *Vaccinium* cover, *Phyllodoce* cover, and microtopographic position using Pearson's correlation analysis and two-tailed Student's t-tests.

**Results**
Along the FCR transect, where we recorded detailed notes for both mature trees and seedlings, we found that mature trees were primarily *A. lasiocarpa* (79 individuals, 83% of all trees), with a minor component of *T. mertensiana* (15 individuals, 16% of all trees), a single *Abies amabalis*, and no mature *X. nootkatensis*. Among seedlings, most were *A. lasiocarpa* trees (30 individuals, 73% of all trees), with a minor component of *T. mertensiana* (8 individuals, 20% of all trees), and only two *A. amabalis* and one *X. nootkatensis*. Along the
STM transect, where we recorded details for only mature trees, we identified five *A. lasiocarpa*, two *T. mertensiana*, and two *X. notkatensis* trees. Of the 65 trees from which we collected samples, 45 were successfully crossdated to establish a master chronology for the study site. The interseries correlation was 0.377, with an average mean sensitivity of 0.427.

The establishment dates suggest two major pulses in establishment for *A. lasiocarpa*, one between 1945 and 1950, and the other between 1960 and 1965 (Figure 4). Both *X. nootkatensis* samples that we collected established more recently in the 1970 to 1980 bins. *T. mertensiana* seedlings established more uniformly over time, and there were no clear periods of higher seedling establishment, though the sample size is too small to state anything conclusively. We do not report establishment dates after 1990 because of the difficulty of determining the exact age of very small seedlings, but the presence of numerous small seedlings indicates ongoing establishment of conifers. No trees established along our transects prior to 1917, though a

![Figure 4.—Histogram of establishment dates. Dates are presented in five-year bins. Species shown are Abies lasiocarpa (ABLA), Tsuga mertensiana (TSME), and Xanthocyparis nootkatensis (XANO).](image-url)
line of older trees not included in our analysis was present immediately to the east of our FCR transect.

Basal diameter was highly variable (3.38±3.29 cm) and was not significantly correlated with establishment year (r = -0.149, p = 0.352) (Figure 5). Average radial growth was low (0.457±0.608 mm) and not significantly correlated with establishment year (r = 0.135, p = 0.401). Tree height was generally low (87.41±29.66 cm) and was statistically significantly negatively correlated with establishment date (r = -0.483, p = 0.008). Tree height and basal area were moderately positively correlated, but this correlation was not significant (r = 0.3621, p = 0.053).

We compared the number of trees that established in a given five-year period with climate during that same period (Figure 6). We selected a suite of climate variables based on their known importance for tree establishment and growth and looked at both annual and growing season (May–September) values. Average total annual precipitation (r = -0.092, p = 0.743) and growing season precipitation (r = 0.166, p = 0.552) were not significantly correlated with the number of seedlings establishing. Average annual temperature was significantly positively correlated with seedling establishment (r = 0.513, p = 0.048). Growing season temperature was only weakly correlated with establishment (r = 0.365, p = 0.178). Average total annual snowfall (r = -0.218, p = 0.434) and October–April average total snowfall (r = -0.191, p = 0.493) were not significantly correlated with establishment rates. Average growing season total snowfall was significantly negatively correlated with establishment numbers (r = -0.652, p = 0.007). Pulses of seedling establishment correspond with years of low summer snowfall and years of very low radial growth (our “marker years” used in crossdating) formed during years of higher-than-average summer snowfall (152.46 mm vs 88.14 mm).

We identified variation in microtopographic position ranging between locally convex and concave surfaces along the FCR transect. This transect was composed of 80 1m² plots, of which 38 contained what we identified as convex topography clustered in two separate ridges along the transect (Figure 7). Locally convex surfaces were generally less than one meter above the surrounding landscape, and appeared to be linear geomorphic features running downslope, likely formed during mass wasting events originating from the steep, rocky slopes above the meadow. The density of conifers, including both seedlings and more mature trees, was higher on convex micro-topographic surfaces (mean = 2.268 trees per m², sd = 2.191) than on concave surfaces (mean = 1.315 trees per m², sd = 1.891), and this difference in means was
Figure 5.—Scatterplots of establishment year vs average growth; establishment year vs basal diameter (cm); establishment year vs height (cm), and tree height (cm) vs basal diameter (cm).
statistically significant ($t = 2.459, p = 0.016$). The trees growing on convex surfaces established earlier in the twentieth century on average (mean year of establishment = 1951, sd = 15.665) than trees on concave surfaces (mean year of establishment = 1964, sd = 11.483), and this difference was significant ($t = 2.376, p = 0.022$). Both *Vaccinium* and *Phyllodoce* were more abundant on convex surfaces, and there was a statistically significant higher total percent shrub cover on convex (mean = 46.121 percent cover, sd = 27.861), rather than concave (mean = 26.552 percent cover, sd = 26.300) surfaces ($t = 3.204, p = 0.002$). Although both shrub cover and density of trees was higher on convex surfaces, there was no statistically significant correlation
Figure 7.—Microsite characteristics for each one-square meter plot sampled along our FCR transect: average tree age (years), average annual tree-ring width (mm), total tree basal area (m$^2$ per hectare), total conifer density (stems per m$^2$), Vaccinium cover (percent), Phyllodoce cover (percent), and micro-topographic setting (convex “ridge” or concave “valley”).
between shrub cover and tree density \( (r = 0.196, p = 0.080) \). Age of trees did not consistently increase with proximity to the older stand of trees—the seed source for establishment—on the eastern side of the transect, as would be expected in a typical gradient of establishment outwards from seed source.

**Discussion**

The moderate correlation among samples’ radial growth measurements and the high mean sensitivity reflect considerable spatial and temporal variability in annual ring widths and made crossdating relatively difficult. In spite of these challenges, we were able to successfully crossdate most of our samples, and we found that annual rings formed during specific “marker” years were often consistently very narrow across all samples. The highly variable annual growth rates were likely due to the temporally and spatially variable stress conditions at the site. Shifting snowpack likely caused many of the abnormal growth rings we observed. When bent by the weight of snow, trees respond by producing larger wood cells on the underside of the bend, forming reaction wood that helps the tree return to an upright position. Some of our samples had multiple lobes of reaction wood pointing in different directions, which partially obscures the shared patterns of narrow and wide rings that would normally be used to crossdate the samples. We found Yamaguchi’s list method to be particularly helpful for crossdating these samples, due to the higher spatial consistency of extremely low radial growth years.

Our results reveal a sustained period of high establishment rates from 1936 to 1970, with the two most prominent pulses from 1945 to 1950 and 1960 to 1965 (Figure 3). These periods of higher establishment coincide with years predicted to have high *A. lasiocarpa* seedling establishment on Mount Rainier, based on climatic characteristics associated with cone production and seedling survival (Henderson 1973), particularly 1944, 1950, 1953, 1956–57, 1960, 1964, and 1969. Interestingly, the establishment pulses we identified do not line up perfectly with those reported for other meadows in the Paradise region. Franklin et al. (1971) reported a peak in establishment between 1928 and 1937, while Rochefort and Peterson (1996) reported establishment pulses from 1935 to 1950, 1955 to 1960, and 1980 to 1985. Variability in the timing of establishment pulses between sites less than 5 km apart suggests a high influence of local site conditions on seedling success. The total absence of trees that established prior to 1917 along our transects shows that this meadow has undergone dramatic changes over the past century. Patches of older trees were present on the northwestern corner and
eastern edge of the meadow, indicating that a lack of seed source or large-scale, stand-replacing disturbances were not the reason for the absence of trees in this area prior to the early twentieth century. Age did not decrease consistently with distance from the older forest patch, suggesting that encroachment is not occurring in a linear fashion outwards from previously established clusters of trees.

Establishment dates were not significantly correlated with basal diameter. This indicates that the conditions most conducive to the establishment of seedlings are not necessarily the same conditions that lead to ongoing rapid radial growth of trees. After trees become established, the interplay between micro-site conditions and weather fluctuations creates variable growth rates among nearby trees, resulting in no correlation between age and size of trees. While radial growth was not correlated with establishment dates, vertical growth was. We found a statistically significant negative correlation between establishment year and tree height (i.e., older trees are generally taller). It may be advantageous to allocate more resources to vertical growth rather than radial growth for trees in settings where snowpack depth can severely limit growth.

Our analysis of the association between climate and establishment dates shows that the survival of seedlings is strongly linked to summer snowfall and annual mean temperature. This subalpine ecotone experiences a high level of inter-annual variability in snowfall and the date of snow melt. On average, the maximum snow depth in June is 289.81 mm, with a range from zero to 635 mm. This means that the start of the snow-free growing season can vary by a month or more between years. We found that the rate of seedling establishment was not significantly correlated with total average annual precipitation and snowfall, but was significantly negatively correlated with May–September total snowfall. Interestingly, neither temperature nor total precipitation during the May–September season was significantly correlated with establishment patterns. These results suggest that growing season snowpack is the strongest limiting factor on the successful establishment of conifer seedlings. Snow and associated cold soil temperature likely inhibit seedling establishment during the brief, snow-free growing season at this altitude (Rochefort et al. 1994). Seedlings cannot establish under a blanket of snow, due to temperature and light constraints (Rochefort et al. 1994), so years with ongoing snowfall into the summer and a short potential growing season may not allow for germination and survival of many seedlings. The lack of a significant relationship with total precipitation indicates
that seedlings are not moisture-limited in this area, likely because of the long-lasting snowpack, which melts and provides plenty of soil water. The extended period of below-average May–September snowpack from 1943 to 1970, during which all but three years were below the long-term average, appears to be a primary reason for the establishment pulses we identified during that same time period. Relatively warm, dry conditions are associated with higher cone production for both *A. lasiocarpa* and *T. metternsiana* (Woodward et al. 1994), so this period’s climate may have aided both seed production and seedling survival. These results indicate that the meadow we sampled may have been maintained by higher summer snowpack prior to the early twentieth century, when conifer seedlings began to encroach.

While the temporal patterns of pulsed seedling establishment events are likely a result of large-scale climatic fluctuations, the high level of spatial heterogeneity in the presence of trees indicates a strong control of microsite conditions on the fate of seedlings. We found that trees were far more common on convex surfaces, where the slightly elevated surface allows for earlier snow melt and warmer soil temperatures, thereby extending the growing season. Trees growing on convex surfaces also had earlier average establishment dates, suggesting the role of micro-topography may have been even more critical at the beginning of the multi-year period of above-average establishment rates that we identified in the mid-twentieth century. Beyond the direct microclimate implications of local micro-topographic setting, there may also be indirect effects via inter-specific biotic interactions. We found that these convex surfaces support higher *Vaccinium* and *Phyllodoce* cover. The woody stems of these low-growing species must persist above-ground through winter season, and are therefore very sensitive to prolonged snowpack, leading to a strong correlation between convex surfaces and the density of woody shrubs. The presence of *Vaccinium* and *Phyllodoce* may facilitate seedling encroachment by moderating soil temperature, increasing summer soil moisture retention, and potentially providing access to beneficial ectomycorrhizal associations (Henderson 1971; Rochefort and Peterson 1996). Disentangling the complex interaction between microclimatic conditions and facilitated succession, both of which are linked to micro-topographic setting, would require further study, but our results suggest that they may both play an important role in shaping the patterns of conifer encroachment.
Conclusion

Our results show that a dramatic reconfiguration of the subalpine ecotone is underway in our study area. The subalpine meadow ecosystem is shrinking in area and becoming increasingly fragmented, due to the encroachment of conifers. Establishment of conifer seedlings occurred in distinct pulses over the twentieth century. These establishment pulses coincide with periods of above-average annual temperature and low summer snowfall, suggesting that cool conditions and late season snowpack play an important role in maintaining meadow ecosystems. The timing of these pulses appears to have been spatially variable on Mount Rainier, likely due to the complex interplay between climatic fluctuations and micro-site characteristics. We found that seedling establishment rates were much higher on locally convex micro-topographic settings and in areas with a dense cover of woody shrubs. Our analysis was limited because we were able to collect samples from only two transects. Future research should expand the spatial and temporal coverage of our work to further investigate the relationship between seedling establishment and vegetation cover, micro-topographic setting, and climatic fluctuations in additional vegetation associations and on different aspects around Mount Rainier National Park. Collecting local microclimatic data would be particularly useful in these analyses. Additional dendrochronological samples would allow for investigation of potential differences in establishment controls for different species and could expand the temporal coverage of our analysis. While our results represent a preliminary analysis, they reveal compelling spatiotemporal patterns of conifer encroachment and suggest potential causal mechanisms that warrant further investigation. This research was completed during the 2016 North American Dendroecological Fieldweek and exemplifies the potential for valuable research contributions that can come from intensive experiential learning programs.

Literature Cited


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