Impacts of Swiss needle cast on overstory Douglas-fir forests of the western Oregon Coast Range

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Abstract

Tree-ring analysis was applied to assess the impacts of the fungal disease Swiss needle cast on the radial growth of mature Douglas-fir (*Pseudotsuga menziesii*) forests in the western Oregon Coast Range. Although considered endemic to the Pacific Northwest, Swiss needle cast has significantly lowered productivity in Douglas-fir forests only in the past twenty to thirty years. To date, studies on Swiss needle cast impacts have almost exclusively involved young (< 30 yrs) plantation trees. To better describe the history of Swiss needle cast and its impacts on older (> 80 yrs) trees, we extracted tree cores from dominant and codominant Douglas-fir and western hemlock (*Tsuga heterophylla*) in three even-aged stands in western Oregon. In the least affected stand growth rates of both species did not significantly differ, while at the most severely diseased site Douglas-fir radial growth was reduced by as much as 85%. Growth reductions likely associated with Swiss needle cast were dated to as early as 1950, though the most severe impacts occurred after 1984. An index of Swiss needle cast severity significantly ($p < 0.01$) related to instrumental records of air temperatures such that warm conditions from March through August were associated with reduced radial growth at the most severely affected site. Overall, this study demonstrates that even mature forests of natural origin are susceptible to severe growth reductions by Swiss needle cast, that warmer spring and summer temperatures are associated with Swiss needle cast impacts, and that the disease appears to be increasing in severity.

Keywords: Swiss needle cast, Pacific Northwest, Douglas-fir, climate change, dendrochronology

1. Introduction

Over the past twenty years, an epidemic of Swiss needle cast, a foliage disease caused by the fungus *Phaeocryptopus gaeumannii,* has emerged in the Oregon Coast Range, significantly lowering productivity in affected Douglas-fir forests (Hansen *et al.*, 2000; Maguire *et al.*, 2002). Fruiting bodies of the fungal pathogen interfere with foliage gas exchange by physically blocking Douglas-fir stomata, thereby reducing or halting photosynthesis and leading to premature needle abscission (Manter *et al.*, 2000). Although mortality is rare, cubic volume growth loss ranges from 23-50% in diseased stands (Maguire *et al.*, 2002). The total area of symptomatic forest in coastal Oregon observed in aerial surveys conducted by the Oregon Dept of Forestry annually since 1996 has been gradually increasing; the area reported in 2009 was 163500 ha (ODF, 2009).

The disease became known as Swiss needle cast because it was first observed in Douglas-fir plantations in Switzerland and Germany in 1925, and subsequently spread throughout central Europe (Boyce 1940). Due to concern about reports of the disease in Europe, surveys for *P. geaumannii* were made in western North America, where it was found to be widespread, although inconspicuous, on native Douglas-fir (Boyce, 1940). Because of its widespread distribution on native Douglas-fir, which preceded the Swiss needle cast outbreak in Europe, and because Douglas-fir is its only known host, Boyce (1940) expressed the opinion that *P. gaeumannii* is probably indigenous to the Pacific Northwest. He also noted that in the Pacific Northwest the pathogen had only a negligible effect on its host, in contrast to the situation in Europe, where severe defoliation due to the disease helped curtail widespread planting of Douglas-fir in Germany (Boyce 1940).

A major question associated with the current epidemic is whether the disease is a recent phenomenon, or whether there have been growth declines of Douglas-fir due to foliage diseases along the western slope of the Oregon Coast Range during the past century. Current impacts of Swiss needle cast have been evaluated almost exclusively in relatively young (<30 years in age) Douglas-fir stands, often in plantation settings (Maguire *et al.*, 2002). Impacts of the disease on older, overstory trees, especially in naturally regenerated stands, remain to be described. Also, all assessments of Swiss needle cast severity span the current outbreak, focusing on the years from approximately 1990 to present (Hansen *et al.*, 2000; Maguire *et al.*, 2002; Stone *et al.*, 2008). Little is known about the history of the disease prior to the current outbreak, and whether it significantly affected growth in earlier decades. Moreover, field and laboratory studies indicate that the disease is associated with springtime and summertime needle wetness as well as wintertime temperatures (Rosso and Hansen, 2003; Manter *et al.*, 2005; Stone *et al.*, 2008). A longer time series of Swiss needle cast impacts would better characterize the development of the disease and provide more statistical power to quantify relationships with climate.

Tree-ring data have been widely used to reconstruct the timing, severity, and spatial extent of insect outbreaks in western conifers (Swetnam and Lynch, 1993; Speer *et al.*, 2001; Case and MacDonald, 2003). However, in this study we explore whether related dendrochronology techniques can be applied as a means by which to assess the long-term history and impacts of a foliar pathogen, Swiss needle cast, on overstory Douglas-fir in the northwestern Oregon Coast Range. More specifically, our objectives are to *i*) describe the effects of Swiss needle cast on the radial growth of mature (>50-yrold), naturally regenerated trees, *ii*) reconstruct the history of Swiss needle cast over the past fifty to seventy years, and *iii*) relate multidecadal time series of Swiss needle cast derived from tree-ring data to instrumental climate records.

2. Methods

Growth-increment analysis was performed on Douglas-fir, the host species for Swiss needle cast, as well as a control species, western hemlock, to better distinguish the impacts of the disease from stand-level disturbances or extreme climate events. Therefore, three even-aged mixed Douglas-fir (*Pseudotsuga menziesii*) -western hemlock (*Tsuga heterophylla*) stands of native origin were selected as study sites in the northwestern Oregon Coast Range (Figure 1). Chosen stands also had no history of logging or thinning, were in excess of 70 yrs in age, and occurred immediately adjacent to younger stands heavily or moderately impacted by the disease. Of the three stands, Tillamook Upper and Lower were located within approximately 3.2 kilometer of one another near Tillamook, OR, while Euchre Mountain was located approximately 70 km to the south, near Lincoln City, OR (Figure 1). At each site, circular, 0.02 ha plots were located along transects through the forest interior at approximately 20 m intervals. Species, diameter, and crown class were recorded for all trees > 10.0 cm dbh (diameter at breast height; 1.3 m). Crown class was partitioned into four categories (dominant, codominant, intermediate, and suppressed) according to the amount of intercepted light (Smith, 1986). For each tree species, a relative importance value was calculated as the average of the relative frequency (presence or absence in plots), relative density (number of individuals), and relative dominance (basal area) (Cottam and Curtis, 1956). Within each 0.02 ha circular plot, one core was extracted from each dominant and codominant western hemlock and Douglas-fir trees. All cores were taken at breast height to avoid rot and buttressing. To increase sample sizes, we also collected cores from several dominant or codominant western hemlock and Douglas-fir trees located just outside plot boundaries.

Cores were dried, mounted, and sanded with increasingly fine sandpaper to reveal the cellular structure. Within each species and site, all cores were then visually crossdated using the "list year" technique to identify any locally absent or false rings in the data set and thereby ensure that all growth increments were assigned the correct calendar year (Yamaguchi, 1991). Once visual crossdating was complete, we measured all growth increments to the nearest 0.002 mm using a Unislide "TA" tree-ring measuring system (Velmex, Inc., Bloomfield, NY). Following measurement, crossdating was statistically verified using the International Tree-Ring Data Bank Program Library program COFECHA, available thorough the University of Arizona Laboratory of Tree-Ring Research http://www.ltrr.arizona.edu/pub/dpl/ (Holmes, 1983; Grissino-Mayer, 2001). In COFECHA, measurement time series were detrended using cubic spline set at a 50% frequency response of 32 years. Within each species and site, every detrended time series was correlated with the mean of the all other detrended time series to yield the interseries correlation. Individuals with an unusually low interseries correlation were checked for potential errors such as missed or false rings. Mean sensitivity was also calculated to describe the high-frequency, between-year growth variability, which for any pair of adjacent years ranged from zero (each year is the same width) to two (when a non-zero value is adjacent to a zero value; i.e. a locally absent increment) (Fritts, 1976).

Once crossdating was verified, original measurement time series were averaged with respect to species and site to produce "ring width" master chronologies. Next, to identify suppressions a running calculation of percent-growth change was applied to each of the original measurement time series. In this "suppression index," percent growth change for a year was equal to (M_1 – M_2) / M_2 in which M_1 equals average growth over the prior 5 years and M_2 equaled average growth over the subsequent 5 years. Sudden reductions in growth resulted in highly positive values. This calculation was also applied to the ring width master chronologies. If the suppression index exceeded 100%, the year with the maximum value was recorded as a moderate suppression, while major a suppression was recorded if the index exceeded 200%. No more than one suppression event could be recorded in a ten-year period. As an additional measure, we calculated percent growth reduction in Douglas-fir relative to the control species, hemlock. At each site, the hemlock measurement master chronology (hemlock) was used, and the calculation was repeated for each Douglas-fir (fir) individual using the formula (fir – hemlock) / hemlock. This calculation was performed for the intervals of 1984 through 2007 and 1996 through 2007.

The difference between Douglas-fir and hemlock ring-width chronologies was calculated to quantify disease-related growth reductions and establish preliminary Swiss needle cast histories at each site. However, we found that estimates of disease history could be refined by comparing Douglas-fir among sites, given that disturbance histories at each of the three locations appeared to be similar. An analysis specific to Douglas-fir would eliminate complications that could arise had hemlock positively responded to Douglas-fir decline or exhibited radically different responses to climate. The analysis was first conducted by subtracting Douglas-fir ring-width chronology at the site with the lowest Swiss needle cast influence (Euchre Mountain) from the Douglas-fir ring-width chronology at the site with the greatest influence (Tillamook Lower).

Although each stand was even-aged, tree ages among stands varied by forty to fifty years. Thus, age-related growth declines had to be removed before growth could be compared, accomplished by developing a "detrended" master chronology at each site. First, each measurement time series was detrended with a negative exponential function to remove age-related growth trends and standardize each mean to a value of one. Exceptions were made for those series in which an exponential function followed a positive trend. Positive slopes would not be related to age, and these individuals were detrended using the series mean (a horizontal line). By detrending with such rigid functions, we attempted to preserve as much long-term variability as possible. Within each site, all detrended Douglas-fir time series were averaged to create master detrended chronologies. Chronology development was conducted using the program ARSTAN http://www.ldeo.columbia.edu/res/fac/trl/public/publicSoftware.html (Cook 1985). A detrended master chronology was also developed for western hemlock at Tillamook Lower as well as for Douglas-fir from Cape Perpetua, a site approximately 65 km south of Euchre Mountain. At 400 years in age, these trees were more than four times the age of western hemlock and Douglas-fir at the other three sites. For these reasons Cape Perpetua was not used as a full replicate, but was still useful in comparisons with the other sites. In particular, the Cape Perpetua Douglas-fir chronology was substituted in place of the Euchre Mountain Douglas-fir chronology to further refine a chronology of Swiss needle cast impact.

A complication with this chronology-development procedure was that many Douglas-fir at Tillamook Lower experienced particularly severe growth declines over the most recent twenty to thirty years, and in many cases negative exponential functions predicted values less than zero. To resolve this issue we used a type of regional curve standardization at Tillamook Lower in which a single function was used to detrend every individual. First, a pith locator (a transparency with concentric circles that matched the curvature and growth rate of the core's growth increments) was used to estimate age at breast height. The earliest growth increment in a core was generally within five years of pith date. Next, each measurement time series was normalized to a mean of zero and standard deviation of one, after which all were aligned with respect to cambial age. A single negative exponential function ($y = 5.24*\exp^{-0.04*x}$) was then fit to the pooled data and used to detrend each measurement time series ($R^2 = 0.81$). Detrended measurement time series were then aligned with respect to calendar year and averaged to create the master chronology.

We correlated the chronology of Swiss needle cast impact with monthly averages of precipitation, temperature, and Palmer Drought Severity Index (1895 – present) for Oregon Region 1 (Coastal Oregon), available at the NOAA NCDC website http://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp# . Monthly averages were used to determine those periods of the year in which environmental variability most strongly affected the Swiss needle cast time series. Given the potentially heavy influence of ocean circulation on the climate of these forests, we also related the Swiss needle cast time series to the Multivariate ENSO Index (MEI) (Wolter and Timlin, 1998). The MEI is the leading principal component of six marine and atmospheric variables in the tropical

Pacific, and was obtained (1950-2005) from the NOAA Earth Systems Research Laboratory (http://www.cdc.noaa.gov/people/klaus.wolter/MEI/). Monthly climate variables were also correlated with Douglas-fir and western hemlock master chronologies at Euchre Mountain and Cape Perpetua. This analysis was conducted to determine baseline climate responses for each species at sites where impacts of Swiss needle cast were presumed to be minimal.

3. Results

Douglas-fir and western hemlock dominated two of the three study sites with the exception of Tillamook Lower, in which Sitka spruce dominated with the highest importance value (Table 1). Sitka spruce and red alder were minor components of Tillamook Upper and absent from Euchre Mountain (Table 1). Among the three sites, Tillamook Lower supported the lowest total basal area and number of stems per hectare (Table 1). Mean plot elevation ranged from 260 m at Tillamook Lower to 520 m at Tillamook Upper, and slopes were comparable among all three sites at fifteen to twenty percent (Table 2). Aspects at Tillamook Lower and Tillamook Upper were southwest, in contrast to northwest-facing slopes at Euchre Mountain (Table 2). Hemlock and Douglas-fir were even-aged within each site, although trees at Euchre Mountain were approximately forty years older than those at Tillamook Upper or Tillamook Lower (Table 2).

Visual crossdating was verified using COFECHA and no dating errors were identified. Interseries correlations as calculated by COFECHA, which reflect the degree of synchrony in growth patterns, were lower for western hemlock than Douglas-fir (Table

2). Also, interseries correlations for each species were highest at Tillamook Lower and lowest at Euchre Mountain (Table 2). No clear trends were evident for mean sensitivity, though all species and sites exceeded 0.2 and values for Douglas-fir at Tillamook Lower were relatively high at 0.4 (Table 2). Locally absent rings occurred only rarely in both species at Euchre Mountain, and none was identified in western hemlock at Tillamook Lower or Tillamook Upper (Table 2). Locally absent rings did, however, occur with much greater frequency in Douglas-fir at Tillamook Lower, and to a lesser extent, in Douglas-fir at Tillamook Upper (Table 2). At these two sites several cores contained a full complement of rings, which facilitated crossdating and identification of locally absent rings. Hemlock master chronologies all significantly ($p < 0.05$) correlated with one another as did Douglas-fir chronologies, corroborating dating accuracy.

Inter-species differences in growth rates were most strongly pronounced at Tillamook Lower, where mean Douglas-fir ring width was significantly ($p < 0.05$) less than the control species, hemlock, during 1950-1951, 1961, 1969, 1972-1974, and 1976 through present (Figure 2A). Early in the measurement chronologies, Douglas-fir ring width was significantly greater than western hemlock, although western hemlock growth did eventually exceed Douglas-fir in 1984 and again from 1999 to 2000 (Figure 2B). No significant differences occurred between hemlock and Douglas-fir at Euchre Mountain (Figure 2C). Also, at Tillamook Lower, Douglas-fir experienced severe and widespread suppression events in 1984 and 1996 (Figure 3A). Almost all Douglas-fir individuals experienced a major suppression in those years, a pattern not shared by hemlock (Figure 3A,B). A similar suppression history was also evident at Tillamook Upper, but the severity of the Douglas-fir suppressions was not as pronounced as at Tillamook Lower, and fewer trees were affected (Figure 3C,D). Neither Douglas-fir nor hemlock experienced major or widespread suppressions at Euchre Mountain (data not shown).

As a final indicator of growth reductions, locally absent rings occurred in a large percentage of Tillamook Lower Douglas-fir, especially in three episodes beginning in 1984, 1996, and again in the mid-2000s (Figure 4A). Locally absent rings began to occur with some frequency at Tillamook Upper in 1996 (Figure 4B). Yet at both sites, hemlock did not contain a single locally absent ring, despite comparable sample sizes (Figure 4C). Too few locally absent rings were noted at Euchre Mountain to compare frequencies between species (Table 2). All indices corroborated that growth reductions for Douglas-fir were most severe at Tillamook Lower, and that these reductions were most pronounced after 1984 (Figures 2-4). Indeed, percent-growth reduction relative to hemlock was greatest and highly significant ($p > 0.001$) at Tillamook Lower, at more than 80% between 1984 and 2007 and almost 90% for the interval of 1996 to 2007 (Figure 5). Percent growth reduction for Douglas-fir at Tillamook Upper was less pronounced, and significant ($p < 0.05$) only from 1996 through 2007. No significant reductions were identified at Euchre Mountain (Figure 5).

Three chronologies of Swiss needle cast impact all indicated that the effects of the disease on radial growth have been increasing over the past five decades (Figure 6). Very similar trends were evident whether the Tillamook Lower Douglas-fir detrended chronology was subtracted from the Tillamook Lower hemlock detrended chronology, the Euchre Mountain Douglas-fir detrended chronology, or the Cape Perpetua Douglas-fir detrended chronology (Figure 6). Thus, growth comparisons between diseased Douglas-fir and undiseased hemlock within sites corroborated growth comparisons between diseased Douglas-fir and relatively undiseased Douglas-fir among sites. These chronologies of Swiss needle cast impact were calculated such that negative values indicate increasing disease impact and reduced tree growth.

For correlations with climate, the difference between the Tillamook Lower Douglas-fir and Cape Perpetua Douglas-fir detrended chronologies was used due to the fact that Swiss needle cast appeared to have the least effect on trees at the southernmost site, and species-specific growth patterns could be better eliminated using Douglas-fir instead of hemlock. For the Swiss needle cast impact chronology, relationships with climate were negative and strongest from March through August with respect to air temperature and MEI (Figure 7A). High values of MEI indicate warm ocean conditions, such that all correlations suggested that warm temperatures in the spring, summer, and early fall are associated with greater Swiss needle cast severity and reduced radial growth. Thus, the inverse of the Swiss needle cast index (index * -1) was calculated to more clearly illustrate that disease progression was consistent with long-term warming trends in mean March through August temperature (Figure 7B). Even when the Swiss needle cast and temperature time series were detrended using cubic splines set at a 50% frequency response of 30 years to remove long-term trends, relationships were still significant ($R^2 = 0.11$; $p < 0.01$).

Correlations between monthly NOAA NCDC temperature, precipitation, and PDSI at Euchre Mountain and Cape Perpetua, the sites with what appeared to be minimal Swiss needle cast impacts, indicated that hemlock and Douglas-fir were both modestly sensitive to summertime (July and August) moisture stress. At Euchre Mountain, hemlock and Douglas-fir significantly ($p < 0.05$) and positively correlated with current and prior July precipitation, while western hemlock positively correlated with prior August and September PDSI. At Cape Perpetua, Douglas-fir positively ($p < 0.05$) correlated with prior July and August precipitation and negatively correlated with current July and prior July to August temperatures. Western hemlock negatively correlated with current June through August temperatures and prior July temperatures. Overall, correlations were weak, and no correlation coefficient exceeded a value of 0.25 (data not shown).

4. Discussion

The tree-ring analyses employed in this study identified substantial growth reductions in Douglas-fir at the two Tillamook sites, consistent with the impacts of Swiss needle cast. Other potential causes of these suppressions could have included stand dynamics or species-specific responses to climate. Yet baseline climate-growth relationships were modest and reflected sensitivity to summertime drought for both species. Thus, contrasting responses to climate was an unlikely explanation for such strong divergences between Douglas-fir and western hemlock. Differences in growth could also have arisen if each species had experienced unique disturbance or developmental histories within the site. However, western hemlock and Douglas-fir were mixed at all three sites, and sampling was spread as evenly as possible throughout each stand. Moreover, all sampled trees were dominant or codominant, and we found no evidence that Douglas-fir was being outcompeted or overtopped by western hemlock. Indeed, the site at which Douglas-fir reductions were the greatest had by far the lowest tree densities or basal areas per hectare. Throughout the tree-ring records, the only time

Douglas-fir experienced greater growth rates than western hemlock was during the first twenty years of the chronologies, especially at Tillamook Upper. Yet this difference could be explained by the tendency of Douglas-fir to more rapidly colonize the site and outgrow western hemlock in the early phases of stand development.

Given their timing, locations, and synchrony, Swiss needle cast was the most likely cause of the profound Douglas-fir growth reductions identified in the tree-ring record. Although the disease is believed to be endemic to the Pacific Northwest, historically Swiss needle cast has only mildly affected Douglas-fir. While comparing the differences in disease severity between Europe and western North America, Boyce (1940) stated: “Within the natural range of Douglas-fir in western North America the fungus has been present for many years, although it passed unnoticed…because there the fungus is either not at all or so negligibly injurious to the host that it is easily overlooked.” However, over the past thirty years has the disease become a significant forest health problem (Hansen *et al.*, 2000). Beginning in the early 1980s, Swiss needle cast was reported as the cause of severe yellowing and needle loss in young Douglas-fir plantations from southwest Washington to western Oregon (Hansen *et al.*, 2000). Also, in a May 1984 memo to the Bureau of Land Management, the US Forest Service Director of Forest Pest Management for the Pacific Northwest Region noted “extensive foliage discoloration and needle loss” in Douglas-fir near Tillamook, OR. Affected Douglas-fir ranged from saplings to old growth, and “close examination of Douglas-fir needles from most trees in the Tillamook area revealed infection by *Phaeocryptopus gaumannii*, cause of Swiss needle cast.”

According to the tree-ring record, Douglas-fir at Tillamook Upper and Tillamook Lower entered a prolonged period of reduced radial growth starting in 1984, coincident with observers' records of widespread needle discoloration and loss in the region (Figures 2, 3, 4). Transient, less severe reductions in Douglas-fir radial growth occurred much earlier at Tillamook Lower, suggesting that Swiss needle cast had a longer history on the landscape. Yet these radial growth suppressions were much less pronounced, and associated foliage yellowing or loss may have been too minor or localized to attract attention. The dramatic growth reductions that occurred in 1984 dated exactly with the first written reports of disease-related impacts on the landscape, suggesting that tree-ring suppressions were indeed the result of Swiss needle cast and that disease had reached unprecedented severity, at least in the context of the past eighty years.

After 1984, the tree-ring record corroborates other lines of evidence that Swiss needle cast is progressively worsening. In an analysis of ten- to thirty-year-old Douglas-fir plantation trees, Maguire *et al.* (2002) found significant losses in cubic volume growth beginning in 1990. In the most severely affected stands, percentage growth loss consistently ranged from thirty to sixty percent, with the greatest losses in 1992 and 1996, the last year included in the study. By 1996 an annual aerial survey of Douglas-fir forests was initiated for the western Oregon Coast Range (Hansen *et al.*, 2000; ODF, 2009). Over the past four years, aerial detection surveys have identified more than 121400 ha of Douglas-fir forests with visible Swiss needle cast symptoms, more than any previous year with the only exception of 2002 (ODF, 2009). On a somewhat longer timescale and from the perspective of radial growth, the tree-ring records developed for this study demonstrate the disease progressed episodically, discretely worsening after 1984 and then again after 1996.

Although increasing severity of the disease is evident, the exact degree of Douglas-fir growth reduction in comparison to western hemlock may have been somewhat overestimated. As Douglas-fir declined, western hemlock could have experienced a gradual growth release and thereby inflated estimates of Douglas-fir suppression. According to a linear regression, mean western hemlock growth rates at Tillamook Lower did significantly ($p = 0.02$) increase from 1984 to present, the time period with the greatest disease impacts. This increase occurred only at Tillamook Lower and averaged 0.41 mm per decade. If this increasing growth rate is removed from the hemlock chronology, the percent difference in growth with Douglas-fir changes only minimally from 84% to 79% for the interval 1984 to 2006, and remains highly ($p>0.001$) statistically significant. Moreover, the increased incidence of severe suppressions and locally absent rings corroborate profound Douglas-fir growth reductions at this site over the past twenty-five years.

Impacts of Swiss needle cast are by no means homogenous across the landscape and vary at a range of spatial scales. In general, Swiss needle cast tends to be more severe near the coast, especially at low-elevation and south-facing aspects with summer drizzle and exposure to summertime fog (Manter *et al.*, 2003; Rosso and Hansen, 2003). Indeed, Tillamook Upper and Lower were both south-facing, of which Tillamook Lower was most heavily impacted, while Euchre Mountain was relatively high in elevation and north-facing (Table 2). Tillamook Lower also contained a large component of Sitka spruce and red alder, indicative of a strong maritime influence. However, no evidence of growth decline due to Swiss needle cast was detected in Douglas-fir at Cape Perpetua despite a south aspect, close proximity to the coast, and an elevation (260 m) identical to that of Tillamook Lower. Douglas-fir at Cape Perpetua were four times as old as western hemlock (and trees at any of the other three study sites), preventing direct comparisons between the two species. Yet no growth suppressions equivalent to those at Tillamook occurred in the 400-year tree-ring record (data not shown). Moreover, yellow foliage and *P. gaeumannii* pseudothecia were evident in younger stands immediately adjacent to the Cape Perpetua and Euchre Mountain study sites. Thus, additional microsite variables as well as stand age are almost certainly involved in the observed patterns of Swiss needle cast severity. For example, older stands may have inherent buffers to the disease associated with lower tree densities, trees with deeper, more shaded crowns, and a highly developed overstory that better protects against environmental extremes. It is also notable that not only were basal areas and frequencies of Douglas-fir low at Tillamook Lower, but so were total basal area and tree frequency across all species (Table 1). Total dominance was half that of Euchre Mountain or Tillamook Upper, suggesting that Tillamook Lower may have been an unusually unproductive site. If this is indeed the case, a combination of particularly unfavorable climatic and edaphic site conditions may help explain the tremendous growth reductions experienced by Douglas-fir over the past thirty years.

To date, analyses of climate and Swiss needle cast have involved laboratory experiments or field studies across broad spatial scales, but over a limited number of years (Rosso and Hansen, 2003; Manter *et al.*, 2005; Stone *et al.*, 2007). By contrast, tree-ring records in this study provided uniquely long time series of growth for comparison with instrumental climate records, but over a limited number of sites. In general, past studies have identified that warmer wintertime temperatures are correlated with greater Swiss needle cast severity, not only in Oregon (Rosso and Hansen, 2003; Manter *et al.*, 2005), but also for Douglas-fir forests in New Zealand (Stone *et al.*, 2007). Spring and summertime needle wetness also appear to favor the disease (Rosso and Hansen, 2003; Stone *et al.*, 2008) as long as summertime temperatures are relatively low (Rosso and Hansen, 2003). Thus, warm winters and cool, wet, and foggy springs and summers should correspond with greater Swiss needle cast severity, and these climate-growth relationships loosely correspond to those identified for tree-ring data.

In this study, an index of the disease was most strongly related to late-winter through springtime temperatures as well as mid-summer temperatures, such that warm temperatures were associated with reduced radial growth and presumably greater disease impact. Notably absent were any relationships with precipitation, PDSI, or wintertime temperatures, and correlations with summertime temperatures were opposite from what was expected. However, the final climate-growth relationships for the disease index must be interpreted with caution. For example, the negative correlations with July and August temperatures may still be an artifact of Douglas-fir's sensitivity to hot and dry summers, especially if Douglas-fir's underlying climate-growth relationships varied between sites. A second consideration is that other studies relating Swiss needle cast to climate have used much younger trees and either relative abundance of *P. gaeumannii* pseudothecia on needles or total foliage retention as metrics of the disease (Rosso and Hansen, 2003; Manter *et al.*, 2005; Stone *et al.*, 2008). By contrast, radial growth is a biological response and an indirect measure of disease in comparison to a direct measure of fungal abundance. Finally, the Swiss needle cast index is based on growth patterns from only two sites, and the climate variables associated with the disease on a landscape scale may not associate as strongly at these single stands. To better address these uncertainties, a larger number of sites must be incorporated to quantify climate influences.

Previous to the current epidemic of Swiss needle cast, another foliage disease of Douglas-fir was considered important; Rhabdocline needle cast, caused by a complex of *Rhabdocline* species (Parker and Reid, 1969; Hansen and Lewis, 1997). Our current understanding of Rhabdocline needle cast is that in western Oregon it is strongly associated with off-site stock, and especially with interior Douglas-fir (*P. menziesii* ssp. *glauca*) seed sources planted in the Oregon Coast Range (Hansen and Lewis, 1997). The disease is also associated with unusually wet spring weather, especially if this continues for several years, and high-humidity micro-sites (Goheen and Willhite, 2006). Although our analysis is focused on impacts from Swiss needle cast, we cannot completely rule out a role from Rhabdocline needle cast in the past. However, growth declines from the early 1980s to present are almost certainly due to Swiss needle cast, given the history of accounts and surveys from the Tillamook study sites and the fact that *Rhabdocline* species infrequently occur in the study area (Hansen *et al.*, 2000).

5. Conclusion

In conclusion, tree-ring chronologies capture multidecadal, annually resolved growth declines in Douglas-fir associated with Swiss needle cast. Previous studies have almost exclusively involved young plantation Douglas-fir with seed from off-site origin. The results of this study indicate that Swiss needle cast can also substantially impact the growth of naturally regenerated overstory trees, even in mixed-species stands. In comparison with hemlock, these growth reductions have exceeded 80% over the last twenty years. Though this estimate may be somewhat inflated if western hemlock experienced growth releases concurrent with Douglas-fir decline, Swiss needle cast nonetheless appears capable of profound reductions in growth-increment width. Moreover, growth declines at Tillamook Lower began several decades prior to the first records of Swiss needle cast outbreaks in the region, providing a longer history of the disease. In addition, these tree-ring data corroborate that the impacts of Swiss needle cast continue to worsen in the western Oregon Coast Range. They also corroborate that Swiss needle cast is associated with climate, especially long-term warming trends during the late winter and early spring.

From a management perspective, the results of this study indicate that naturally regenerated older trees are susceptible to Swiss needle cast, and that younger trees will not simply “outgrow” the disease. Growth may be substantially reduced, even in trees more than 100 years in age. From an ecological perspective, coastal forests are among the most productive in the world, and continuing intensification of Swiss needle cast could alter forest composition, dynamics, and carbon sequestration. More replicates will be necessary to better estimate the synchrony of radial growth losses across the landscape, the timing at which significant losses began, and the sites that are most vulnerable. In addition, stands with older trees should be sampled to determine whether declines occurred prior to the 20th century. For now, however, this study demonstrates that Swiss needle cast is a significant pathogen even in mature forests and that tree-ring analysis is an important resource for quantifying the historical dynamics of this disease.

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Figure Legends

Figure 1. Locations of the three study sites for this analysis, Tillamook Upper, Tillamook Lower, and Euchre Mountain. Tillamook Upper and Lower are only 1 km apart

and are not separated at this scale. Cape Perpetua, the location of an additional Douglas-fir chronology, is also noted.

Figure 2. Tree-ring chronologies for each of the three stands. Chronologies were developed by averaging all measurement time series with respect to species and site for A) Tillamook Lower, B) Tillamook Upper, and C) Euchre Mountain. 95% confidence intervals are included. Shaded areas denote years in which Douglas-fir growth is significantly lower than that of hemlock. For all three sites, the only period in which Douglas-fir growth is greater than hemlock was at Tillamook Upper between 1940 and 1948.

Figure 3. The percentage of trees with a suppression index that exceeded 100% (moderate suppression) and 200% (major suppression) at A) Tillamook Lower Douglas-fir, B) Tillamook Lower western hemlock, C) Tillamook Upper Douglas-fir, and D) Tillamook Upper western hemlock. The suppression calculation was also applied to the master chronologies.

Figure 4. The percentage of Douglas-fir with a locally absent ring at A) Tillamook Lower and B) Tillamook Upper. C) The total number of Douglas-fir trees included in the analysis.

Figure 5. The percent difference between mean hemlock growth (in mm) that of each Douglas-fir (in mm). Percent difference was calculated as Douglas fir minus hemlock, and the difference divided by hemlock. Negative values indicate low growth in Douglas-fir relative to hemlock. Growth was compared over two intervals: from 1984 to 2008 and also from 1996 to 2008. 95% confidence intervals are shown.

Figure 6. The difference between the detrended master chronology of Douglas-fir at Tillamook Lower and the detrended master chronologies of i) western hemlock at Tillamook Lower, ii) Douglas-fir at Euchre Mountain, and iii) Douglas-fir at Cape Perpetua. All chronologies were first normalized to a standard deviation of one and a mean of zero over the common interval of 1930 to 2006. Negative values indicate low growth for Tillamook Lower Douglas-fir. Heavy lines are smoothing splines to emphasize decadal trends.

Figure 7. A) Correlations between the Swiss needle cast index (the difference between the Tillamook Lower and Cape Perpetua Douglas-fir chronologies) and monthly-averaged air temperature (temp) and Multivariate ENSO Index (MEI). Months span the prior (lagged) November through current December. * indicates significant correlations ($p < 0.01$). B) Relationship between average March through August temperature and the inverse of the Swiss needle cast index ($R^2 = 0.22$; $p < 0.001$) (both normalized to mean = 0; std dev = 1). Warm temperatures are associated with reduced radial growth and presumably favorable disease conditions.

Table 1. Frequency, density, and dominance values for overstory species at the three study stands

A) Tillamook Lower

Species	Frequency (12 plots)	Density (stems / ha)	Dominance (m^2 / ha)	Relative frequency	Relative Density	Relative dominance	Relative importance
Alnus rubra	1	8.3	1.9	4.2	3.4	1.1	2.9
Picea sitchensis	9	91.7	80.6	37.5	37.9	46.6	40.7
Pseudotsuga menziesii	5	41.7	22.9	20.8	17.3	13.3	17.1
Tsuga heterophylla	9	100.0	67.4	37.5	41.4	39.0	39.3
Totals	24	241.7	172.8	100.0	100.0	100.0	100.0

B) Tillamook Upper

Species	Frequency (5 plots)	Density (stems / ha)	Dominance (m^2 / ha)	Relative frequency	Relative Density	Relative dominance	Relative importance
Alnus rubra	2	30.0	12.2	15.4	6.0	3.6	8.3
Picea sitchensis	2	50.0	38.7	15.4	10.0	11.4	12.3
Pseudotsuga menziesii	4	150.0	154.0	30.8	30.0	45.2	35.3
Tsuga heterophylla	5	270.0	135.6	38.5	54.0	39.8	44.1
Totals	13	500.0	340.5	100.0	100.0	100.0	100.0

C) Euchre Mountain

Species	Frequency (6 plots)	Density (stems / ha)	Dominance (m^2 / ha)	Relative frequency	Relative density	Relative dominance	Relative importance
Pseudotsuga menziesii	6	208.3	343.6	50.0	69.4	81.6	67.0
Tsuga heterophylla	6	91.7	77.7	50.0	30.6	18.4	33.0
Totals	12	300.0	421.3	100.0	100.0	100.0	100.0

Table 2. Site and chronology attributes

	elevation	aspect	slope	chronology	interseries correlation[1]	mean sensitivity[2]	number of cores	pith date[3]	absent rings[4]
Tillamook Lower	260 m	210° (SSW)	15%	Douglas-fir	0.65	0.41	23	1927	78
				western hemlock	0.43	0.26	21	1932	0
Tillamook Upper	520 m	230° (SW)	20%	Douglas-fir	0.56	0.22	21	1931	12
				western hemlock	0.38	0.22	19	1925	0
Euchre Mountain	410 m	330° (NNW)	15%	Douglas-fir	0.48	0.21	21	1882	2
				western hemlock	0.35	0.28	19	1887	4

[1] The average correlation between each detrended measurement time series (using a 22-year cubic spline) and the average of all other detrended measurement time series as output by COFECHA

[2] An index of high-frequency variability that ranges from 0 (no variability) to 2 (highly variable), as output by COFECHA

[3] Mean pith date at breast height

[4] Frequency per thousand of locally absent rings

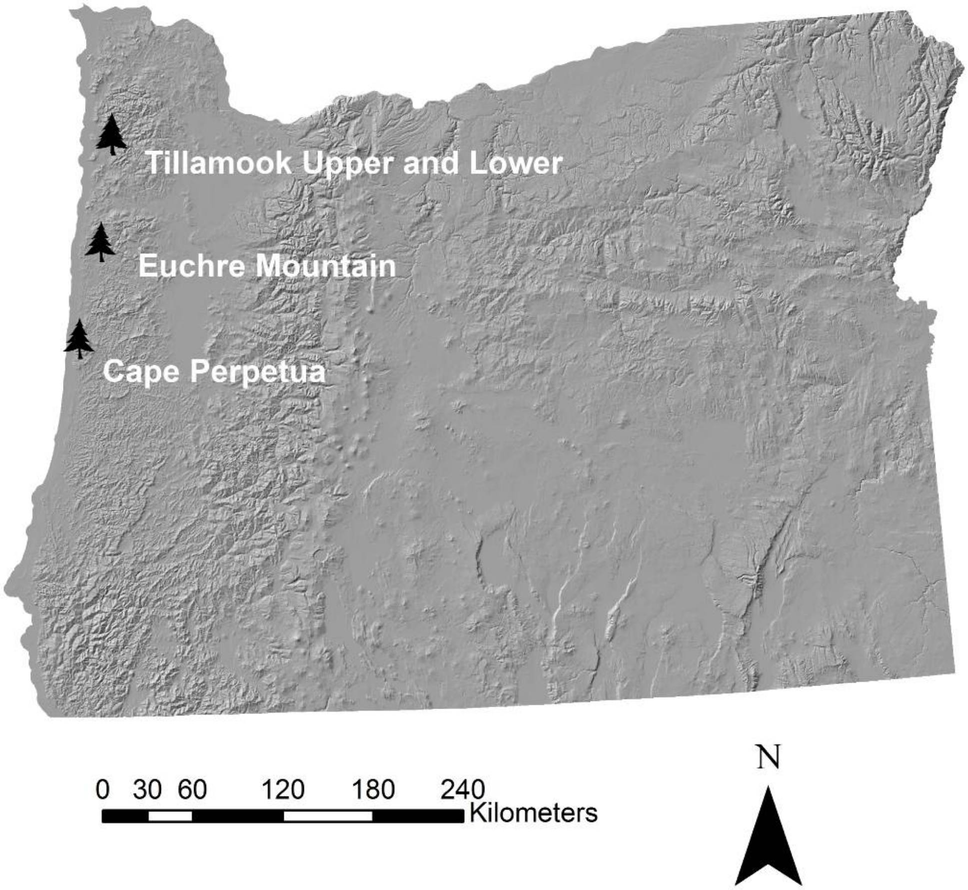

Tillamook Upper and Lower
Euchre Mountain
Cape Perpetua
0 30 60 120 180 240
Kilometers
N

Figure 1

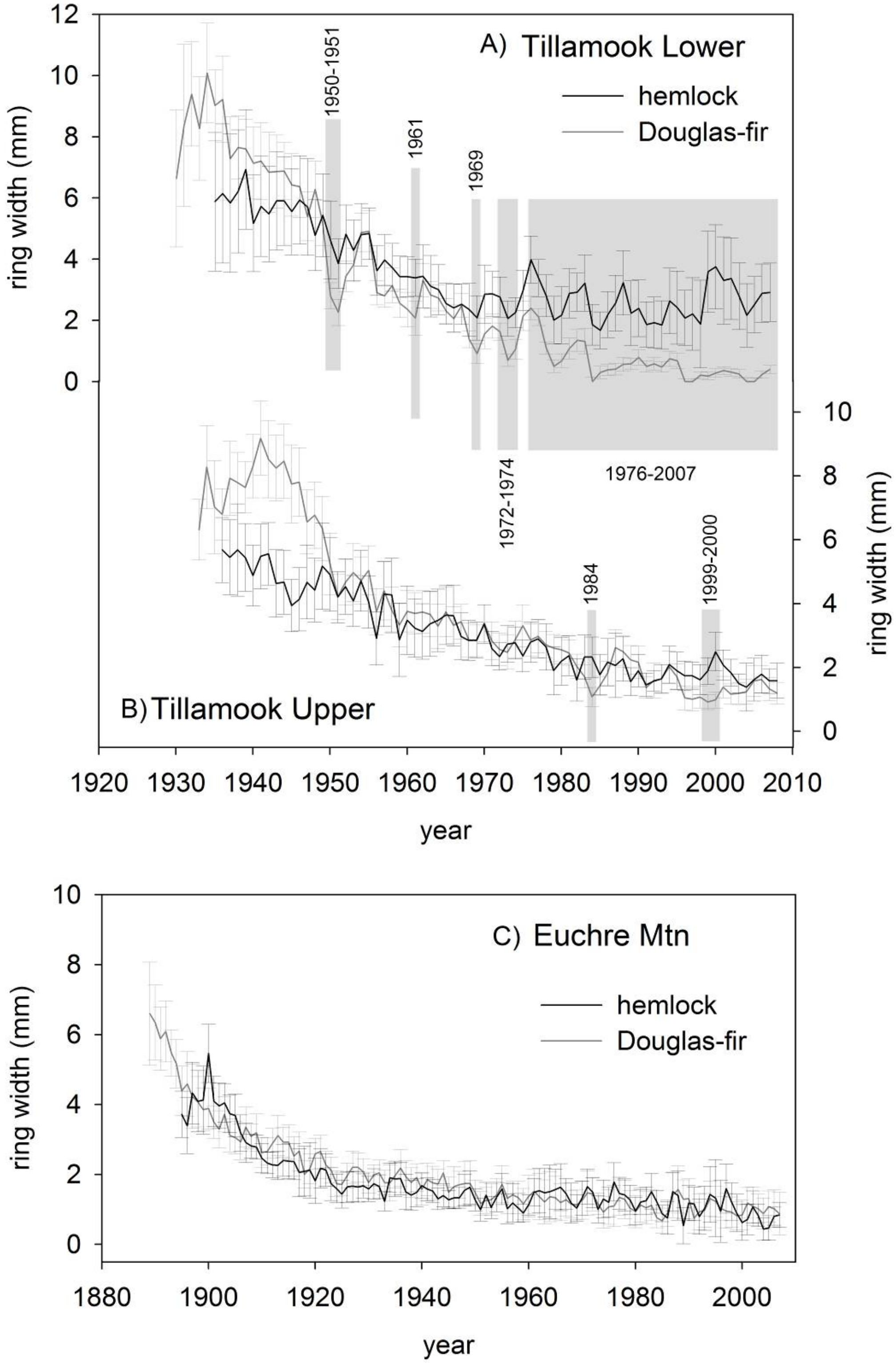

A) Tillamook Lower
hemlock
Douglas-fir
ring width (mm)
12
10
8
6
4
2
0
1950-1951
1961
1969
1972-1974
1976-2007
B) Tillamook Upper
1984
1999-2000
ring width (mm)
10
8
6
4
2
0
1920
1930
1940
1950
1960
1970
1980
1990
2000
2010
year
C) Euchre Mtn
hemlock
Douglas-fir
ring width (mm)
10
8
6
4
2
0
1880
1900
1920
1940
1960
1980
2000
year

Figure 2

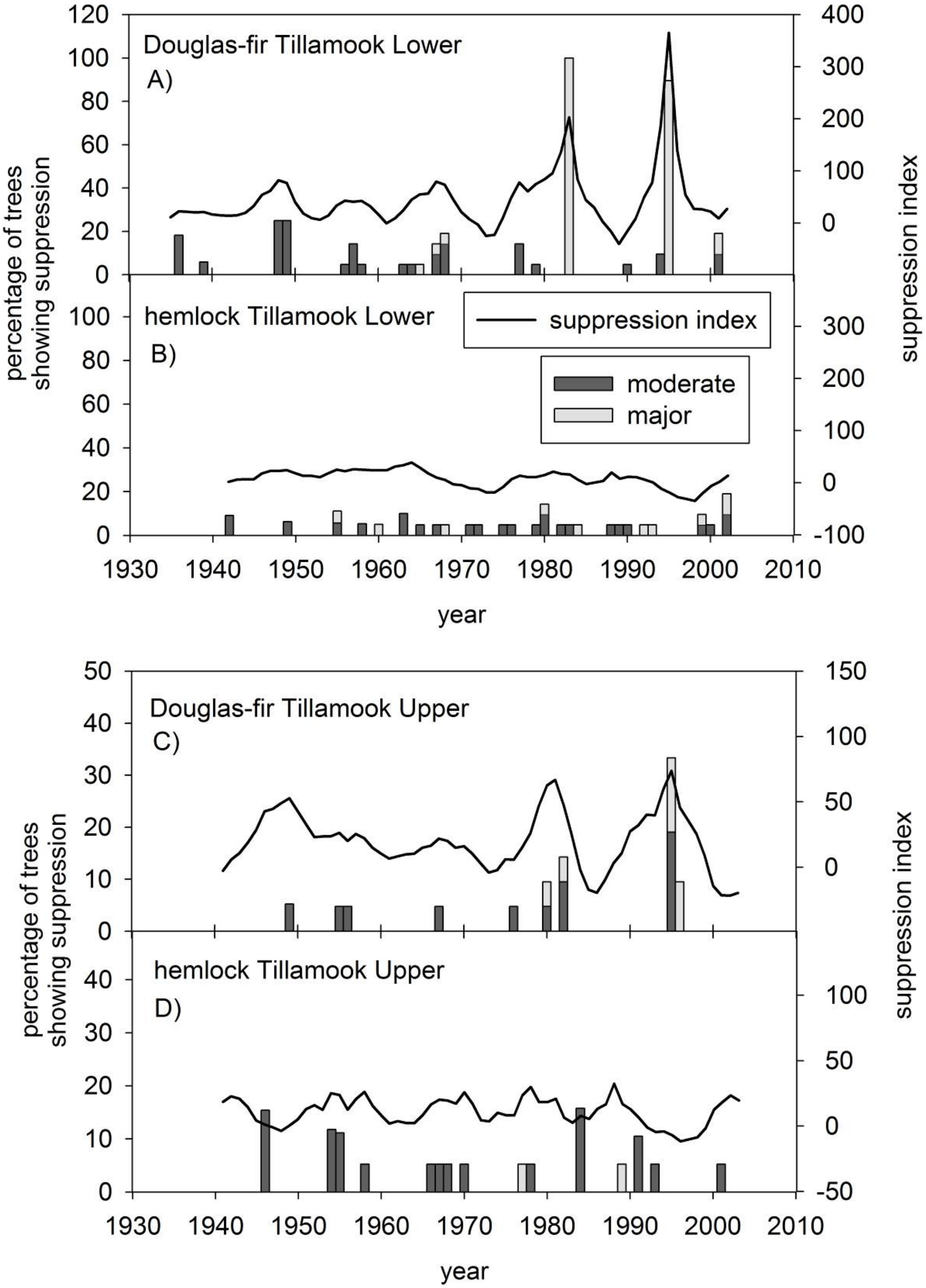

Douglas-fir Tillamook Lower
A)
hemlock Tillamook Lower
B)
suppression index
moderate
major
Douglas-fir Tillamook Upper
C)
hemlock Tillamook Upper
D)
percentage of trees showing suppression
suppression index
year
120
100
80
60
40
20
0
400
300
200
100
0
-100
50
40
30
20
10
150
50
-50
1930
1940
1950
1960
1970
1980
1990
2000
2010

Figure 3

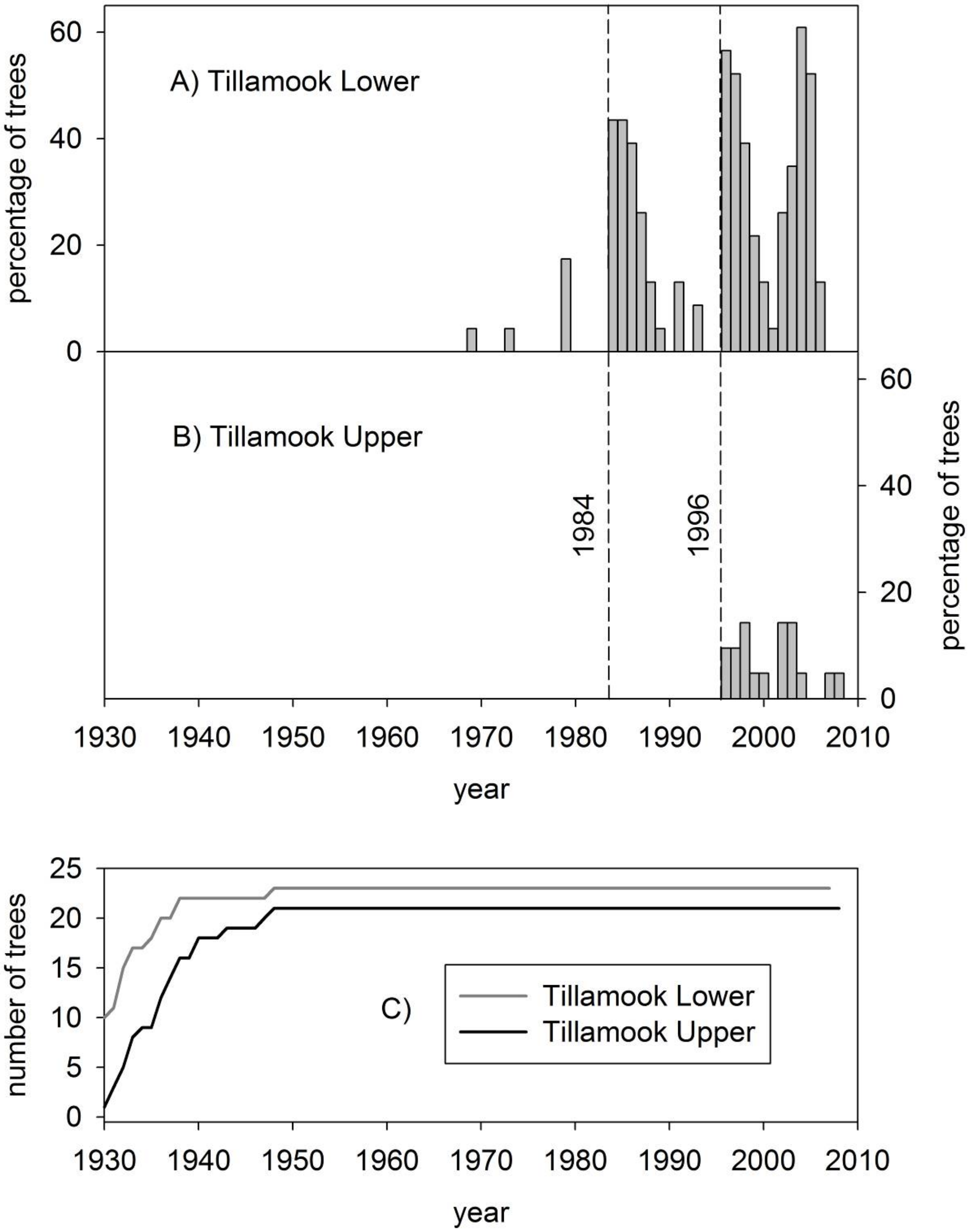
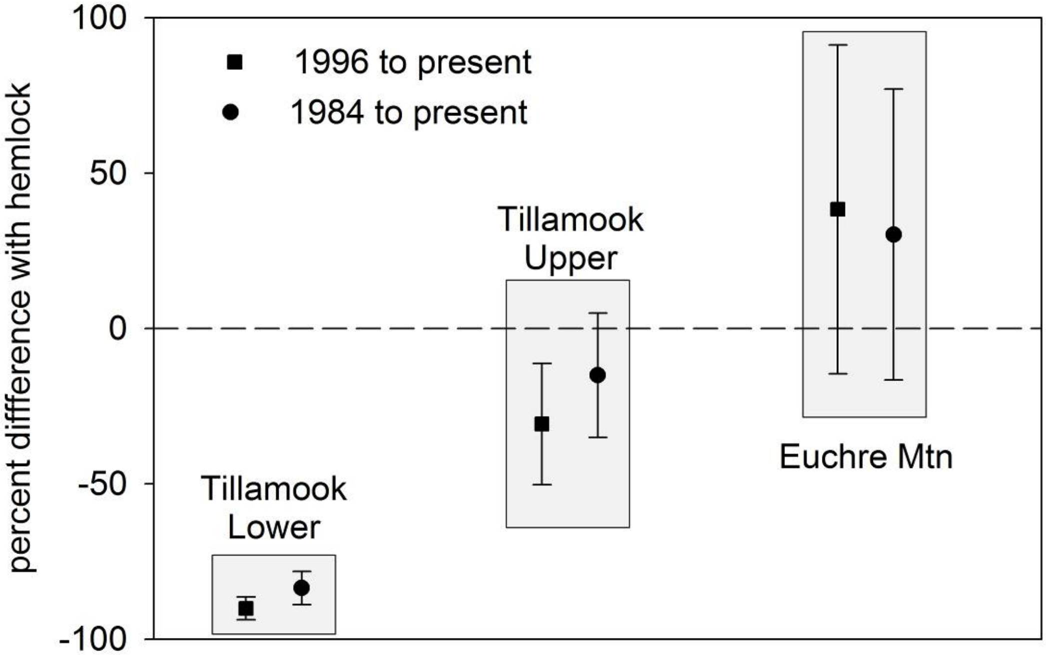

A) Tillamook Lower
B) Tillamook Upper
percentage of trees
60
40
20
0
1984
1996
1930
1940
1950
1960
1970
1980
1990
2000
2010
year
C)
Tillamook Lower
Tillamook Upper
number of trees
25
20
15
10
5
0
year

Figure 4



100
50
0
-50
-100
percent difference with hemlock
■ 1996 to present
● 1984 to present
Tillamook Lower
Tillamook Upper
Euchre Mtn

Figure 5

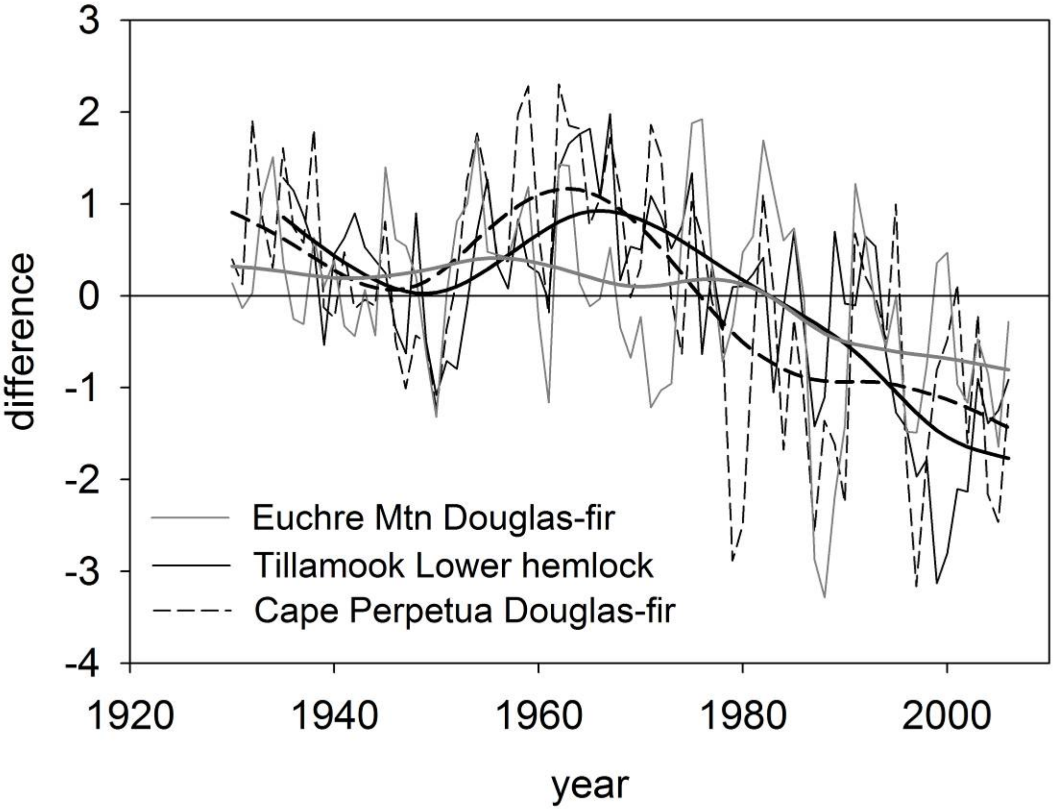

3
2
1
0
-1
-2
-3
-4
difference
1920
1940
1960
1980
2000
year
Euchre Mtn Douglas-fir
Tillamook Lower hemlock
Cape Perpetua Douglas-fir

Figure 6

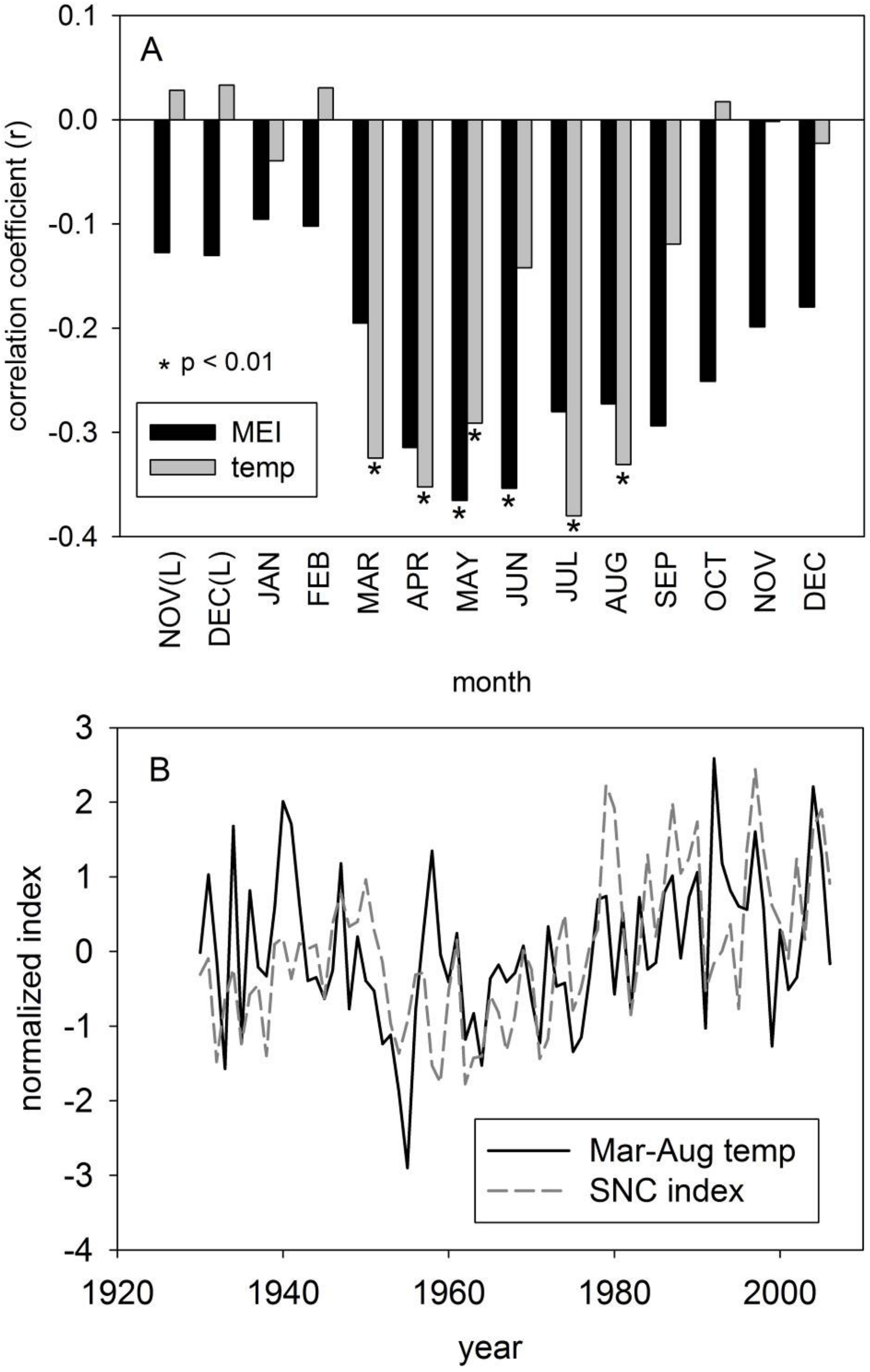

A
correlation coefficient (r)
0.1
0.0
-0.1
-0.2
-0.3
-0.4
* p < 0.01
MEI
temp
*
NOV(L)
DEC(L)
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
month
B
normalized index
3
2
1
0
-1
-2
-3
-4
Mar-Aug temp
SNC index
1920
1940
1960
1980
2000
year

Figure 7