

Article

The Long-Term Effects of Wind Disturbance on a Sitka Spruce-Western Hemlock Forest

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Abstract: Wind is an important disturbance in many forested regions, but research has largely focused on immediate to short-term (<10 years) effects on species composition and structure of stands and landscapes. We used a set of ten, 0.4-ha plots established in 1935 and measured every 5–13 years to examine the cumulative effects of multiple wind disturbance events in the coastal forests of Oregon. Since 1935 there have been ten documented wind events in coastal Oregon with hurricane-force winds. Most of the eight windstorms since 1962 noticeably influenced at least one plot; however, no individual storm clearly influenced all plots. Net rate of biomass accumulation of plots was negative when biomass mortality exceeded 29–41 Mg/ha per 5-year period (or 3.4%–5.8% per 5 years). In contrast, wind disturbance did not clearly reduce NPP (Net Primary Production) in any plot until biomass mortality exceeded 50%. Major wind-related mortality episodes in individual plots did not necessarily strongly influence the average loss of biomass across all plots. For example, a biomass loss of 88% in one plot resulted in an average loss of only 3.4% across all plots. In contrast, the cumulative effect of multiple plots with repeated wind-related mortality did decrease biomass at the multi-plot level. Depending on the plot, wind caused 16%–59% of the total mortality over time, and the proportion of wind-related mortality has increased 5- to 8-fold since 1940. The majority (80%) of wind-related mortality was “immediate”, but some trees survived up to 35 years after being significantly wind damaged. Despite western hemlock having a wind-related mortality rate that was at least twice that of Sitka spruce, the number of stems of the former species increased over time. This trend may be related to the predominant recovery mechanism which was the release of existing small trees and the fact that the majority of ingrowth was western hemlock. This study suggests that wind disturbance is a heterogeneous, gradual process and that while individual events have a detectable impact on structure and function, the largest impacts, at least in systems where it reoccurs each decade, are cumulative.

Keywords: cumulative effects; disturbance; forest regeneration; mortality; long-term change; permanent plots; windthrow

1. Introduction

Many processes lead to periodic pulses of mortality in forest stands and landscapes which can result in changes of forest structure and function that are evident for decades to centuries [1]. These disturbance effects are dependent on the spatial scale examined, as well as the spatial heterogeneity of the disturbance: the death of a few trees can lead to significant change at the scale of 100 m², but may be viewed as part of “normal” mortality at the scale of more than 1 ha. Different disturbances may lead to similar cumulative mortality over broad regions, but those with diffuse spatial patterns will have less-apparent broad-scale impact on structure and function than those that are concentrated. The realization that disturbance expresses itself differently depending on hierarchical

level has meant that perspectives on disturbance have evolved from the simple idealized case in which these disturbances completely “reset” the system to one in which disturbances create heterogeneous mosaics of structural and functional change [2].

The coastal forests of Oregon provide an example of the heterogeneous, hierarchical mosaic of disturbance. In this region, fire and wind are the primary processes causing major episodes of mortality that lead to long-term structural and functional change. In some ways, fire and wind disturbance are opposites in terms of temporal and spatial patterns. Fires are infrequent to rare in this region given the wet climate, with an approximate return interval of 230 years [3], but when climatic and weather conditions are favorable, fires do occur, and they are often severe because of the high accumulation of fuels [4]. In contrast, winds of sufficient velocity to fell trees occur most every year in the region, while severe wind events with hurricane-level winds in excess of 119 km per hour (74 miles per hour), occur on average once every 25 years for any given location [5]. Fire disturbance can be quite extensive, but even historically large, severe fires such as the Tillamook and Nestucca burns modified only a small fraction ($\approx 6\%$) of the Oregon Coast Range landscape [6,7]. In comparison, high wind events, such as the 1962 Columbus Day Storm, can impact areas larger than the Oregon coastal region [8,9], even though patches of high mortality are often localized [10]. Thus, despite influencing over 20 times more area than the 1933 Tillamook burn, the 1962 Columbus Day Storm killed a similar volume of timber: 11 billion board feet versus 10 billion board feet, respectively [6–8].

The broad-scale spatial and temporal patterns created by these two types of disturbances in coastal Oregon have been examined by Harcombe et al. [11], as has the importance of wind-related mortality on forest growth [12,13]. However, there has not been a detailed examination of how repeated wind disturbance has influenced these forests at a fine scale over long time periods. Indeed, as noted by Mitchell [14], “the long-term and cumulative impacts of recurrent windthrow are often over looked by scientists and managers”. We therefore conducted a descriptive study using a set of ten, 0.4-ha plots established in 1935 and measured periodically since then to address the following questions regarding wind at the scale of the individual plot (0.4 ha) and all plots (4.0 ha):

1. Is there a correspondence between major windstorms, defined as those with hurricane-strength winds, and the occurrence of major tree mortality periods?
2. What is the magnitude of major tree mortality periods and at what magnitudes are there net losses in tree density and biomass?
3. What are the specific mechanisms of overall (e.g., suppression) and wind-related mortality (e.g., breakage, uprooting, and crushing), and how many trees involved in the latter are associated with “immediate” versus delayed mortality?
4. To what degree are pulses of tree ingrowth related to major tree mortality periods, and what is the time lag in tree ingrowth after a major tree mortality period?
5. How does net primary productivity (NPP) respond to the magnitude of mortality?

2. Materials and Methods

2.1. Study Area

The plots examined in this study are located in the Cascade Head Experimental Forest north of Otis, Oregon (45.08° N 124.00° W). The elevation ranges from approximately 210 to 500 m and topography of the plot locations is gentle with most slopes less than 20 degrees and most aspects south to southwest. Soil depth was at least 1 m in each plot (Table S1). Distance from the Pacific Ocean ranges from 1.7 to 9.2 km, with the majority of plots more than 5 km from the coast (Figure 1). The climate is classified as warm-summer Mediterranean in the Köppen system, with a mean annual temperature of 10.0 °C and an annual precipitation of 2450 mm. The dominant vegetation consists of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Sitka spruce (*Picea sitchensis* (Bong.) Carrière), although farther inland Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western red cedar (*Thuja plicata* Donn ex

D. Don) are common. In addition, red alder (*Alnus rubra* Bong.) is often present in disturbed stands. Mean site index of western hemlock in the plots is 43.9 m at 100 years of age.

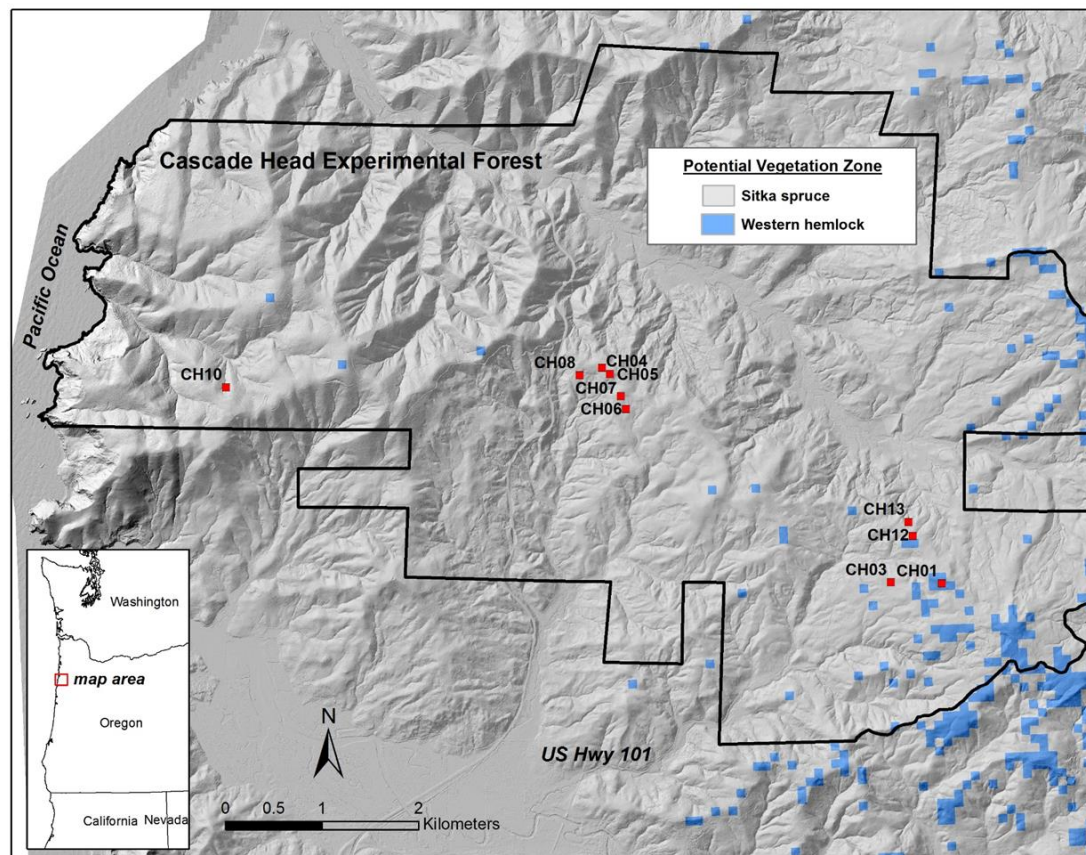


Figure 1. Permanent plot locations in Cascade Head Experimental Forest, Otis, OR, USA, established in 1935 by the US Forest Service.

2.2. Wind Events

Hurricanes do not occur in this region; however, hurricane-force winds (≥ 119 km per hour or ≥ 74 miles per hour) can occur in deep low-pressure systems that initially form in the tropics and approach the Pacific coast from the southwest (thus the regional term “sou-westers”). Although we have no direct record of wind speeds in the plots, we were able to identify major wind events since 1950 from historical records published online [5,15]. We focused on regionally documented storms with winds or gusts reaching at least 119 km per hour (74 miles per hour), of which there have been 10 since 1951, with an estimated return interval of 25 years (Table 1).

Table 1. Windstorms of the central and northern coast of Oregon with gusts of at least 119 km/h (Category 1 hurricane on the Saffir-Simpson Hurricane Wind Scale).

Date	Storm Name	Peak Gusts (mph)	Peak Gusts (kph)	Pressure (mb)
December 2007	Great Coastal Gale	125	201	986
January 2006	Unnamed	103	166	
December 1995	Sinatra Day Storm	100	161	954
January 1993	Inauguration Day Storm	90–100	145–161	976
November 1981	The Double Windstorms	90–100	145–161	960
October 1967	Unnamed	90+	145+	977
March 1963	The Spring Gale	80–100	129–161	982
October 1962	Columbus Day Storm (Typhoon Freda)	130+	209+	960
November 1958	Unnamed	131	211	
December 1951	Unnamed	100	161	

2.3. Plot Measurements

The ten plots we examined were first established in 1935 in 85-year-old forests dominated by Sitka spruce and western hemlock. The initial intent of establishing the plots was to understand growth and yield of this forest type [16]. Although the plots were located subjectively, they represent the range of species composition as well as stand structures present in this location and provide a long-term record of the effects of disturbance in this forest. The plots are 0.404 ha and were slope-corrected during the initial survey. All trees 5.0 cm DBH (diameter at breast height) and larger were tagged with numbered aluminum tags secured with nails. Initial tree densities in the plots ranged from 373 to 884 trees per ha (TPH) and a total of 6448 trees were measured over the course of the study. Tree species and DBH were recorded for all live trees, and the height of a subsample of trees was determined with a measuring tape and clinometer. At 5- to 13-year intervals, the plots were measured and checked for mortality for a total of 12 times amounting to 34,687 tree visits (Table S2). In addition, a mortality check without DBH measurement was conducted on all plots in 1961. Repeat censuses included measurement of DBH using a diameter tape, the tagging and measurement of ingrowth trees that had reached the minimum DBH of 5.0 cm, and documenting tree mortality. During mortality checks, each tree living in previous years was revisited and its status as live or dead was determined. Dead trees were defined as those with no green foliage; however, in the case of trees wind snapped near the base, some green foliage may have been present. The cause of mortality was noted (e.g., suppression, wind, insects) and after 1982, the symptoms associated with the cause were also noted.

2.4. CH06 Reconstruction

One of the plots, CH06, was severely impacted by the 1962 Columbus Day Storm, after which it was salvage-logged and temporarily abandoned until 2005, a period during which the other nine plots were measured seven times. For CH06 we reconstructed the number of trees, bole biomass, ingrowth, mortality, change in biomass, and NPP_b (net primary production of boles) for the missing measurements using tree core data and surveys of post-storm survivors and regeneration. A total of 70 trees alive in 2005 were cored to their pith to determine the time that they reached 5 cm DBH and the rate at which their DBH grew. The majority of these trees established after the 1962 storm; however, three of the trees that survived the windstorm and subsequent timber salvage were also cored to determine their DBH growth rates. In addition, we established eight 30 by 2-m belt transects distributed systematically across the plot and surveyed all dead trees that had reached a DBH of at least 5 cm before dying, noting the species, position (standing versus downed), state of decay, and DBH. We also surveyed the entire plot for trees that survived the windstorm and salvage but had died by 2005, noting the tag number, species, state of decay, and DBH. For all trees that were alive in 2005 we used the core-based growth data to “un-grow” the trees for each virtual measurement period until the tree reached the minimum DBH of 5 cm. For trees that had established after the windstorm, but subsequently died, we assumed that the trees with the largest DBH had established earlier than the ones with the smallest DBH. We then used the relative DBH distribution of the ingrowth based on cored trees to assign the dead trees to ingrowth for different virtual measurement intervals. These trees were then assigned a time interval that they would have died by assuming that the smaller DBH trees would have died before the larger ones. The estimated time these trees lived (period of mortality versus the period of ingrowth) was used with the DBH at the time of death to estimate the growth rate of these trees and estimate the DBH at the virtual measurement intervals. For trees established before the windstorm, but that died afterward, we assumed that the majority of them would have died in the 1983–1998 period based on their extent of decay. The DBH of these trees at the intervals they were alive was estimated by “un-growing” the trees using their DBH at the time of death and the average DBH growth rate of surviving trees.

2.5. Data Analysis

The net change in bole biomass was estimated from the bole biomass at time_{n+x} minus the bole biomass at time_n divided by the number of years (x) between measurements. NPP_b was estimated by summing the change in live bole biomass (including ingrowth) and biomass of mortality for an interval and dividing by the number of years between measurements.

The number of tree stems and biomass were expressed on a per-hectare basis. Bole biomass was estimated with allometric equations from BIOPAK [17]. In addition to biomass at any one time, we computed the biomass associated with ingrowth and mortality. We report ingrowth as the number of stems or biomass for the interval between measurements, and mortality as the annual percentage of trees or biomass dying over the period. Because measurement intervals varied from 5 to 13 years, we standardized mortality rates to an annual basis using the negative compound interest formula of Sheil et al. [18]: $M = 1 - (1 - (N_D/N_L))^{1/t}$, where M is the annual mortality rate, N_D is the number of dead trees during a given measurement interval, N_L is the number of live trees at the previous measurement, and t is the interval of time in years.

While average mortality over an interval is adequate for capturing “typical” or “background” mortality in forests, it underestimates mortality during episodic events such as windstorms. We therefore estimated the percentage of mortality associated with wind events by only considering wind-related mortality causes when they were noted; in the case of CH06 in 1962, all mortality was assumed to be caused by wind. It should be noted that prior to 1982 mortality causes were general in nature and after that more detailed subcategories of causes were noted. For example, after 1982, mortality causes associated with wind included windthrow, windsnap/broken tops, and crushing by falling trees that were assumed to have been toppled by wind. Prior to that time these were all classified as wind mortality.

Given the initial, non-random sampling design, it was not appropriate to use standard statistical tests of significance. We therefore examined how individual plots behaved and also examined trends across plots (i.e., the multi-plot level). For the latter we characterized variation using box and whisker plots indicating the median, the 25th and 75th percentiles (interquartile range), values no more or less than 1.5 times the interquartile range, and outliers. Since it was impossible to experimentally exclude wind, the effects of wind disturbance on biomass were examined by comparing plots with and without major impacts from wind disturbance. We also examined which factors might be associated with plots with and without major impacts from wind disturbance. However, given the low number of plots examined, we were not able to conduct a rigorous statistical analysis.

3. Results

3.1. Correspondence between Major Windstorms and Major Tree Mortality Periods

Most storms since 1962 (Table 1) seem to have notably influenced at least one plot, but none of the plots had major mortality events (i.e., greater than 1% per year) associated with each windstorm (Figure 2, Table S3). CH06 had a major biomass decline associated with the 1962 or 1963 storms, as indicated by an average rate of biomass mortality of 26% per year between 1955 and 1963. However, since much of this mortality occurred within a year, the mortality associated with the 1962 Columbus Day Storm was probably around 88%, based on the estimated biomass before and after this event. Despite the close proximity of four other plots to CH06 (which are also on similar south-facing slopes as CH06), mortality in the other plots associated with the Columbus Day Storm was less than 1% per year for biomass mortality (range 0.23%–0.78% per year) and less than 1.5% per year for TPH mortality (range 0.71%–1.35% per year). However, the rest of the plots seem to have been influenced by other storms occurring since 1962. For example, CH13 had a major biomass mortality pulse of 2.88% per year (3.53% per year for TPH) that may have been associated with a 1971 storm event in which wind speeds did not apparently reach the 119 km/h threshold used in Table 1. A subsequent pulse of biomass mortality of 4.32% per year in CH13 was associated with the 1981 storms. If the majority of

this biomass mortality in CH13 was associated with the wind events, then about 14% and 22% of the biomass was lost to these two events, respectively. CH01 and CH08 appear to have been influenced by the 1993, 1995, and 2007 storms, with 25% to 65% of the biomass killed between 1993 and 2008. Despite the occurrence of ten major storms since 1950, and despite their proximity to other plots, three of the plots (CH04, CH05, and CH10) seem to have not experienced major wind-related mortality over the 78-year study period, although each has had trees die from wind-related causes.

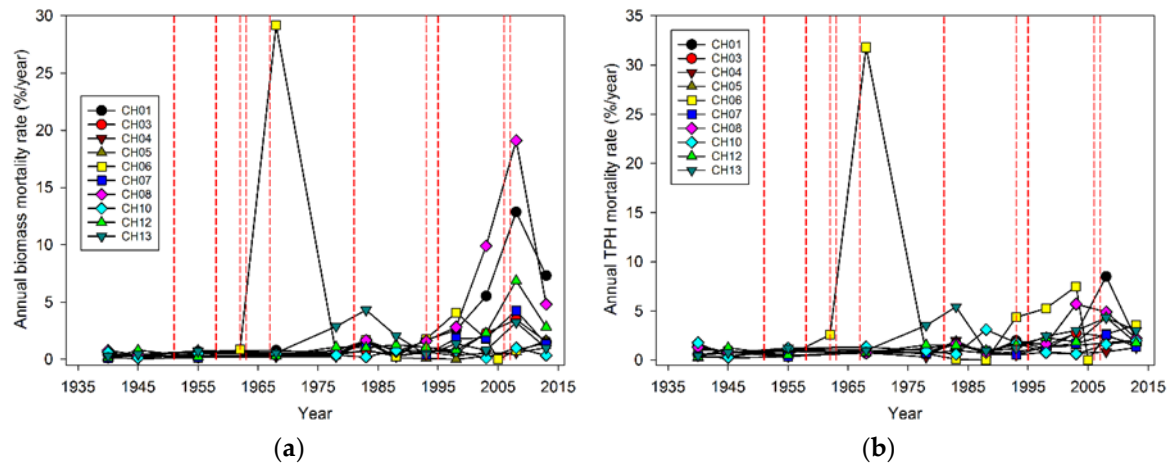


Figure 2. Annual rate of tree mortality (%/year) in each of the ten permanent plots based on (a) bole biomass, and (b) number of trees. The red vertical lines indicate major wind events.

At the plot scale (0.04 ha) the magnitude of wind-related biomass mortality over a 5-year period, the interval of most measurements, ranged from near 0% to more than 88%. However, at the multi-plot scale (here defined as the average condition across the ten plots), the magnitude of biomass mortality related to major windstorms ranged from less than 1.3% (or 0.26% per year) from 1940 to 1945 to a high of 26.5% (or 5.3% per year) from 2003 to 2008 (Figure 3, Table S4). For periods in which there is just “background” mortality, including occasional trees killed by wind, the rate of biomass mortality at the plot scale is less than 1% per year or about 5% over a 5-year measurement period. A similar pattern emerged when trees per ha were considered.

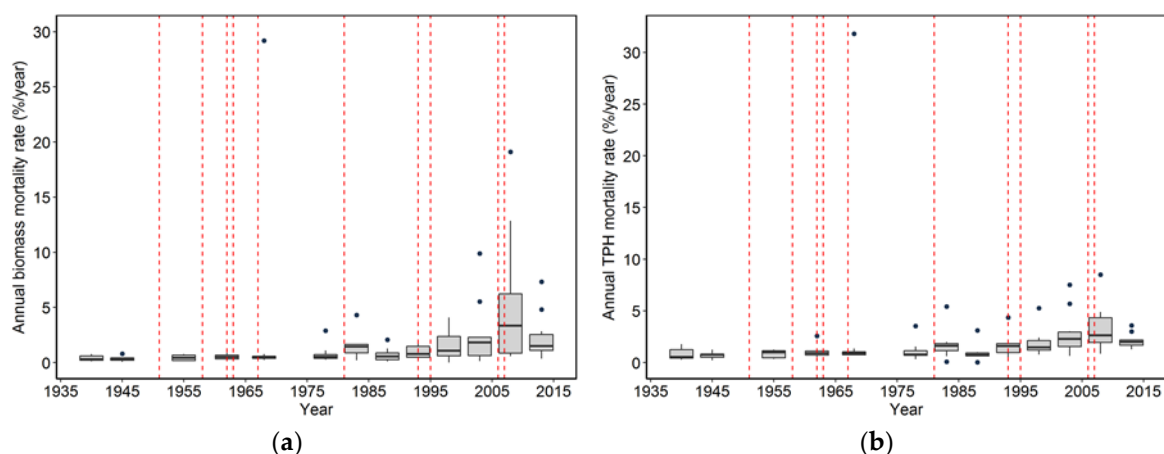


Figure 3. Median and range of the annual rate of tree mortality (%/year) across ten permanent plots based on bole biomass (a), and number of trees per ha (b). Mortality values for 1962 are interpolated for all stands except CH06 which was reconstructed. The red vertical lines indicate major wind events.

3.2. Magnitude of Mortality Causing Live Biomass and TPH to Decrease

In most plots (e.g., CH01, CH03, CH06, CH07, CH08, CH12, CH13), one can detect storms that caused sufficient biomass mortality to negate gains in live biomass; however, this method is not sensitive enough to estimate a threshold amount of mortality needed to cause a biomass decline (Figure 4). An examination of the annual net biomass accumulation versus annual mortality indicates that when biomass mortality exceeds 5.8–8.2 Mg/ha/year (or 29–41 Mg/ha per 5-year period), then the net rate of biomass accumulation is negative (Figure 5). Given the biomass present over the observation period, a biomass mortality percentage of 3.4%–5.8% per 5 years would likely lead to a biomass decline at the plot level.

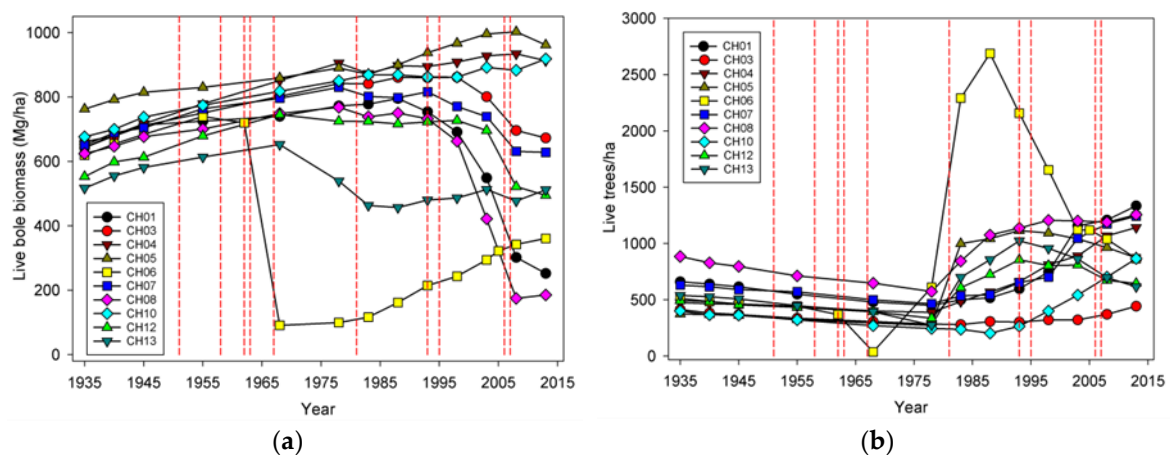


Figure 4. Long-term trends in bole biomass (Mg) per hectare (a) and number of trees per hectare (b) in each of the ten permanent plots at Cascade Head Experimental Forest, Otis, OR, USA. The red vertical lines indicate major wind events.

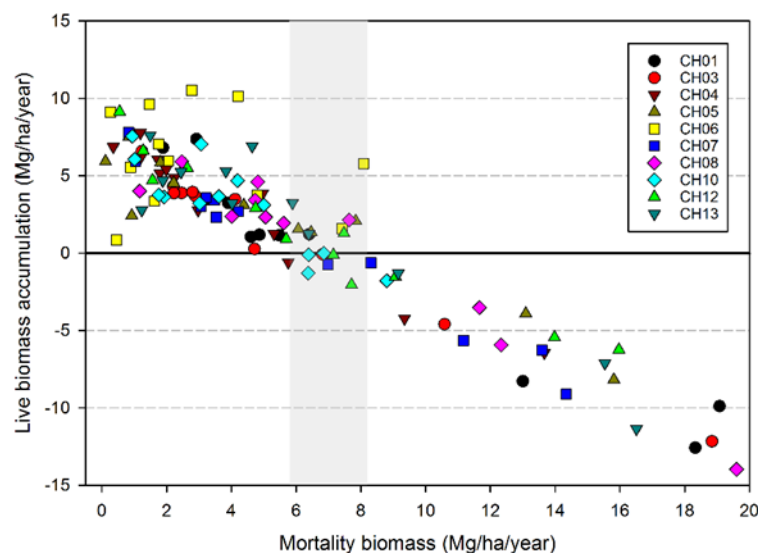


Figure 5. Live biomass accumulation vs mortality biomass, with mortality biomass restricted to <20 Mg/ha/year (outliers go to ~90 Mg/ha/year; see Figure S1 for full range of values). The gray bar indicates uncertainty in the value of mortality that leads to a negative live biomass accumulation (5.8–8.2 Mg/ha/year).

The cumulative effects of wind disturbance on biomass might be best seen by comparing plots with and without major impacts from wind disturbance (Figure 6). Biomass for the three plots that were not impacted by major wind disturbance generally continued to increase (approximately 32%) between 1935 and 2013, with only two intervals at which biomass declined slightly. In contrast, the seven plots that experienced major wind-related losses increased biomass until 1962, and subsequently had major biomass decreases between 1962 and 1968, as well as between 1998 and 2008. The biomass of this set of plots in 2013 was the lowest in the 78-year period of observations and 28% less than in 1935 when the dominant trees were 85 years old. These plots also had a preponderance of initial biomass comprised of western hemlock (74%–97%).

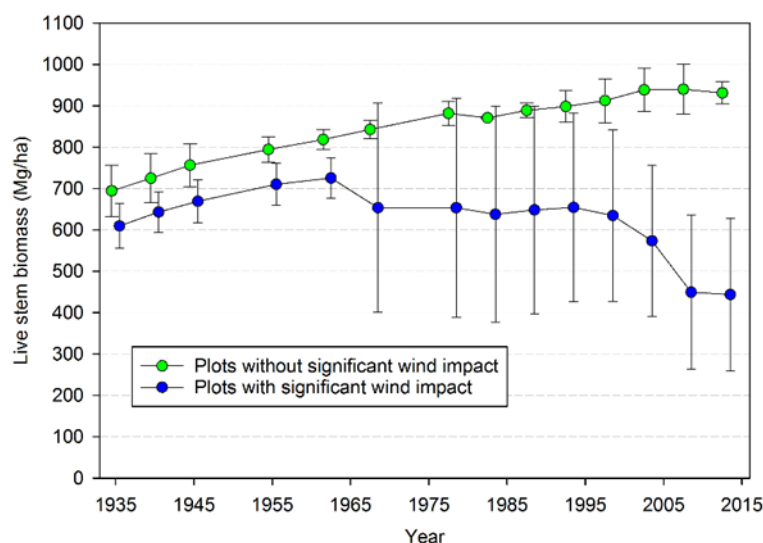


Figure 6. Average live biomass (with standard deviations) in plots not significantly impacted by wind ($n = 3$, green circles) vs those significantly impacted by wind ($n = 7$, blue circles).

Until 1978, TPH declined in all plots, and with the exception of CH06, there were no sudden declines obviously associated with major windstorms (Figure 4). After 1978, there appear to be two distinct temporal patterns in TPH. In CH05, CH06, CH12, and CH13, TPH increased and then declined, whereas in the other plots TPH increased, but did not decline.

At the multi-plot scale, major mortality episodes related to wind in individual plots had little effect on the median multi-plot biomass (Figure 7). For example, the 88% biomass loss in CH06 associated with the Columbus Day Storm led to a mean decrease of only 3.4% of live biomass across all plots. The same is true of CH13, which lost approximately 33% of its biomass to wind between 1968 and 1983, but this amounted to a biomass decline of less than 0.5% at the multi-plot level over that time period. In contrast to the effects of wind mortality in one plot, the cumulative effect of having multiple stands with wind-related mortality drove down the overall biomass at the multi-plot level. For example, between 1998 and 2013, when half of the plots (CH01, CH03, CH07, CH08, and CH12) experienced major wind-related mortality losses, biomass across all ten plots decreased by an average of 14.8%. However, biomass need not decline for wind to have had an influence. For the 1955–2003 period, the main effect of major windstorms at the multi-plot level may have been to constrain increases in live biomass, rather than lead to a decline.

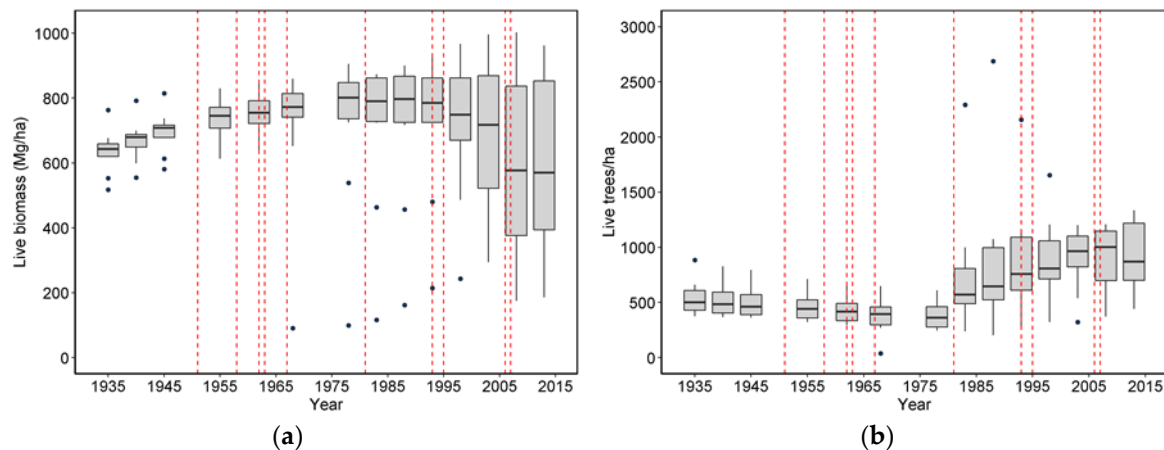


Figure 7. Median and range of live bole biomass (Mg) per hectare (a) and number of trees per hectare (b) across ten permanent plots at Cascade Head Experimental Forest, Otis, OR, USA. Values for 1962 are interpolated for all stands except CH06 which was reconstructed. The red vertical lines indicate major wind events.

In contrast to biomass, the main effect of wind may have been to magnify the increase in TPH at the multi-plot level (Figure 7). For example, after 1978 TPH roughly doubled, with about 22% of that increase related to ingrowth in CH06 following the major mortality event in 1962. In total, nearly 5000 new ingrowth trees were added to the study since 1978, with a plot-level average of approximately of 1250 TPH.

3.3. Mortality Mechanisms and Duration of Mortality Process

In terms of tree density and biomass, the proportion of mortality caused by wind has varied greatly over time for individual plots at a single census, ranging between 0% and 100% (Figure S2). For the entire period of observation since 1935, wind caused 16%–51% of the TPH mortality for each plot and 20%–59% of the biomass mortality (Figure 8). A total of 1,410 trees succumbed to wind; of these, 52% died standing with broken main stems, and 41% were uprooted. Suppression, the other major form of identifiable mortality in our study, caused 6%–63% of the mortality across all years for each plot; the latter (63%) occurred between 1988 and 2003 in CH06 among densely stocked ingrowth, which regenerated prolifically following the 1962 storm. Considering all plots together, the proportion of biomass mortality related to wind has generally increased over time, from 7%–17% between 1940 and 1945, to 61%–85% between 2008 and 2013 (Figure 9).

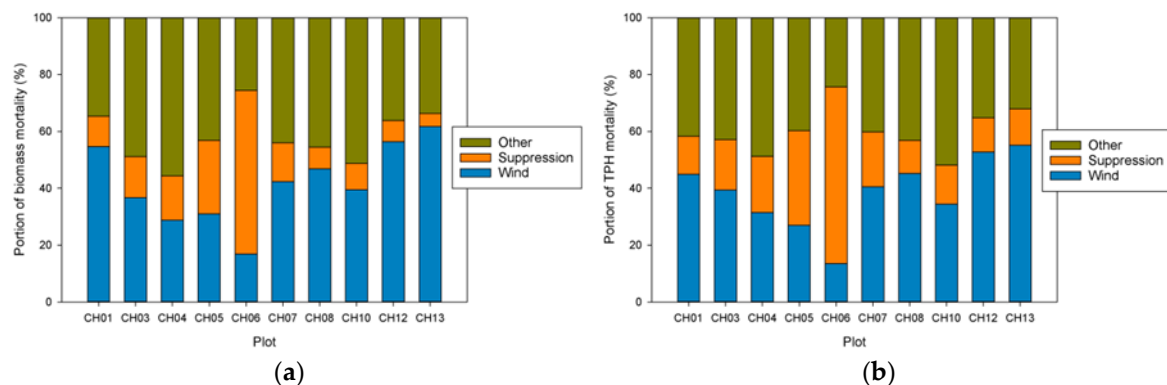


Figure 8. Tree mortality in terms of biomass (a) and trees per ha (b) resulting from wind, suppression and other or unknown causes over the entire measurement interval (1935–2013) in each permanent plot.

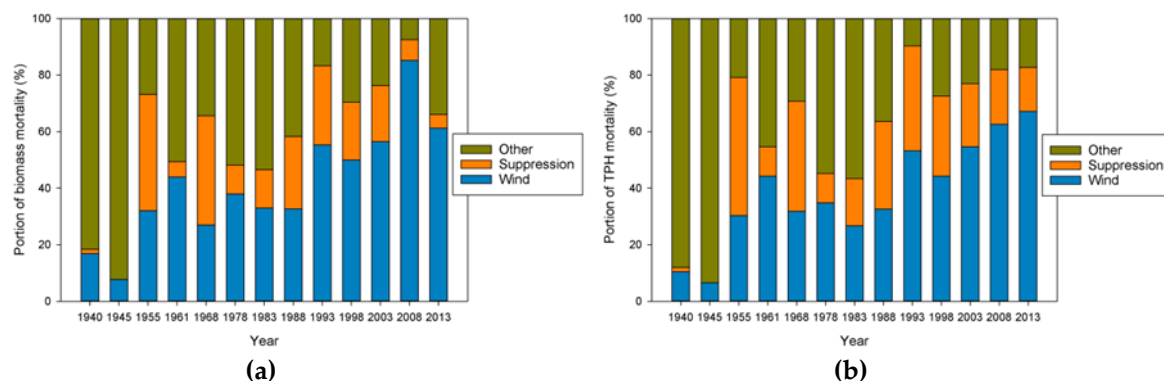


Figure 9. Tree mortality in terms of biomass (a) and trees per ha (b) resulting from wind, suppression and other or unknown causes across ten permanent plots over time.

The biomass mortality rate of western hemlock related to wind was, depending on the time period, 2 to 30 times higher than that of Sitka spruce. For TPH, the wind-related mortality rate for hemlock was up to 25 times that of Sitka spruce. The largest difference between species for biomass and TPH mortality rates occurred after 1988, the period during which wind disturbance influenced the most plots. For both species, the proportion of mortality caused by wind increased with diameter. For example, for trees 5 to 25 cm DBH, the fraction of mortality related to wind was 39% and 50% for Sitka spruce and western hemlock, respectively. In contrast, for trees with DBH greater than 75 cm, the fraction of wind-related mortality increased to 80%–90% for the same species, respectively.

Wind-related mortality rates (as opposed to proportion of total mortality described above) during periods with major storms were generally highest for the intermediate DBH size classes for Sitka spruce, but increased with DBH size class for western hemlock. In the case of Sitka spruce, wind-related mortality rates for 25–50 cm and 50–75 cm DBH trees were on average 2.7 and 3.6 times greater than the >100 cm size class, respectively (Figure S3). For the smallest DBH class (i.e., 5–25 cm), wind-related mortality rates of Sitka spruce were on average an order of magnitude lower than the intermediate DBH size classes. For western hemlock, the wind-related mortality rate of the three intermediate DBH size classes (25–50, 50–75, and 75–100 cm) was, on average, 1.8–2.4 times higher than the smallest DBH size class. These rates were also higher than the largest DBH size class (100 cm); however, because there were very few western hemlocks of this size (i.e., 2), it was difficult to reliably quantify the wind-related mortality rate for this DBH size class.

Although wind-related mortality can be relatively rapid (<1 year) when a stem snaps or fully uproots, a considerable amount of this mortality can take 5 or more years after the event. Trees damaged by windstorms can be separated into those that were broken but not immediately killed, downed by uprooting, and struck by falling boles or tops. Field notes indicate that 319 trees were damaged by wind between 1978 and 2013, with 41% broken, 27% downed, and the remaining 32% struck. A total of 32% of these damaged trees died within 5 years, 40% within 10 years, and 45% within 35 years, suggesting that a substantial fraction of trees impacted by windstorms can survive for decades. Thus, wind-related effects on structure and function are not necessarily immediate or captured by mortality statistics per se.

3.4. Relationships of Tree Ingrowth and Major Tree Mortality Periods

Ingrowth did not appear in great numbers in any of the plots until 1978 (Figure S4). Aside from CH06, the increase in ingrowth appeared to have been a response to the long-term changes in stand structure and commensurate resource availability. That is, regeneration had established over time in many of these stands and grew very slowly until 1978, when it reached the minimum size of 5 cm DBH. Stands CH04, CH05, and CH10 have all had major periods of ingrowth, but have not lost major amounts of biomass in windstorms. The most noticeable increase in ingrowth following wind mortality occurred in CH06, which had over 1600 trees per ha appear in a 5-year period, roughly twice the

maximum periodic ingrowth observed in other plots. The number of ingrowth trees per measurement period was often very high. For stands without major wind-related mortality events, it was 200 to 800 trees per ha in a 5-year period. For stands with major wind-related mortality, ingrowth was 400 to 500 trees per ha in a 5-year period.

For the stands that have had major biomass losses due to windstorms (CH06 and CH13) there was a lag between the storm and the ingrowth pulse. This is clearest for CH06, which seems to have had about a 10-year lag. For CH13 the lag might have been of similar duration. For plots that had ingrowth already occurring, the lag could be less than 5 years because the trees were already close to the minimum size and the openings created by wind allowed the trees to grow faster.

In terms of ingrowth biomass there was also an increase after 1978; however, ingrowth biomass is low (Figure 10), because the trees are so small that even a very large number of them do not form much biomass. In terms of NPP, ingrowth biomass generally comprised less than 10% of NPP, with a few exceptions that ranged from 12 to 22%.

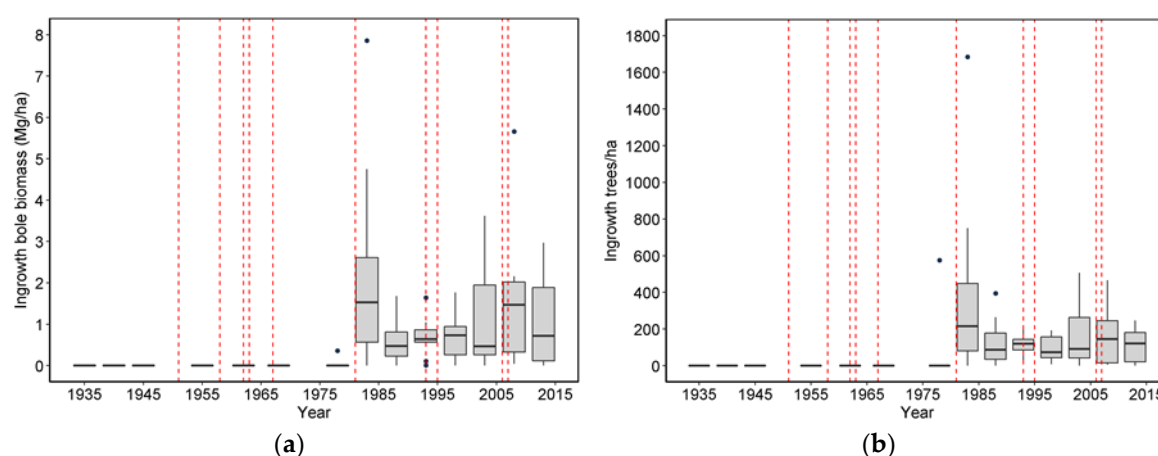


Figure 10. Median and range of ingrowth across ten permanent plots, expressed as bole biomass (Mg) per hectare (a), and trees per hectare (b). The red vertical lines indicate major wind events.

When all plots are considered, the majority of TPH ingrowth has been western hemlock (92% since 1983). This is generally true for plots with impacts from major windstorms as well as for those without. The one exception to this pattern is CH10, which has had Sitka spruce as a major share (93%) of its new trees. The predominance of western hemlock ingrowth (99%) in CH06, the plot with the highest wind mortality losses, is notable given the belief that Sitka spruce would regenerate more successfully in larger openings [19].

3.5. Changes in Species Composition

Over time and across all plots, the proportion of biomass in Sitka spruce has generally increased, whereas for TPH it has decreased (Figure 11). Specifically, the proportion of biomass comprised of Sitka spruce increased from 39.5% in 1935 to 49.3% in 2013, whereas for TPH it decreased from 27.5% in 1935 to 15.2% in 2013. The latter related to both a decrease in trees per ha in Sitka spruce as well as a substantial increase in western hemlock ingrowth.

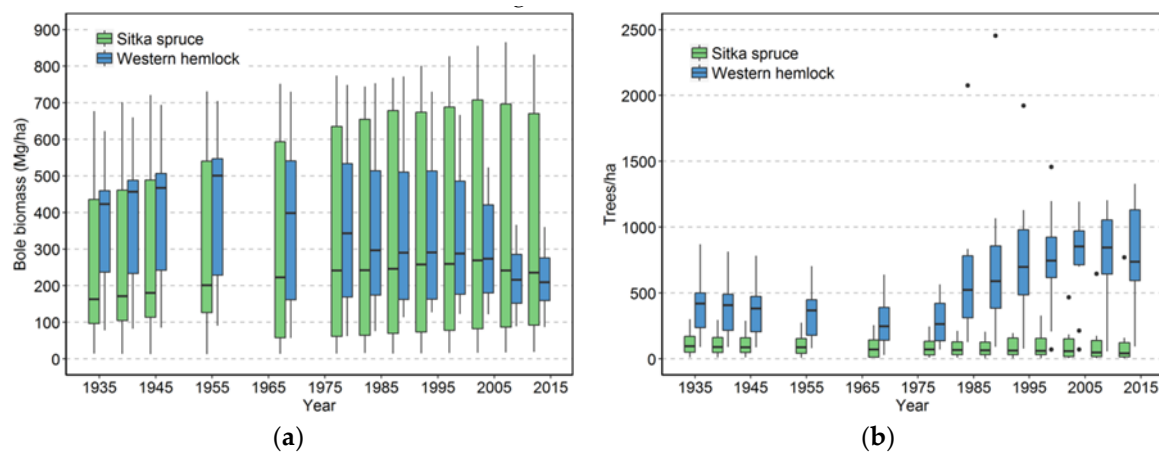


Figure 11. Biomass (a) and trees per ha (b) for the two major tree species over time.

3.6. NPP_b Response to Magnitude of Mortality

Between 1955 and 1978 there seems to have been a slow rate of decline in NPP_b in most of the plots (Figure 12). Since 2007, NPP_b appears to be increasing in some of the plots; some of these were subject to wind-related mortality (CH13) and others were not (CH10). Unless the wind mortality is greater than 50%, there did not seem to be much of an effect on NPP_b . For CH06, NPP_b of the trees was reduced to close to zero by the wind-related mortality (and probably the subsequent salvage). NPP_b then greatly increased on this plot exceeding the values of all the other plots as the ingrowth fully established (14.35 Mg/ha/year by 2003). CH13, which despite losing almost 30% of its biomass to mostly wind-related mortality between 1968 and 1983, experienced little change in NPP_b related to this disturbance (although in the most recent period NPP_b increased to a point similar to that in 1940). At the multi-plot level, mean NPP_b has been relatively stable since 1955, vacillating between 6.1 and 8.9 Mg/ha/year despite the impact of at least six major windstorms (Figure 12). This is in contrast to the steady decline in NPP_b from 1940 to 1955, prior to the majority of known major storms since 1935, when the plots were established. The range in median NPP_b was generally lower than variation from plot to plot, and the variability around median NPP_b has generally increased over time. Much of this plot to plot increase in variation was related to wind disturbance in CH06.

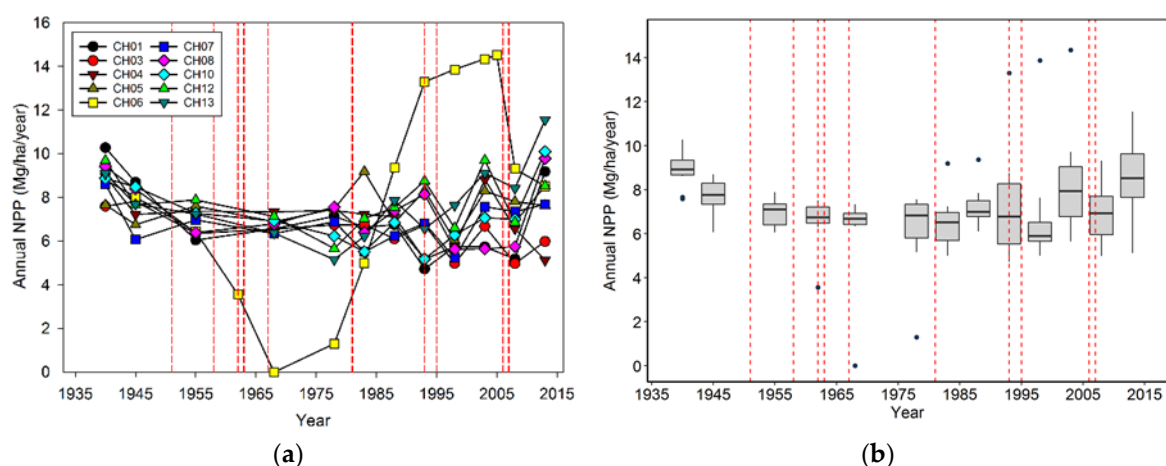


Figure 12. Net primary productivity (NPP) of boles (Mg/ha/year) (Mg/ha/year) in each of the ten permanent plots (a) and median across ten permanent plots (b). The red vertical lines indicate major wind events.

4. Discussion

Wind is an important disturbance agent in many forested regions of the globe, though its effects on forest structure vary with the frequency, intensity and duration of each event, as well as the interaction with topography and antecedent conditions such as soil moisture [14,20]. The majority of research on wind-related effects on forests has focused on the period immediately after an event, characterizing damage and mortality and how these change the species composition and structure of stands over the short-term (<10 years). Few studies have examined subsequent changes over the long term and fewer yet have examined the effects of multiple wind disturbance events [14]. Our study is one of the few that has examined multiple wind disturbance events over multiple decades (i.e., 78 years) in the same plots. Inference from our findings to the whole study area is limited, because the plots were not located randomly or systematically across the study area; however, they do provide some sense of the degree to which the effects of wind disturbance are synchronous versus asynchronous over a broad area. Thus, our results potentially provide new insights into the impact of wind disturbance on forests over time and at multiple spatial scales.

Although studies of wind disturbance generally focus on hurricanes in the eastern portion of North America, wind is also important in the Pacific Northwest, particularly along the Pacific coast and in the Coast Range where storms rival hurricanes in intensity and impact [21]. In some Pacific Northwest forests, wind is the dominant disturbance because fires are extremely rare [22]. The Cascades Mountains, the crest of which parallels the coast roughly 200 km inland from the coast, restrict the eastern extent of these storms. For example, little damage was observed from the 1962 Columbus Day Storm east of the Cascades [8].

Wind disturbance has been characterized as spatially heterogeneous, creating patches of severely impacted forest that are mostly less than 2 ha in extent [20,23] but dispersed over a wide area. This is consistent with our observations, in which major wind events influenced plots somewhere in the study area, but rarely across all plots at once. Harcombe et al. [11] examined a nearby forest landscape dominated by Sitka Spruce and western hemlock using aerial photography. They found that wind could create openings multiple ha in size, although even these were comprised of mixtures of high- and low-severity patches. They also found that openings from one event were often spatially adjacent to those created by previous or subsequent events. If these previous and subsequent events are in close temporal proximity, a larger, effectively homogeneous patch might be created. On the other hand, if wind disturbance events are separated by decades, landscape-level heterogeneity may be increased.

While the severity of wind disturbance depends on the scale being examined, Foster and Boose [23] observed a maximum mortality of 75% for areas ranging in size from 0.15 to 0.6 ha. Our maximum estimate is 88% for an area of 0.4 ha (plot CH06) in the 1962 Columbus Day Storm, but most of the events impacting our plots caused far lower losses in terms of magnitude. Our estimate of the maximum magnitude of wind-related mortality may be too high given that salvage logging followed the wind disturbance in CH06, compounding losses in trees and biomass [24]. However, it is likely that the majority of trees were sufficiently damaged in CH06 to have eventually died from wind-related effects on tree vigor such as snapped tops and crushing. The observation that wind-related mortality events rarely kill the majority of stems is consistent with the notion that wind disturbance along the Pacific coast is a very “inefficient” disturbance, meaning that with the exception of very small spatial extents, it does not cause anything approaching complete tree mortality [20].

Our analysis focused on mortality losses of trees and biomass caused by wind. Nonetheless, there were other changes brought about by wind disturbance in these plots such as defoliation, branch losses, and damage to stems. We did not quantify defoliation or branch loss, and although both forms of damage occurred, we believe these were relatively small compared to what was observed in regions with broad-leaved species. This may be due to the fact that needle-shaped leaves are less resistant to the wind than broad ones and that the branches of excurrent tree forms (typical of gymnosperms) may be less exposed than those of decurrent forms (typical of angiosperms). It is also likely that the majority of branch loss in the coastal Northwest is associated either with stems snapping or wind-fallen

stems impacting other stems. Our records indicate that 319 trees were damaged by wind between 1978 and 2013, as opposed to 1,233 trees that died directly from wind-related mortality. The majority of wind-related effects (80%) therefore resulted in “immediate” mortality. Of those trees that were damaged, 144 (about 45%) died within 35 years, which means that in these coastal Northwest forests only a small share (144 of 1552, or 9%) of the trees dying from wind are associated with indirect causes.

Ruth and Yoder [25] observed that Sitka spruce and Douglas-fir were more wind-firm than western hemlock. We also observed species differences, with western hemlock having at least an order of magnitude higher mortality rate than Sitka spruce, depending on the time interval examined. We found that the effects of size, as indicated by DBH, were species dependent, even though the smallest DBH size class for both species had low wind-related mortality rates. Trees of small size are likely protected from the full force of the wind either by surrounding larger trees or boundary layer effects [14,20]. For Sitka spruce, the largest-diameter trees appeared to be more wind-firm than the intermediate-sized ones. For western hemlock, the wind-related mortality rate appeared to increase with DBH, although it is possible the few largest western hemlocks were more wind-firm than intermediate-sized ones. These findings on size-class responses to wind mortality (i.e., intermediate highest versus largest highest) have been observed in other studies [20]. Moreover, although we reported the average effects by DBH size class in the results, the ranking of mortality rates by DBH class was not the same over time, suggesting that the effect of DBH on wind-related mortality varies over time (Figure S3). This means that while the smallest DBH class is likely to have the lowest wind-related mortality rate, any of the larger DBH size classes can have the highest rate depending on the features of a particular storm. Specifically, a low-intensity storm might preferentially kill the large trees with stems or roots compromised by decay, whereas the most intense storms might kill the majority of all large diameter stems regardless of condition.

Wind-related mortality has become increasingly important in these plots as the dominant trees have grown and aged, from 85 years at the time of plot establishment (1935) to 163 years of age at last measurement (2013). Although none of the plots was severely impacted by wind until the forest reached an age of 112 years, it is likely that areas within this landscape were impacted at a younger age. The windstorm in 1951 did not seem to impact the plots we examined; however, there were stands in the Cascade Head Experimental Forest that were impacted by this storm, particularly along the boundaries of recent harvest areas [25]. Moreover, CH06, which had a mortality event in 1962 that was severe enough to cause a new, even-aged cohort of trees to establish, also had a major wind-related mortality loss in 2007 effectively at an age of 45 years. While age is often correlated with the extent of wind damage and mortality, other structural features of the local topography and forest stand are likely more important [20,26]. In the case of CH06, the area impacted in 2007 was relatively open, suggesting wind could penetrate this part of the plot. Most of the other plots were relatively intact and evenly stocked by trees for many decades after plot establishment, and thus may have been less susceptible to wind disturbance until gaps began to develop at an older age. In the case of CH08 and CH13, which were impacted by multiple storm events, an earlier event created openings that likely enhanced the impact of subsequent events. This is similar, albeit at a smaller spatial scale, to the spreading of wind-related openings observed by Harcombe et al. [11] and along cutting boundaries by Ruth and Yoder [25].

Everham and Brokaw [20] list four pathways or mechanisms for recovery following wind disturbance: regrowth, recruitment, release, and repression. Although some foliage and branches were lost in wind disturbance and these likely regrew, the primary process of regrowth in the forests we studied is likely related to sprouting of branches along snapped stems (Sitka spruce can produce epicormic branches). However, a relatively small number of trees suffered broken stems (125), and about half of these died. In comparison, approximately 5000 trees were tagged as ingrowth over the course of the study, indicating that recruitment and release are much more important in these forests. It should be noted that while ingrowth was certainly influenced by wind-related mortality, it also occurred, sometimes prolifically, in plots without major wind-related mortality. Since we did

not track seedlings in these plots it was difficult to distinguish recovery via new recruitment versus recovery via release of existing (pre-disturbance) tree seedlings. To some extent, these two mechanisms could be distinguished by the lag between wind disturbance and the ingrowth pulse; in the case of CH06, the lag of 10 years indicated a substantial contribution to recovery by recruitment. However, in most of the other plots a lag was not readily apparent, and a pulse of ingrowth started before wind disturbance impacted most of the plots. This suggests that for most plots, the predominant recovery mechanism was via the release of existing small trees. For the most part, we did not observe the process of repression being important despite a fairly dense understory of herbs and shrubs that developed in openings created by wind.

As noted by Foster and Boose [23], the majority of studies examining succession following wind disturbance consider either small gap-sized areas or large areas of catastrophic disturbance, but largely ignores situations between these extremes which happen to be quite common. In the case of gap-sized disturbances, regrowth and expansion of surviving trees could lead to little change in density, regeneration, composition, NPP, or biomass at the stand level. With larger gaps, these variables may change over time; if the disturbance repeats in other locations in the stand, wind disturbance may maintain the forest live biomass in quasi-equilibrium [19,27,28]. In cases where severe wind mortality impacts an entire stand, a “typical” successional scenario might be a major pulse of mortality followed by pulse of ingrowth followed by a second period of increased mortality due to competition/suppression. Also, if the disturbance is severe enough, then there could be a decrease in woody-related NPP, followed by an increase, and quite possibly a decrease as the new stand develops [29]. While we observed this temporal pattern of NPP in CH06, that was the exception. The changes in the plots we observed strongly suggest that the majority of stands do not undergo solely either gap or catastrophic wind-related mortality; instead there are more subtle changes in ingrowth, mortality, and NPP that are hard to distinguish from stands not undergoing wind disturbance. Moreover, at the landscape level, even individual catastrophic events do not necessarily have an impact on overall species composition, tree density, biomass, ingrowth, mortality, or NPP. Rather it is the accumulation of multiple events in previously and newly disturbed stands that have the largest impact on these variables.

Of all the variables we examined in this forest, NPP seems the least responsive to wind-related disturbance. In part this result may have been due to our use of a 5–10-year measurement interval to determine NPP_t; had we determined this variable annually, then we might have observed a greater and more short-lived reduction after wind disturbance. Therefore, one could make the case at the plot scale that there is a dip in NPP after major wind mortality and then a rebound that overshoots the long-term average. However, this only seems to have occurred when mortality was very high (CH06), while for most of the plots, temporal changes in NPP were muted. Moreover, at the multi-plot scale, NPP was even more stable than that observed at the plot level. Since we did not include the NPP of trees smaller than 5.0 cm dbh, non-woody parts (i.e., foliage) nor understory vegetation, NPP is probably less influenced by wind-related disturbance than our analysis indicates. In this particular environment, water, light, and nutrient resources are relatively abundant, thus surviving or establishing trees and understory plants will use them, keeping NPP relatively high at both the plot and multi-plot scale.

The effects on species composition also seem to be minimal and counterintuitive. The limited amount of change is probably a function of the limited number of species present in this system. The only truly early successional tree species, red alder, is not particularly abundant in these plots, although stands dominated by alder do occur nearby [30]. The counterintuitive result is that the climax species, western hemlock, is increasing its numbers more than Sitka spruce, a species thought to require large gaps for regeneration [19]. In this moist, resource-rich environment, western hemlock is not restricted to the later stages of succession and can successfully regenerate in open settings as well as in shade. Moreover, western hemlock can maintain itself in the understory without substantial growth for many decades. Both attributes give this species an advantage over Sitka spruce in terms of numbers. Sitka spruce's advantage appears to be in its longevity and possibly its wind firmness

relative to western hemlock [25]. This likely explains why the proportion of biomass is increasing in Sitka spruce, but the proportion of TPH is increasing in western hemlock. This pattern may be similar to that observed in the Rocky Mountains where Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) was able to maintain itself in the presence of subalpine fir (*Abies lasiocarpus* (Hook.) Nutt.), not by abundantly reproducing after disturbances, but by having a lower mortality rate than subalpine fir [28].

Input-output balances are important in understanding how both TPH and biomass have evolved in this landscape. When NPP, biomass mortality, and net change in biomass are considered for all the plots, biomass mortality has generally exceeded NPP_b since 1968, leading to an overall loss of biomass since that time (Figure S5). The opposite is true for TPH, with ingrowth generally exceeding stem mortality since 1978, even in plots not impacted significantly by wind disturbance (Figure S6). For the three plots that were not impacted by major wind disturbance there is some evidence that the rate of biomass accumulation has gradually slowed over time and that mortality became approximately equal to NPP_b (Figure S7). In contrast, mortality generally exceeded NPP_b since 1968 in the seven plots that have experienced major wind-related losses (Figure S7). Examination of the possible factors responsible for the divergence of plots with and without major wind disturbance suggests that initial species composition was more important than soil depth or aspect. Soil depth in all the plots exceeded 1 m and deeper than the root depth of these species, thus shallow soils did not seem to be an explanation. Two of the plots not strongly influenced by wind (CH04 and CH05) had SW aspects, the predominant direction of strong winds. The remaining plot with little wind disturbance (CH10) had a NW aspect and may have been protected, but one of the plots strongly influenced by wind CH13 had a N aspect suggesting that northerly aspects can be subject to wind disturbance in this landscape. In fact, all aspects except for E (which were not sampled) appeared to have plots with major wind impacts. Those plots without strong wind disturbance effects all had at least 65% of their initial biomass comprised of Sitka spruce. In contrast, only one of the plots with major wind disturbance (CH03) had the majority of initial biomass comprised of Sitka spruce (62%); the remaining plots had 74%–97% of their initial biomass comprised of western hemlock. Thus, at least for this landscape, an initial predominance of more wind-susceptible species (i.e., western hemlock) may eventually lead to greater changes in biomass than if wind-firm species (Sitka spruce) predominate. It is not clear if there will be additional decreases of biomass in these plots, or whether biomass will gradually increase again as released trees and newly regenerated ones gain biomass. The critical factor is likely the near-term reoccurrence of major impacts from wind or other disturbance: if, on one hand, additional major losses recur in the near future, then biomass may reach a new, lower steady-state as hypothesized by Acker et al. [13]. On the other hand, if future losses are low because these plots are now more wind resistant (which we view as unlikely) or major windstorms do not occur for many years (also unlikely), then biomass would likely begin to significantly increase.

Wind and fire are significant disturbances in the Pacific Northwest region, but leave contrasting imprints on the forests because of differences in their temporal and spatial patterns, and also because of their different biological legacies. As noted by Harcombe et al. [11], in the coastal landscape fire creates a long-term stage upon which wind disturbances play out, gradually imposing a new pattern as wind effects accumulate. Because wind disturbance leaves a significant legacy of either surviving large trees or advanced regeneration, forest response following wind disturbance events can be more rapid compared to fire. Therefore, one might think of wind as a slow disturbance (particularly when events occur in series) coupled to a rapid response. Fire might be thought of in the opposite manner as a fast disturbance coupled to a slow recovery process given that it can remove seed sources and advanced regeneration. This suggests that to fully understand forest structure and function one needs to examine how multiple disturbances interact over broad areas and long durations.

5. Conclusions

An examination of observations from ten, 0.4 ha permanent plots over a 78-year period on the Oregon coast indicated the following:

1. Most wind storms since 1961 with gusts ≥ 119 km/h have noticeably impacted at least one plot, but none of these windstorms has noticeably impacted all ten. This meant that the primary impact of wind, at least on biomass, was cumulative;
2. To cause a detectable biomass decline, mortality must exceed 29–41 Mg/ha per 5-year period (or 3.4%–5.8% per 5 years);
3. Depending on the plot, wind caused 16%–59% of the total mortality over the 78-year observation period. The proportion of wind-related mortality has increased 5- to 8-fold since 1940 suggesting this disturbance is an increasingly important driver of change;
4. The majority (80%) of wind-related mortality was “immediate”, but some trees survived up to 35 years after being significantly damaged by wind, suggesting this disturbance influences forest structure in ways not captured by mortality alone;
5. While biomass has generally declined since 1962, the number of trees per ha has increased on all plots. The majority of plots with major biomass declines were initially dominated by western hemlock, which may be related to the observation that western hemlock had a wind-related mortality rate that was at least twice that of Sitka spruce;
6. The number and biomass of ingrowth trees increased substantially after 1978, and in most plots regardless of wind impact. The appearance of these “new” trees led to the observed increase in trees per ha as well as the increase in the proportion of western hemlock stems in most of the plots;
7. NPP_b was only noticeably impacted by wind disturbance when biomass loss exceeded 50%, which meant that most major windstorms had little detectable impact on individual plot NPP_b . This may be related to observations that growth of surviving trees and seedlings was the primary recovery mechanism from wind disturbance.

These observations all suggest that wind, like many natural disturbances, does not reset an ecosystem completely. Although often described in a simple manner as producing either a small gap or large patch of complete mortality, wind disturbance is in reality a messy, gradual process impacting forest structure and function. In addition, while individual events certainly can have a detectable impact, wind’s largest impact, at least in systems where it is frequently reoccurring, is cumulative as one event alters one part of the landscape and another event alters another part of the landscape, and so on eventually causing forest structure and function to change at the landscape level.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1999-4907/10/2/119/s1>, Figure S1, Live biomass accumulation vs mortality biomass, with mortality biomass for full range of values. Figure S2, Proportion of mortality of biomass (upper) and trees (lower) related to wind for individual plots, Figure S3, Wind-related annual mortality rate expressed on a biomass (left) or trees (right) basis for Sitka spruce (upper) and western hemlock (lower) for diameter and breast height (DBH) size classes over time, Figure S4, Long-term trends in plot-level ingrowth, expressed as bole biomass (Mg) per hectare (upper), and number of trees per hectare (lower), Figure S5, Input-output balances for biomass (upper) and trees per ha (lower) across ten permanent plots, Figure S6, Annual mortality TPH, ingrowth TPH, and change in live TPH in plots not significantly impacted by wind (upper, $n = 3$) vs those significantly impacted by wind (lower, $n = 7$), Figure S7, Annual biomass accumulation, mortality, and NPP (Net Primary Production) in plots not significantly impacted by wind (upper, $n = 3$) vs those significantly impacted by wind (lower, $n = 7$), Table S1, Physiographic, topographic and soils information for ten plots at Cascade Head Experimental Forest, Table S2, History of measurements and mortality assessments from ten, 0.4-ha plots at Cascade Head Experimental Forest, Table S3, Plot level data summaries, Table S4, Means (standard deviations) of data from 10 plots at Cascade Head Experimental Forest.

Author Contributions: Conceptualization, M.E.H. and R.J.P.; methodology, M.E.H. and R.J.P.; software, M.E.H. and R.J.P.; validation, M.E.H. and R.J.P.; formal analysis, R.J.P.; investigation, M.E.H. and R.J.P.; resources, M.E.H. and R.J.P.; data curation, R.J.P.; writing—original draft preparation, M.E.H.; writing—review and editing, M.E.H. and R.J.P.; visualization, R.J.P.; supervision, M.E.H.; project administration, M.E.H.; funding acquisition, M.E.H. and R.J.P.

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Supplemental material: Figures

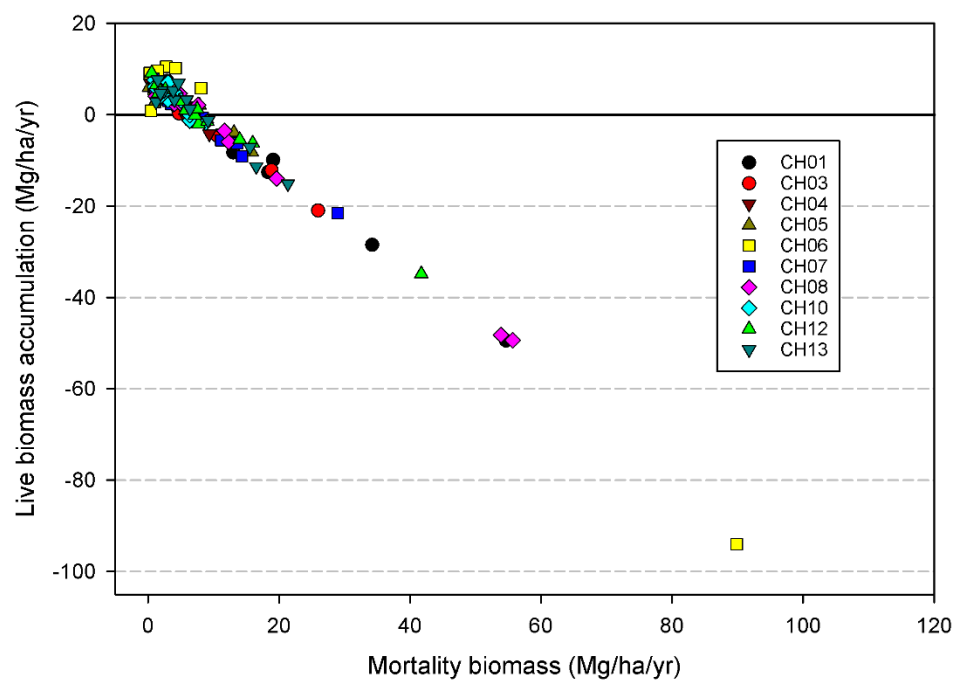


Figure S-1. Live biomass accumulation vs mortality biomass, with mortality biomass for full range of values.

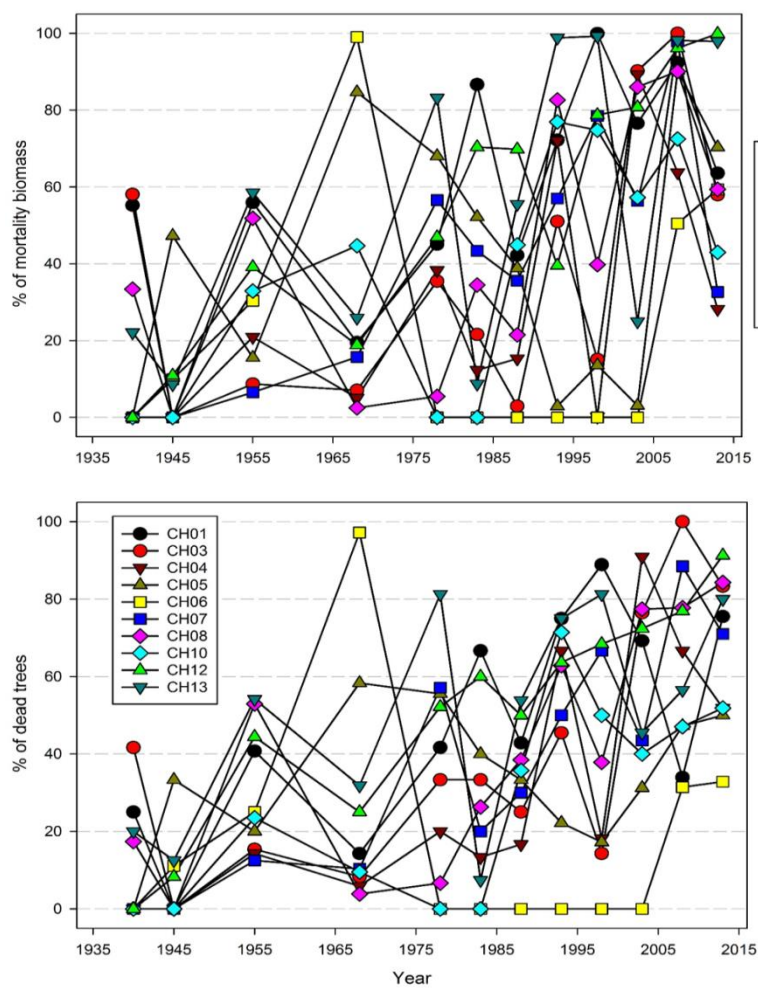


Figure S-2. Proportion of mortality of biomass (upper) and trees (lower) related to wind for individual plots.

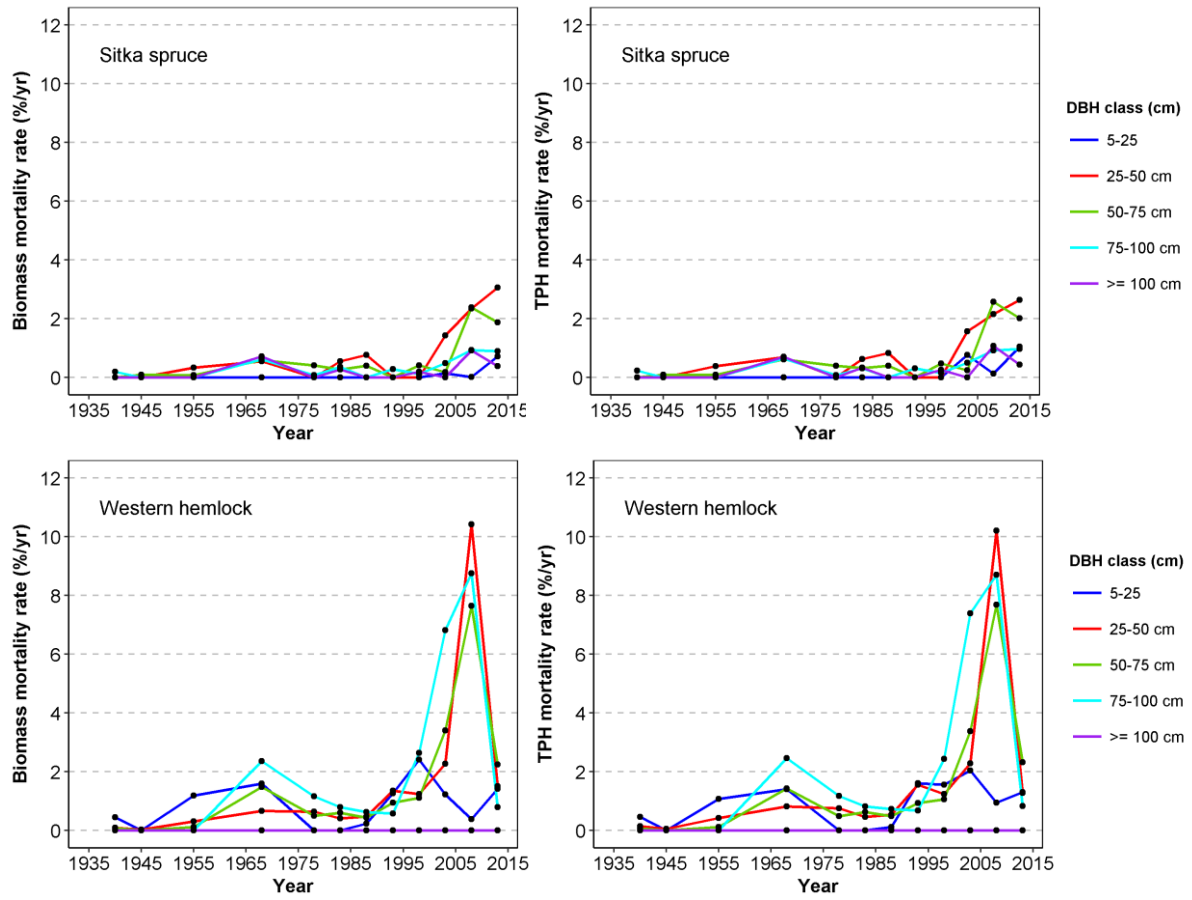


Figure S-3. Wind-related annual mortality rate expressed on a biomass (left) or trees (right) basis for Sitka spruce (upper) and western hemlock (lower) for diameter at breast height (DBH) size classes over time.

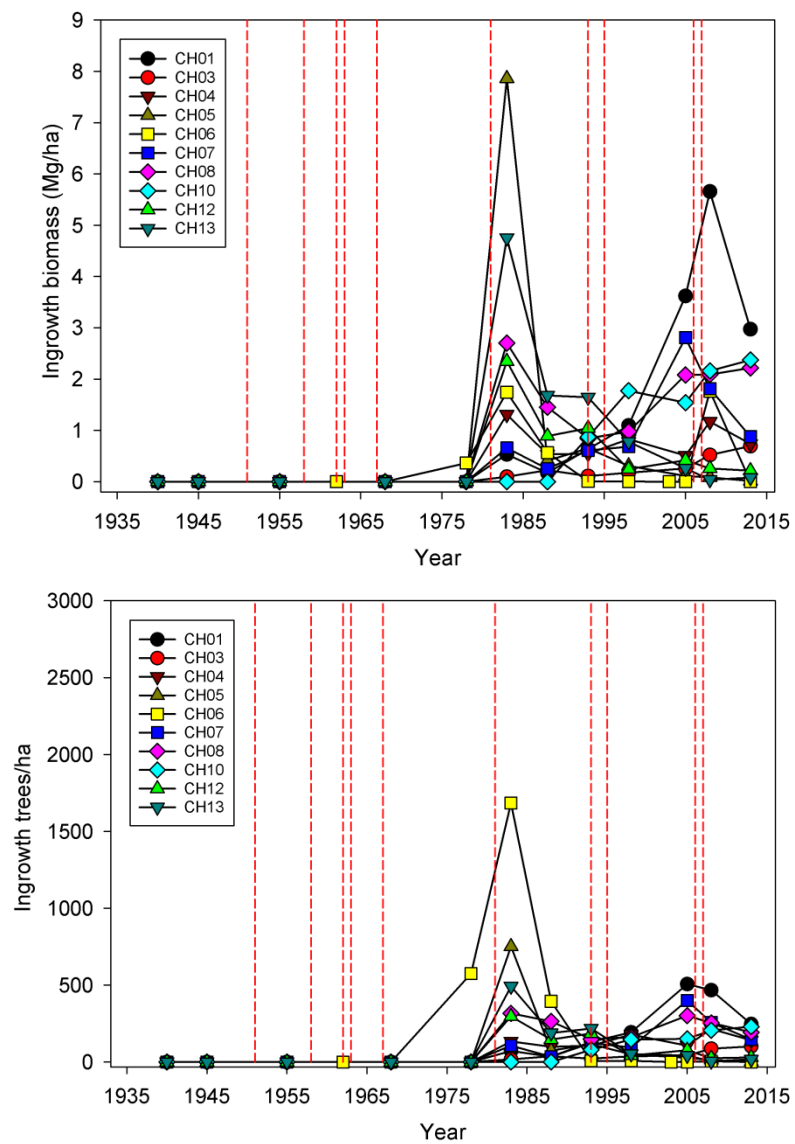


Figure S-4. Long-term trends in plot-level ingrowth, expressed as bole biomass (Mg) per hectare (upper), and number of trees per hectare (lower) for individual plots.

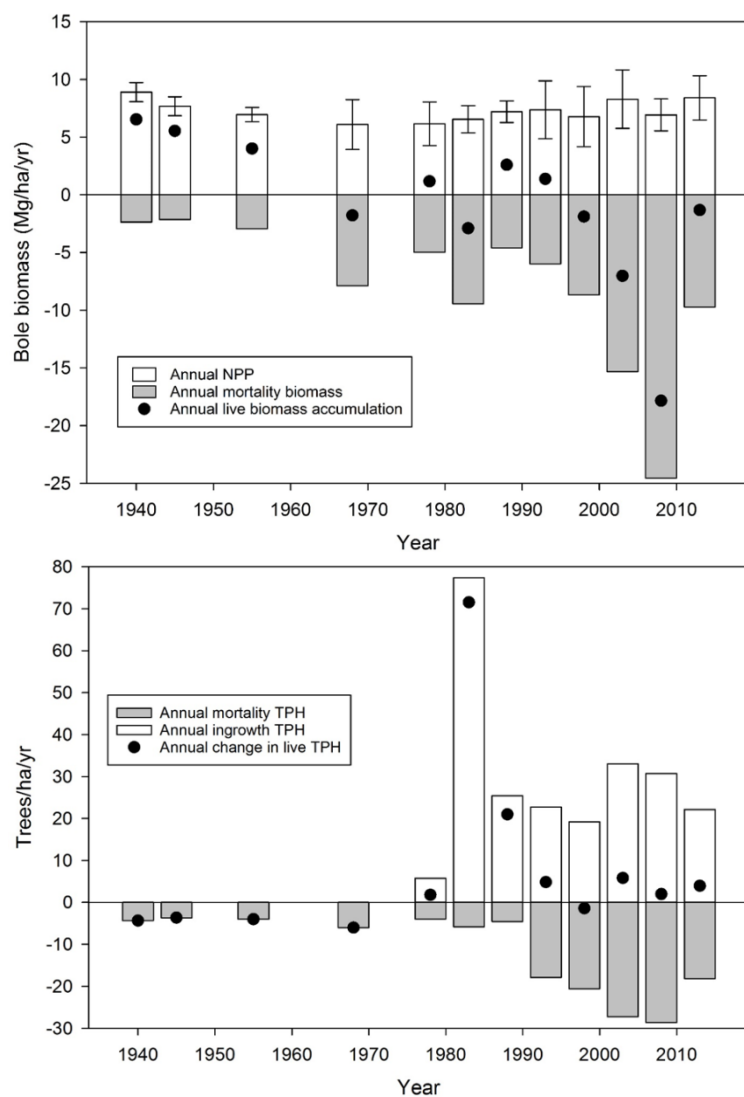


Figure S-5 Input output balances for biomass (upper) and trees per ha (lower) across ten permanent plots.

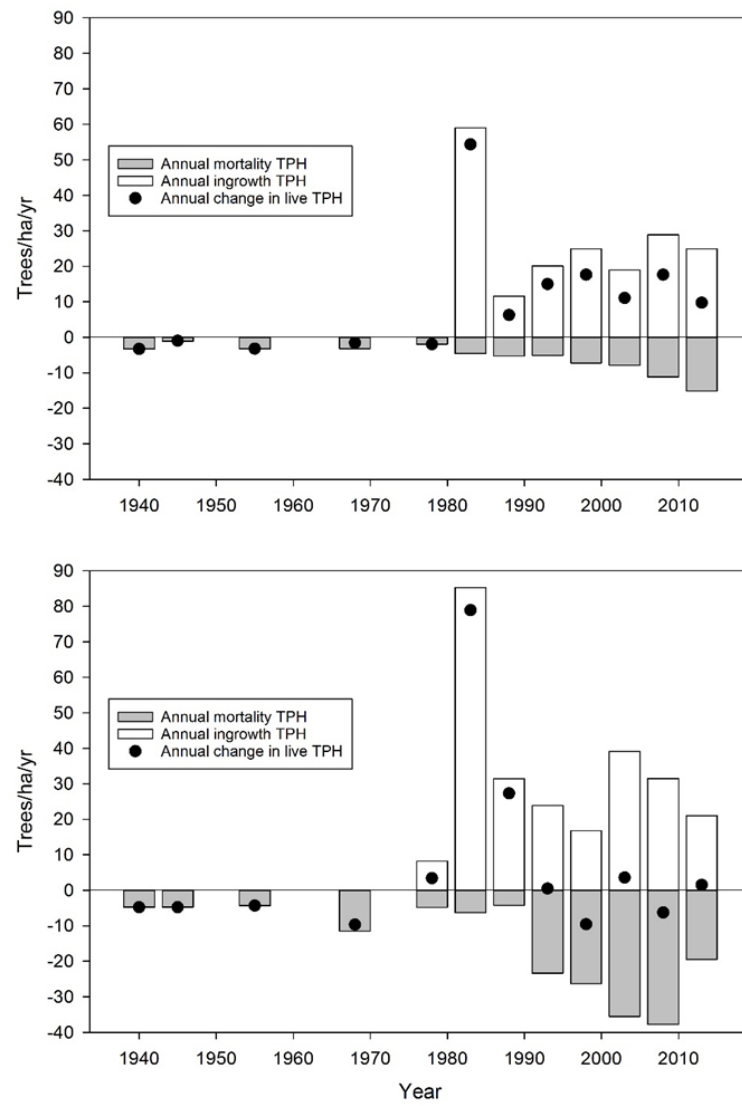


Figure S-6. Annual mortality TPH, ingrowth TPH, and change in live TPH in plots not significantly impacted by wind (upper, n=3) vs those significantly impacted by wind (lower, n=7).

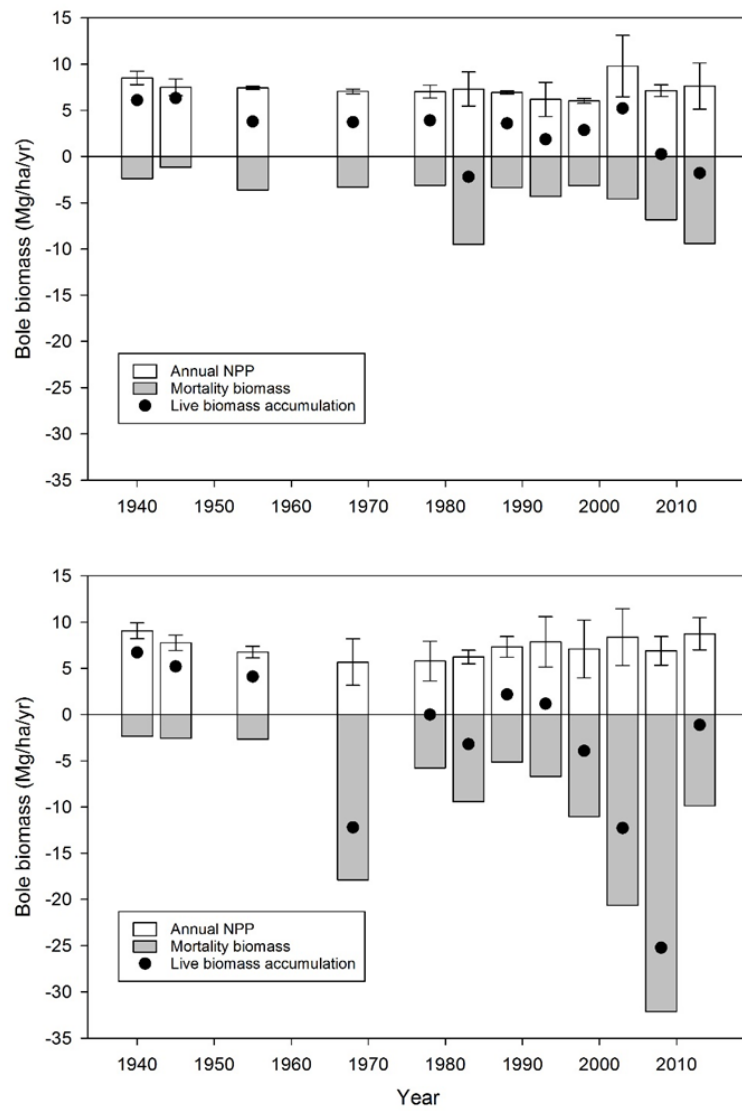


Figure S-7. Annual biomass accumulation, mortality and NPP (Net Primary Production) in plots not significantly impacted by wind (upper, n=3) vs those significantly impacted by wind (lower, n=7).

Table S-1. Physiographic, topographic and soils information for ten plots at Cascade Head Experimental Forest.

Plot	Area (ha)	Latitude	Longitude	Elev (m)	Slope (deg)	Aspect	Soil texture	Soil depth (B, m)	Parent material
CH01	0.4048	45.0456	-123.8973	298	16	S	silty clay loam	1.0-1.4	diorite, sandstone
CH03	0.4048	45.0457	-123.9040	236	8	W	silty clay loam	1.0-1.3+	sandstone, siltstone
CH04	0.4048	45.0648	-123.9413	294	12	SW	silty clay loam	1.3+	sandstone, siltstone
CH05	0.4048	45.0653	-123.9423	288	9	SW	silty clay loam	1.2+	sandstone, siltstone
CH06*	0.4048	45.0615	-123.9391	253	14	SW	silty clay loam	1.2+	sandstone, siltstone
CH07	0.4048	45.0627	-123.9398	277	25	S	silty clay loam	1.2+	sandstone, siltstone
CH08	0.4048	45.0646	-123.9453	252	25	S	silty clay	1.5+	sandstone, siltstone
CH10	0.4048	45.0631	-123.9917	312	37	NW	silty clay loam	0.9-1.3+	sandstone, siltstone
CH12	0.4048	45.0500	-123.9012	262	4	SW	silty clay loam	1.2-1.4+	sandstone, siltstone
CH13*	0.4048	45.0513	-123.9018	231	19	N	silty clay loam	1.2-1.4+	sandstone, siltstone

* CH06 and CH13: soil information is from nearby plots (CH07 for CH06, CH12 for CH13).

Table S-2. History of measurements and mortality assessments from ten, 0.4-ha plots at Cascade Head Experimental Forest.

Year	Activity
1935	Plots established: plot boundaries surveyed, trees ≥ 5.0 cm tagged and measured
1940	Tagged trees measured, mortality documented, ingrowth tagged and measured
1945	Tagged trees measured, mortality documented, ingrowth tagged and measured
1955	Tagged trees measured, mortality documented, ingrowth tagged and measured
1961	Mortality assessment, dead trees noted
1968	Tagged trees measured, mortality documented, ingrowth tagged and measured
1978	Tagged trees measured, mortality documented, ingrowth tagged and measured
1983	Tagged trees measured, mortality documented, ingrowth tagged and measured
1988	Tagged trees measured, mortality documented, ingrowth tagged and measured
1993	Tagged trees measured, mortality documented, ingrowth tagged and measured
1998	Tagged trees measured, mortality documented, ingrowth tagged and measured
2003	Tagged trees measured, mortality documented, ingrowth tagged and measured
2005	Reconstruction of CH06: live and dead trees measured, trees cored and aged
2008	Tagged trees measured, mortality documented, ingrowth tagged and measured
2013	Tagged trees measured, mortality documented, ingrowth tagged and measured

Table S-3 Plot level summaries.

Table S-3a. Plot-level data summary for CH01.

Plot	Year	Interval	Ingrowth		All live trees		Mortality		Mortality rate (%/yr)		NPP ¹ (Mg/ha/yr)
			Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	
CH01	1935				659.58	642.54					
CH01	1940	5	0.00	0.00	639.82	679.36	19.76	14.59	0.61	0.46	10.28
CH01	1945	5	0.00	0.00	615.12	713.39	24.70	9.43	0.78	0.28	8.69
CH01	1955	10	0.00	0.00	548.42	725.24	66.70	48.61	1.14	0.70	6.05
CH01	1961*	6	0.00	0.00	508.90	732.58	39.52	38.40	1.24	0.90	7.62
CH01	1968	7	0.00	0.00	479.25	739.92	29.64	32.20	0.85	0.64	5.65
CH01	1978	10	0.00	0.00	449.60	772.35	29.64	38.98	0.64	0.54	7.14
CH01	1983	5	71.64	0.53	499.01	778.12	22.23	27.41	1.01	0.72	6.64
CH01	1988	5	34.58	0.17	516.30	795.57	17.29	16.31	0.70	0.42	6.75
CH01	1993	5	130.93	0.63	597.83	754.17	49.41	65.02	1.99	1.69	4.72
CH01	1998	5	192.69	1.09	746.05	691.28	44.47	91.65	1.53	2.56	5.75
CH01	2003	5	506.42	3.62	1156.13	548.93	96.34	171.02	2.73	5.53	5.74
CH01	2008	5	466.90	5.66	1208.00	301.73	415.02	273.12	8.51	12.86	5.18
CH01	2013	5	247.04	2.97	1333.99	252.26	121.05	95.40	2.09	7.32	9.19

1-Net Primary Productivity

Table S-3b. Plot-level data summary for CH03.

Plot	Year	Interval	Ingrowth		All live trees		Mortality		Mortality rate (%/yr)		NPP (Mg/ha/yr)
			Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	
CH03	1935				412.55	661.37					
CH03	1940	5	0.00	0.00	382.91	678.78	29.64	20.56	1.48	0.63	7.59
CH03	1945	5	0.00	0.00	368.08	711.70	14.82	6.17	0.79	0.18	7.82
CH03	1955	10	0.00	0.00	335.97	750.57	32.11	24.63	0.91	0.35	6.35
CH03	1961	6	0.00	0.00	323.62	776.46	12.35	13.22	0.62	0.30	6.52
CH03	1968	7	0.00	0.00	306.32	802.35	17.29	20.14	0.78	0.37	6.58
CH03	1978	10	0.00	0.00	284.09	841.82	22.23	28.00	0.75	0.35	6.75
CH03	1983	5	17.29	0.10	279.15	841.32	22.23	34.27	1.62	0.83	6.75
CH03	1988	5	37.06	0.22	306.32	860.73	9.88	11.11	0.72	0.27	6.10
CH03	1993	5	22.23	0.11	301.38	860.35	27.17	34.07	1.84	0.80	6.74
CH03	1998	5	37.06	0.17	321.15	861.71	17.29	23.57	1.17	0.55	4.99
CH03	2003	5	42.00	0.26	321.15	800.89	42.00	94.22	2.76	2.29	6.68
CH03	2008	5	86.46	0.52	370.55	696.04	37.06	129.73	2.42	3.47	4.98
CH03	2013	5	101.28	0.69	442.19	673.03	29.64	52.92	1.65	1.57	5.98

Table S-3c. Plot-level data summary for CH04.

Plot	Year	Interval	Ingrowth		All live trees		Mortality		Mortality rate (%/yr)		NPP (Mg/ha/yr)
			Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	
CH04	1935				474.31	643.78					
CH04	1940	5	0.00	0.00	464.43	682.66	9.88	5.94	0.42	0.19	8.96
CH04	1945	5	0.00	0.00	459.49	717.02	4.94	1.74	0.21	0.05	7.22
CH04	1955	10	0.00	0.00	442.19	778.78	17.29	11.95	0.38	0.17	7.37
CH04	1961	6	0.00	0.00	424.90	815.02	17.29	10.38	0.66	0.22	7.77
CH04	1968	7	0.00	0.00	400.20	851.27	24.70	12.53	0.85	0.22	6.97
CH04	1978	10	0.00	0.00	387.85	905.45	12.35	19.85	0.31	0.24	7.40
CH04	1983	5	133.40	1.31	484.19	873.27	37.06	68.34	1.99	1.56	7.23
CH04	1988	5	98.81	0.53	568.18	897.64	14.82	11.21	0.62	0.26	7.12
CH04	1993	5	106.23	0.55	659.58	894.70	14.82	28.78	0.53	0.65	5.17
CH04	1998	5	177.87	0.83	810.28	908.60	27.17	14.84	0.84	0.33	5.75
CH04	2003	5	106.23	0.51	889.33	927.90	27.17	24.81	0.68	0.55	8.82
CH04	2008	5	214.92	1.17	1067.19	934.17	37.06	26.57	0.85	0.58	6.57
CH04	2013	5	140.81	0.74	1141.30	913.07	66.70	46.72	1.28	1.02	5.12

Table S-3d. Plot-level data summary for CH05.

Plot	Year	Interval	Ingrowth		All live trees		Mortality		Mortality rate (%/yr)		NPP (Mg/ha/yr)
			Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	
CH05	1935				373.02	762.63					
CH05	1940	5	0.00	0.00	368.08	791.90	4.94	9.04	0.27	0.24	7.66
CH05	1945	5	0.00	0.00	360.67	814.60	7.41	11.06	0.41	0.28	6.75
CH05	1955	10	0.00	0.00	323.62	830.05	37.06	60.64	1.08	0.77	7.61
CH05	1961	6	0.00	0.00	316.21	844.61	7.41	5.53	0.39	0.11	3.35
CH05	1968	7	0.00	0.00	293.97	859.17	22.23	54.85	1.04	0.95	9.92
CH05	1978	10	0.00	0.00	271.74	890.19	22.23	43.81	0.78	0.52	7.48
CH05	1983	5	750.99	7.86	998.02	870.65	24.70	65.47	1.89	1.52	9.19
CH05	1988	5	74.11	0.41	1042.49	900.14	29.64	4.78	0.60	0.11	6.85
CH05	1993	5	116.11	0.65	1114.13	937.58	44.47	4.12	0.87	0.09	8.31
CH05	1998	5	49.41	0.31	1091.90	967.20	71.64	0.54	1.32	0.01	6.03
CH05	2003	5	27.17	0.11	1040.02	995.84	79.05	12.84	1.49	0.27	8.29
CH05	2008	5	12.35	0.08	963.44	1002.59	88.93	32.30	1.77	0.66	7.81
CH05	2013	5	2.47	0.01	872.04	961.66	93.87	79.07	2.03	1.63	7.63

Table S-3e. Plot-level data summary for CH06.

Plot	Year	Interval	Ingrowth		All live trees		Mortality		Mortality rate (%/yr)		NPP (Mg/ha/yr)
			Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	
CH06	1935				511.36	619.04					
CH06	1940	5	0.00	0.00	484.19	654.31	27.17	8.77	1.09	0.29	8.81
CH06	1945	5	0.00	0.00	461.96	684.09	22.23	10.30	0.94	0.32	8.02
CH06	1955	10	0.00	0.00	442.19	739.56	19.76	8.83	0.44	0.13	6.43
CH06	1961	6	0.00	0.00	429.84	749.00	12.35	44.53	0.47	1.03	9.00
CH06	1968	7	0.00	0.00	37.07	90.84	392.78	629.10	29.54	23.03	0.00
CH06	1978	10	574.72	0.36	609.27	99.35	2.47	4.49	0.69	0.51	1.30
CH06	1983	5	1684.54	1.74	2291.37	116.19	2.47	8.10	0.08	1.69	4.99
CH06	1988	5	394.41	0.57	2688.15	161.75	2.47	1.30	0.02	0.23	9.37
CH06	1993	5	7.41	0.01	2157.99	214.40	537.47	13.85	4.36	1.77	13.30
CH06	1998	5	7.41	0.00	1654.11	243.32	511.29	40.41	5.26	4.09	13.87
CH06	2003	5	0.00	0.00	1118.91	294.03	535.10	21.02	7.52	1.79	14.35
CH06	2008	5	4.94	1.77	1037.55	342.13	86.46	7.32	1.60	0.50	11.09
CH06	2013	5	0.00	0.00	864.62	360.75	172.92	23.95	3.58	1.44	8.51

Table S-3f. Plot-level data summary for CH07.

Plot	Year	Interval	Ingrowth		All live trees		Mortality		Mortality rate (%/yr)		NPP (Mg/ha/yr)
			Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	
CH07	1935				629.94	650.22					
CH07	1940	5	0.00	0.00	615.12	689.18	14.82	4.13	0.48	0.13	8.62
CH07	1945	5	0.00	0.00	590.42	704.24	24.70	15.30	0.82	0.45	6.07
CH07	1955	10	0.00	0.00	570.65	763.51	19.76	10.42	0.34	0.15	6.97
CH07	1961	6	0.00	0.00	531.13	779.73	39.52	25.29	1.19	0.56	6.92
CH07	1968	7	0.00	0.00	499.01	795.94	32.11	24.71	0.89	0.46	5.85
CH07	1978	10	0.00	0.00	464.43	830.16	34.58	34.70	0.72	0.44	6.89
CH07	1983	5	106.23	0.66	533.60	801.86	37.06	55.83	1.65	1.38	5.51
CH07	1988	5	34.58	0.25	543.48	798.12	24.70	34.91	0.94	0.89	6.23
CH07	1993	5	123.52	0.61	652.17	816.10	14.82	16.09	0.55	0.41	6.82
CH07	1998	5	93.87	0.68	701.58	770.53	44.47	71.71	1.40	1.82	5.23
CH07	2003	5	400.20	2.81	1044.96	739.15	56.82	67.96	1.67	1.83	7.32
CH07	2008	5	256.92	1.81	1173.42	631.28	128.46	144.62	2.59	4.26	7.35
CH07	2013	5	145.75	0.88	1242.59	628.14	76.58	41.54	1.34	1.35	7.68

Table S-3g. Plot-level data summary for CH08.

Plot	Year	Interval	Ingrowth		All live trees		Mortality		Mortality rate (%)		NPP
			Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	
CH08	1935				884.39	624.25					
CH08	1940	5	0.00	0.00	827.57	647.30	56.82	24.06	1.32	0.78	9.42
CH08	1945	5	0.00	0.00	795.45	676.88	32.11	12.35	0.79	0.38	8.39
CH08	1955	10	0.00	0.00	711.46	700.64	83.99	40.11	1.11	0.61	6.39
CH08	1961	6	0.00	0.00	694.17	724.69	17.29	7.01	0.41	0.17	5.18
CH08	1968	7	0.00	0.00	647.23	748.75	46.93	33.12	1.00	0.67	8.17
CH08	1978	10	0.00	0.00	573.12	768.23	74.11	56.11	1.21	0.78	7.56
CH08	1983	5	316.21	2.70	842.39	738.55	46.94	61.66	1.69	1.66	6.40
CH08	1988	5	264.33	1.45	1074.60	750.20	32.11	25.28	0.77	0.69	7.39
CH08	1993	5	148.22	0.84	1136.36	732.60	86.46	58.32	1.66	1.61	8.14
CH08	1998	5	160.57	0.98	1205.53	662.71	91.40	98.01	1.66	2.83	5.62
CH08	2003	5	301.38	2.08	1200.59	421.62	306.32	269.33	5.69	9.91	5.65
CH08	2008	5	254.45	2.09	1188.24	174.70	266.80	278.44	4.90	19.43	6.31
CH08	2013	5	192.69	2.22	1254.94	185.41	125.99	38.18	2.22	4.81	9.78

Table S-3h. Plot-level data summary for CH10.

Plot	Year	Interval	Ingrowth		All live trees		Mortality		Mortality rate (%/yr)		NPP (Mg/ha/yr)
			Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	
CH10	1935				400.20	676.50					
CH10	1940	5	0.00	0.00	365.61	699.94	34.58	20.95	1.79	0.63	8.88
CH10	1945	5	0.00	0.00	363.14	737.69	4.94	4.68	0.27	0.13	8.49
CH10	1955	10	0.00	0.00	321.15	774.34	42.00	36.11	1.22	0.50	7.28
CH10	1961	6	0.00	0.00	296.45	796.12	24.70	11.53	1.32	0.25	5.55
CH10	1968	7	0.00	0.00	269.27	817.89	27.17	34.98	1.36	0.64	8.11
CH10	1978	10	0.00	0.00	244.57	850.05	24.70	30.16	0.96	0.37	6.23
CH10	1983	5	0.00	0.00	237.15	868.83	7.41	8.78	0.61	0.21	5.51
CH10	1988	5	0.00	0.00	202.57	868.81	34.58	34.27	3.10	0.80	6.85
CH10	1993	5	79.05	0.87	264.33	862.33	17.29	31.86	1.77	0.74	5.08
CH10	1998	5	145.75	1.77	400.20	861.79	9.88	31.93	0.76	0.75	6.28
CH10	2003	5	150.69	1.54	538.54	892.08	12.35	5.03	0.63	0.12	7.06
CH10	2008	5	205.04	2.16	701.58	883.11	42.00	43.97	1.61	1.01	7.00
CH10	2013	5	229.74	2.37	864.62	918.31	66.70	15.31	1.98	0.35	10.10

Table S-3i. Plot-level data summary for CH12.

Plot	Year	Interval	Ingrowth		All live trees		Mortality		Mortality rate (%/yr)		NPP (Mg/ha/yr)
			Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	
CH12	1935				491.60	552.87					
CH12	1940	5	0.00	0.00	484.19	598.56	7.41	2.74	0.30	0.10	9.69
CH12	1945	5	0.00	0.00	454.55	613.16	29.64	23.73	1.26	0.81	7.66
CH12	1955	10	0.00	0.00	432.31	679.25	22.23	12.74	0.50	0.21	7.88
CH12	1961	6	0.00	0.00	410.08	712.22	22.23	15.82	0.88	0.39	8.13
CH12	1968	7	0.00	0.00	392.79	745.18	17.29	10.94	0.61	0.22	6.27
CH12	1978	10	0.00	0.00	335.97	724.69	56.82	77.07	1.55	1.09	5.66
CH12	1983	5	296.44	2.34	607.71	724.14	24.70	35.75	1.52	1.01	7.04
CH12	1988	5	145.75	0.89	723.81	716.47	29.64	45.32	1.00	1.28	7.53
CH12	1993	5	185.28	1.04	854.74	722.87	54.35	37.38	1.55	1.07	8.76
CH12	1998	5	42.00	0.24	802.87	727.40	93.87	28.47	2.30	0.80	6.60
CH12	2003	5	76.58	0.42	807.81	696.16	71.64	79.85	1.85	2.30	9.72
CH12	2008	5	24.70	0.26	671.94	521.92	160.57	208.50	4.34	6.87	6.85
CH12	2013	5	29.64	0.21	644.76	494.68	56.82	69.90	1.75	2.83	8.53

Table S-3j. Plot-level data summary for CH13.

Plot	Year	Interval	Ingrowth		All live trees		Mortality		Mortality rate (%/yr)		NPP (Mg/ha/yr)
			Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	
CH13	1935				538.54	517.05					
CH13	1940	5	0.00	0.00	526.19	555.06	12.35	7.44	0.46	0.29	9.09
CH13	1945	5	0.00	0.00	506.42	581.29	19.76	12.21	0.76	0.44	7.69
CH13	1955	10	0.00	0.00	447.13	613.50	59.29	40.20	1.24	0.71	7.24
CH13	1961	6	0.00	0.00	407.61	632.97	39.52	35.30	1.53	0.98	9.13
CH13	1968	7	0.00	0.00	392.79	652.43	14.82	8.60	0.53	0.20	4.01
CH13	1978	10	0.00	0.00	274.21	538.88	118.58	165.13	3.53	2.88	5.16
CH13	1983	5	491.60	4.75	699.11	463.27	66.70	106.71	5.42	4.32	6.22
CH13	1988	5	187.75	1.68	854.74	456.76	32.11	45.76	0.94	2.06	7.85
CH13	1993	5	217.39	1.64	1022.73	480.15	49.41	9.41	1.18	0.42	6.56
CH13	1998	5	51.88	0.78	956.03	486.43	118.58	31.94	2.43	1.37	7.64
CH13	2003	5	42.00	0.26	862.15	512.92	135.87	19.14	3.02	0.80	9.13
CH13	2008	5	4.94	0.04	696.64	477.33	170.45	77.69	4.31	3.23	8.42
CH13	2013	5	17.29	0.08	615.12	511.90	98.81	23.20	3.01	0.99	11.55

Table S-4. Means (standard deviations) of data from 10 plots at Cascade Head Experimental Forest (*continued on next page*).

Year	Interval	Ingrowth		All live trees		Mortality		Mortality rate (%/yr)		NPP (Mg/ha/yr)
		Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	Trees/ha	Biomass (Mg/ha)	
1935				537.55 (153.51)	635.02 (66.75)					
1940	5	0	0	515.81 (145)	667.71 (62.78)	21.74 (15.83)	11.82 (7.67)	0.82 (0.55)	0.37 (0.24)	8.90 (0.83)
1945	5	0	0	497.53 (137.19)	695.41 (64.45)	18.53 (10.03)	10.70 (6.1)	0.70 (0.32)	0.33 (0.21)	7.68 (0.81)
1955	10	0	0	457.51 (123.86)	735.54 (60.29)	40.02 (22.96)	29.42 (18.29)	0.84 (0.38)	0.43 (0.26)	6.96 (0.62)
1961	6	0	0	434.29 (119.76)	756.34 (60.14)	23.22 (12.28)	20.70 (14.16)	0.87 (0.42)	0.49 (0.35)	6.92 (1.82)
1968	7	0	0	371.79 (162.68)	710.38 (226.1)	62.50 (116.42)	86.12 (191.29)	3.74 (9.07)	2.74 (7.13)	5.74 (3.83)
1978	10	57.47 (181.74)	0.04 (0.11)	389.48 (130.55)	722.12 (242.74)	39.77 (34.63)	49.83 (45.06)	1.11 (0.91)	0.77 (0.78)	6.16 (1.88)
1983	5	386.83 (513.08)	2.20 (2.46)	747.17 (590.09)	707.62 (240.94)	29.15 (18.77)	47.23 (30.37)	1.75 (1.42)	1.49 (1.10)	6.55 (1.18)
1988	5	127.14 (124.41)	0.62 (0.56)	852.07 (705.67)	720.62 (235.62)	22.73 (10.97)	23.03 (16.39)	0.94 (0.81)	0.7 (0.6)	7.20 (0.94)
1993	5	113.64 (65.31)	0.70 (0.46)	876.13 (544.53)	727.53 (221.36)	89.57 (158.96)	29.89 (20.14)	1.63 (1.10)	0.92 (0.59)	7.36 (2.52)

1998	5	95.85 (67.54)	0.69 (0.53)	868.97 (388.42)	718.10 (217.39)	103.01 (147.86)	43.31 (32.75)	1.87 (1.31)	1.51 (1.30)	6.78 (2.6)
2003	5	165.27 (175.89)	1.16 (1.28)	897.96 (282.89)	682.95 (232.21)	136.27 (163.12)	76.52 (84.80)	2.80 (2.21)	2.54 (3.03)	8.28 (2.54)
2008	5	153.16 (153.00)	1.56 (1.67)	907.86 (282.06)	596.50 (283.13)	143.28 (119.89)	122.23 (102.05)	3.29 (2.29)	5.29 (6.26)	7.16 (1.74)
2013	5	110.67 (94.85)	1.02 (1.10)	927.62 (305.77)	589.92 (279.71)	90.91 (41.14)	48.62 (26.06)	2.09 (0.72)	2.33 (2.15)	8.41 (1.92)