

Assessing tree mortality in an old-growth forest:
Wind River Forest Dynamics Plot 2010-2012

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Abstract

Analyzing tree mortality data is essential to understanding how the forest dynamics change over time and will allow better management of the forest ecosystem. This study investigated the biotic, mechanical and stress factors associated with death in the Wind River Forest Dynamics Plot (WFDP). The study area is a 25.6 hectare (800 m × 320 m) permanent sample plot located in old-growth *Pseudotsuga menziesii*—*Tsuga heterophylla* forest in the Gifford Pinchot National Forest, Washington state. Forest tree composition (31,167 live stems ≥ 1 cm dbh) is predominantly *Acer circinatum*, *Tsuga heterophylla*, *Abies amabilis*, *Taxus brevifolia*, *Pseudotsuga menziesii*, *Thuja plicata*, and *Abies grandis*. The overall mortality rate for all species was 1.6% in 2010-2011 and 1.1% in 2011-2012. As predicted for a *Pseudotsuga menziesii*—*Tsuga heterophylla* old-growth temperate forest, large-diameter (≥ 100 cm dbh) *P. menziesii* are dying and being replaced predominately with smaller *Tsuga heterophylla*. If mortality continues at the current rate, there will be less than 10 *P. menziesii* ≥ 100 cm dbh alive in the year 2180.

Introduction

The Wind River Forest Dynamics Plot (WFDP) is a 25.6 hectare (800 m × 320 m) permanent sample plot located in old-growth Douglas-fir (*Pseudotsuga menziesii*)—western hemlock (*Tsuga heterophylla*) forest in the Cascade Range of Washington state. This 500 year-old forest is located 371 m above sea level and 20 km north of the Columbia River in the Gifford Pinchot National Forest, within the T.T. Munger Research Natural Area (Shaw *et al.* 2004). The plot was established during the summers of 2010 and 2011.

In accordance with the Smithsonian's Center for Tropical Forest Science protocol, all woody stems (trees and shrubs) greater than or equal to (\geq) one centimeter in diameter at breast height (dbh) are tagged and mapped (Condit 1998). In total, the plot comprises 31,167 live stems \geq 1 cm at dbh, or 1.37 m. Forest tree structure is predominantly western hemlock (*Tsuga heterophylla*), Pacific silver fir (*Abies amabilis*), Pacific yew (*Taxus brevifolia*), Douglas-fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*) and grand fir (*Abies grandis*). Understory species with diameter \geq 1 cm at dbh include beaked hazelnut (*Corylus cornuta* var. *californica*) and vine maple (*Acer circinatum*). Plant nomenclature follows Hitchcock and Cronquist (1973). As for the impact of mammalian species, the plot lies within the range of a large herd of elk (*Cervus canadensis*).



Figure 1. Tagged tree in Wind River Forest Dynamics Plot.

Tree death is a complex process as the causes and patterns often vary (Franklin *et al.* 1987). Tree mortality consists of removing genetically unique individuals from the stand, but these dead trees provide habitat and decomposed material to surrounding

organisms as a standing snag or fallen woody debris. By assessing tree mortality on an annual basis, we can determine the composition changes over time in the structure of the forest. Along with rates of recruitment and growth, mortality is essential to understanding the long-term stand dynamics. Tree mortality analysis can determine if the balance of recruitment against mortality will be sufficient to sustain individual species populations, forest ecosystem services and the overall biomass. Large permanent sample plots, like WFDP, monitor the magnitude of climate effects and insect outbreaks in a forest ecosystem through annual mortality checks. Collecting annual data exposes forest ecosystem shifts over time by differentiating climatic shifts from temporal variability, and the sample size (31,167 live stems ≥ 1 cm dbh) of the WFDP plot is large enough to examine mortality by species and size class. The observed changes in forest composition found in WFDP can be used to improve the understanding and management of similar regional and global forests.

Predictions for mortality rates

The structure of a natural, old-growth *P. menziesii*—*Tsuga heterophylla* forest follows ecosystem, community, and population trends that can be used to predict stand age, composition and productivity (Franklin *et al.* 2002). The data from WFDP—a late-successional temperate forest—should demonstrate that if mortality continues at a similar rate in WFDP, there will be a gradual shift from a forest once dominated by large-diameter *P. menziesii* to one dominated by smaller-diameter *Tsuga heterophylla*. After a stand-replacement fire approximately 500 years ago, *P. menziesii* was able to establish in the region (Gray and Franklin 1997). As a shade-intolerant species, it is typical for *P. menziesii* to dominate early-successional forests in the Pacific Northwest post-disturbance. However,

with no stand-replacement disturbances occurring in the last several centuries and gaps in the forest canopy allowing sunlight to reach the forest floor, it is expected that the 2010-2012 mortality data will display forest composition slowly shifting to shade-tolerant species like *Tsuga heterophylla*, *Taxus brevifolia*, and *A. amabilis*.

Materials and Methods

The eastern and western portions of the WFDP were established in the summers of 2010 and 2011, respectively. All freestanding woody stems ≥ 1 cm dbh were identified, mapped, and tagged, following measurement protocol established by the global Smithsonian Network (Condit 1998). Field crews within the 25.6 ha sampling area fulfilled a complete inventory of all WFDP trees in 2012 by checking for in-growth (trees ≥ 1 cm dbh), as well as the location accuracy and vigor of all tagged trees. For any live tree at previous inventory and found newly dead, a full mortality check was done to determine the factors associated with death (FADs) and overall tree condition (Table 1). This involved recording the tag number, re-measuring the dbh and stem height, confirming the species, assessing the stem and root condition, and determining the portion of the tree supported by the ground. We then identified FADs by inspecting each tree mortality for biotic factors such as beetle entry and exit holes, beetle frass, fungal fruiting bodies, and any mechanical damage visible on the outside of the tree. We peeled off the bark near 1.37 m and at the base of the tree to check for possible sapwood damage, examining it for beetle galleries and mycelial fans. If no biotic or mechanical factors appeared to be the culprit, stress from suppression and competition was considered as the primary FAD. The data recorder wrote down the FAD codes determined from the mortality check and then the tree tag was hammered into the

bark to confirm that the mortality check had been completed. This was done for all 20 m × 20 m grid cells within the plot.

Table 1. Tree condition and factors associated with dead (FAD) codes used by field surveyors in WFDP.

Tree Condition	Description	FAD	Description
<u>Crown</u>		40	Unknown
01	Dead needles or leaves present	<u>Biotic</u>	
02	Earlier loss of crown portion	50	Suppression
03	Foliage damage	51	Animal Damage
04	Spike top/ top dieback	52	Mistletoe
05	Crown flat topped	<u>Disease</u>	
06	Mistletoe plants observed	61	White pine blister rust
07	Witches brooms	62	Rot—specify
<u>Bole/Branches/Roots</u>		63	Canker
13	Rotten wood	64	Other (specify)
14	Mycelia/ rhizomorphs/ fungal fruiting body	65	Unknown
15	Rot at break	<u>Insect</u>	
16	Pitch tube on bole	71	Bark (specify if possible)
17	Beetle galleries	72	Defoliating (specify if possible)
18	Exit/entrance holes	73	Other (specify)
19	Conks	<u>Physical</u>	
20	Swelling	80	Uprooted by falling tree parts
21	Canker	81	Uprooted (note cause)
22	Evidence of scale	82	Broken stem by falling tree parts
23	Tree is hollow	83	Broken stem (note extent/cause)
24	Pitching	84	Crown damage
25	Pitch sheets	85	Crushed by falling tree parts
26	Oozing wounds	86	Crushed (note cause)
27	Bark sloughing	87	Lightning
28	Scar on bowl	88	Other (note cause)
29	Girdling	89	Tree located, removed from plot
30	Woodpecker/ Sapsucker activity	<u>Fire</u>	
31	Snow/ ice damage	91	Crown scorch
<u>Other</u>		92	Bole/stem char
36	Tree dead several years	93	Crown or bole/stem combustion
37	Tree dead above breast height, live below	94	Other (specify)
38	Tree not found		

Once the field survey was completed, I entered the mortality data and associated comments into Microsoft Excel. I interpreted the codes and any additional comments made by the field recorder to determine the principal FAD for all mortalities occurring on the

eastern portion of the plot from 2010-2012 and the western portion of the plot from 2011-2012. They were placed into four categories of mortality: biotic, mechanical, stress and unknown. While the presence of a biotic FAD—tree-killing pathogens, insects or vertebrate—can sometimes lead to an



Figure 2. Evidence of windthrow.

automatic placing of the mortality into the biotic category, the WFDP plot is unique in that evidence of the fir engraver (*Scolytus ventralis*) was often found under the bark, but the galleries were frequently not large enough to be considered the main factor of death.

Because the beetles will often colonize dead trees, it was necessary to take into account all factors listed on the field data sheets to select biotic, mechanical, stress or unknown factors. Other common biotic factors in WFDP included mistletoe, black fungus under the bark, white mycelial fans from *Armillaria* and *Phellinus weirii* (Furniss 1997). Mechanical factors entailed physical damage to the tree, such as evidence of crushing, snapping or uprooting. Often, biotic factors weaken the tree and predispose a tree to mechanical failure so it was important to establish which factor ultimately killed the tree (Franklin *et al.* 2002). Stress, or suppression, is a density-dependent mortality in that the trees growth is restricted by crowding or insufficient photosynthesis. For some dead trees, the FAD was unknown because the mortality factors identified were not deemed sufficient to kill tree and field inspection yielded no definitive evidence of causal factors. These were often standing dead trees absent of biotic and mechanical damage, and with ample sunlight. I then calculated mortality rates for 2011-2012, using the equation:



Figure 3. Evidence of laminated root rot (*Phellinus weirii*)

$$m_1 = 100 [1 - (N_1 / N_0)]^{1/t}$$

where m_1 is the one-year mortality rate, N_0 is the number of stems alive in 2011, N_1 is the number of stems alive in 2012 that were alive in 2011, and the $t = 1$ is the number of years between measurements (Lutz and Halpern 2006). Because the plot was implemented over two field seasons, the western half of the plot had a one-year interval between measurements and the eastern half of the plot had a two-year interval between measurements. In order to determine the mortality rate for 2010-2011 for the eastern portion of the plot, it was necessary to make the assumption that mortality rates were equal throughout the entire 25.6 ha of the plot. This was done by calculating the one-year mortality rate of the western portion of the plot from 2011-2012. Then, using those mortality rates I found the assumed number of trees still alive at the beginning of 2011 in the eastern portion of the plot:

$$\text{Assumed \# Trees} = N_2 / (1 - m_1)$$

Because we are assuming the mortality rate for 2011-2012 is the same for the eastern and western portion of the plot, we can use the assumed number of trees alive in 2011 to find the 2010-2011 mortality rate by using the total number of trees (N_0) identified in the 2010 plot installation:

$$m = 100 [1 - (\text{Assumed \# Trees} / N_0)]$$

The assumption of equal mortality in 2011-2012 for both portions of the plot resulted in the 1-year mortality rates for both 2010-2011 and 2011-2012, allowing for more robust mortality analysis and comparisons.

Results

Mortality rates

Mortality rates were analyzed by species and four size classes: $1 \text{ cm} \leq \text{dbh} < 10 \text{ cm}$, $10 \text{ cm} \leq \text{dbh} < 50 \text{ cm}$, $50 \text{ cm} \leq \text{dbh} < 100 \text{ cm}$ and $\text{dbh} \geq 100 \text{ cm}$. Species that had more than

Table 2. Tree species, by Garrison code, observed for eastern (2010-2012) and western (2011-2012) portion of WFDP, categorized by total trees n , size class, and total mortalities by species (Garrison *et. al.* 1974).

Species	2010—2012 EASTERN						2011—2012 WESTERN					
	n	$1 \leq \text{dbh} < 10 \text{ (cm)}$	$10 \leq \text{dbh} < 50 \text{ (cm)}$	$50 \leq \text{dbh} < 100 \text{ (cm)}$	$\text{dbh} \geq 100 \text{ (cm)}$	Morts.	n	$1 \leq \text{dbh} < 10 \text{ (cm)}$	$10 \leq \text{dbh} < 50 \text{ (cm)}$	$50 \leq \text{dbh} < 100 \text{ (cm)}$	$\text{dbh} \geq 100 \text{ (cm)}$	Morts.
ABAM	1764	1563	186	15	0	34	2653	1869	748	35	1	15
ABPR	37	10	15	12	0	3	11	7	4	0	0	0
ABGR	7	0	2	5	0	0	4	1	0	3	0	0
ACCI	5122	5080	42	0	0	175	6044	5991	53	0	0	91
ACGL	1	1	0	0	0	0	0	0	0	0	0	0
ALRU	2	1	1	0	0	0	6	3	3	0	0	0
AMAL	0	0	0	0	0	0	7	7	0	0	0	0
COCOC	259	258	1	0	0	10	382	382	0	0	0	9
CONU	79	64	15	0	0	8	102	78	24	0	0	1
GASH	13	13	0	0	0	0	1	1	0	0	0	1
HODI	4	4	0	0	0	0	15	15	0	0	0	1
OECE	2	2	0	0	0	0	0	0	0	0	0	0
MEFE	0	0	0	0	0	0	15	15	0	0	0	0
PIMO	2	0	1	0	1	0	4	0	0	3	1	0
PSME	374	2	4	126	242	3	200	2	14	116	68	1
RHMA	20	20	0	0	0	0	438	438	0	0	0	4
RHPU	0	0	0	0	0	0	1	1	0	0	0	1
ROGY	1	1	0	0	0	0	0	0	0	0	0	0
RUSP	1	1	0	0	0	0	0	0	0	0	0	0
TABR	1018	369	646	3	0	55	1078	385	686	7	0	14
THPL	166	18	53	55	40	2	35	4	10	15	6	0
TSHE	4705	2378	1589	697	41	72	5287	2498	1954	780	55	41
VAME	1	1	0	0	0	0	0	0	0	0	0	0
VAOV	53	53	0	0	0	1	12	12	0	0	0	0
VAPA	756	756	0	0	0	18	485	485	0	0	0	2

19 mortalities include *Abies amabilis*, *Acer circinatum*, *C. cornuta* var. *californica*, *Taxus brevifolia*, and *Tsuga heterophylla* (Table 2). While *Vaccinium parvifolium* had a relatively large number of mortalities, 95% of the mortalities had $\text{dbh} < 2\text{cm}$ and thus were not

considered for further investigation. *P. menziessi* had only four mortalities, however, they all occurred in trees > 100 cm dbh. Hence, they are included in further analysis to illustrate the shifting forest composition in the WFDP.

Temporal Variation in Mortality

Under the aforementioned assumption that the mortality rates in any single year are the same for the eastern and western portions of the plot, the mortality rates for 2010-2011 and 2011-2012 were calculated (Table 3).

Table 3. Temporal variation of mortality rates for common woody stems ≥ 1 cm dbh in WFDP.

Species	Family	2010-2011	2011-2012
<i>Abies</i> (all species)	Pinaceae	1.5%	0.6%
<i>Acer circinatum</i>	Sapindaceae	1.9%	1.5%
<i>Corylus cornuta</i> var. <i>californica</i>	Betulaceae	1.5%	2.4%
<i>Pseudotsuga menziesii</i>	Pinaceae	0.3%	0.5%
<i>Taxus brevifolia</i>	Taxaceae	4.1%	1.3%
<i>Thuja plicata</i>	Cupressaceae	1.2%	0.0%
<i>Tsuga heterophylla</i>	Pinaceae	0.8%	0.8%
Other	N/A	2.0%	0.9%
Overall	N/A	1.6%	1.1%

The overall mortality rate was 1.6% in 2010-2011 and 1.1% in 2011-2012 for all species. The mortality rate for the *Abies* genus (*Abies amabilis*, *Abies grandis*, *Abies procera*) was 2.5 times higher in 2010-2011 than 2011-2012. *Taxus brevifolia* follows a similar trend, as the 2010-2011 mortality rate was 3.2 times higher than the 2011-2012 mortality rate. *Thuja plicata*, on the other hand, had a mortality rate of 1.2% in 2010-2011 but 0.0% in 2011-2012. *Acer circinatum*, *P. menziesii*, and *Tsuga heterophylla* had similar—within 0.4%—mortality rates for both time intervals.

Characteristics of Mortality

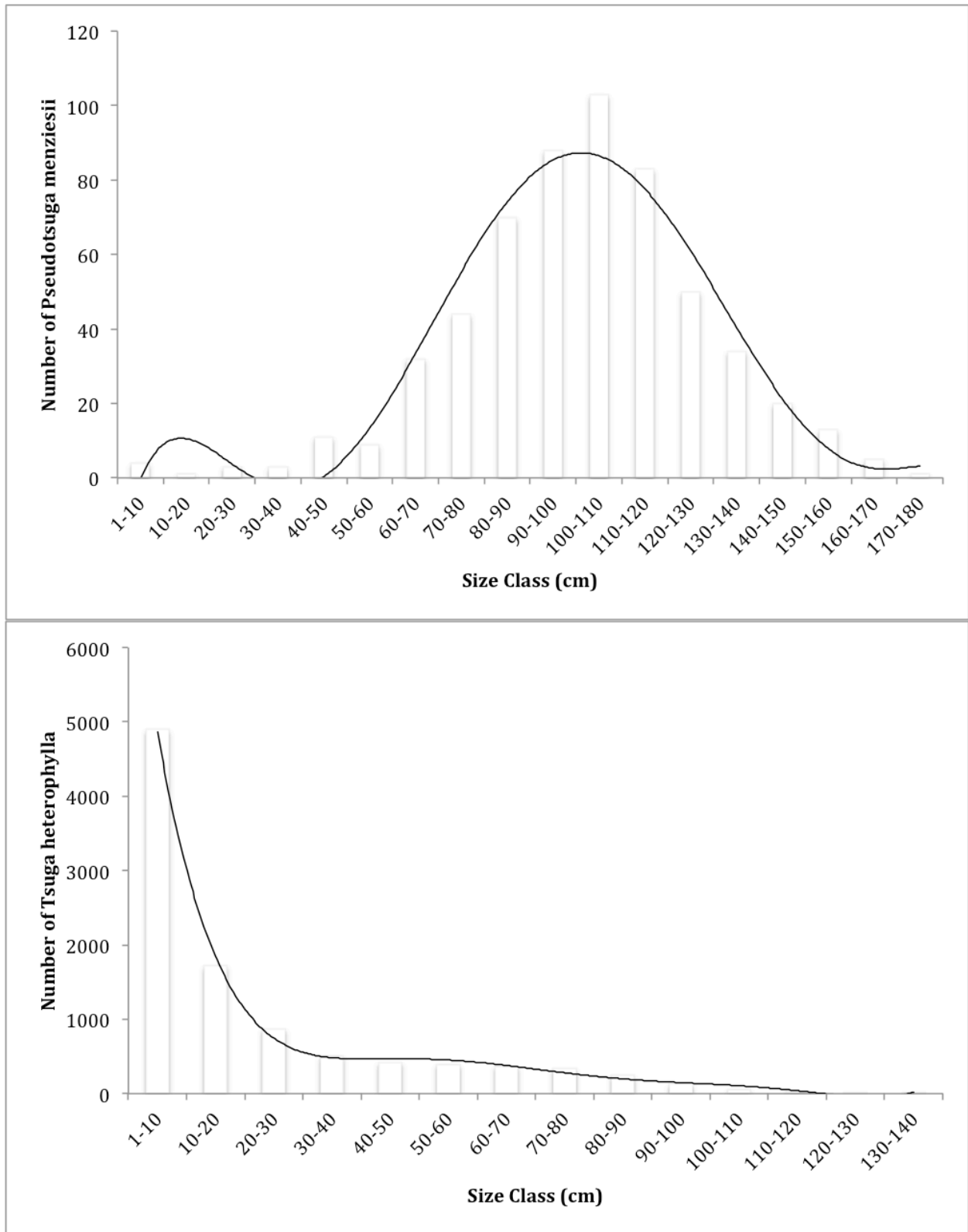
The mortality rates for *Acer circinatum*, *Tsuga heterophylla*, *Taxus brevifolia*, and *P. menziesii* vary by size class in the WFDP old-growth temperate forest (Table 4).

Table 4. Mortality rate by diameter class for selected species.

Species	2010—2011 EASTERN					2011—2012 WESTERN				
	Overall	1 ≤ dbh	10 ≤ dbh	50 ≤ dbh	dbh ≥ 100	Overall	1 ≤ dbh	10 ≤ dbh	50 ≤ dbh	dbh ≥ 100
	Rate	< 10 (cm)	< 50 (cm)	< 100 (cm)	(cm)	Rate	< 10 (cm)	< 50 (cm)	< 100 (cm)	(cm)
<i>Acer Circinatum</i>	1.9%	2.0%	0.0%	N/A	N/A	1.5%	1.5%	1.9%	N/A	N/A
<i>Pseudotsuga menziesii</i>	0.3%	0.0%	0.0%	0.0%	1.2%	0.5%	0.0%	0.0%	0.0%	0.0%
<i>Taxus brevifolia</i>	4.1%	7.0%	2.5%	0.0%	N/A	1.3%	2.1%	0.9%	0.0%	N/A
<i>Tsuga heterophylla</i>	0.8%	0.1%	0.4%	3.7%	0.0%	0.8%	0.7%	0.7%	1.0%	1.8%

By comparing the species by diameter class, two important observations should be noted. Firstly, *Taxus brevifolia* has a high mortality rate of 7.0% for stems 1 cm ≤ dbh < 10 cm and 2.5% for stems 10 cm ≤ dbh < 50 in 2010-2011. Another key observation from the size class breakdown was that 1.2% of the total *P. menziesii* ≥ 100 cm dbh died from 2010-2011. While this consists of only three trees of 242 in the large-diameter size class on the eastern portion of the plot, young *P. menziesii* trees are not replacing this biomass. Only two *P. menziesii* < 27 cm are found in the eastern portion of the plot where the mortalities are occurring. As predicted for a *P. menziesii*—*Tsuga heterophylla* old-growth forest by Winter *et al.*, large *P. menziesii* are dying off and not being replaced (2002). Instead, the abundance of shade-tolerant species like *Tsuga heterophylla* are increasing as evidence by the 2378 stems ≤ 10 cm dbh on the eastern portion of the plot (Table 2). The diameter distribution for *P. menziesii* was highest for size classes between 90 and 120 cm dbh (Figure 4).

Figure 4. Diameter distribution of *Pseudotsuga menziesii* and *Tsuga heterophylla* in the WFDP plot.



Mortality by principal cause and diameter class were made by species and year.

(Tables 5, 6).

Table 5. Mortality rate by factor associated with death (FAD) for selected species under the aforementioned assumption of uniform mortality for 2011-2012.

Species, Year	Biotic	Mechanical	Stress	Unknown
<i>Acer circinatum</i>				
2010-2011	1.0%	0.3%	0.1%	0.0%
2011-2012	0.6%	0.6%	0.8%	0.1%
<i>Pseudotsuga menziesii</i>				
2010-2011	0.0%	0.5%	0.0%	0.0%
2011-2012	0.8%	0.0%	0.0%	0.0%
<i>Taxus brevifolia</i>				
2010-2011	0.6%	0.5%	0.3%	0.0%
2011-2012	2.1%	1.1%	0.7%	0.2%
<i>Tsuga heterophylla</i>				
2010-2011	0.3%	0.3%	0.2%	0.0%
2011-2012	0.1%	0.1%	0.5%	0.0%

For 2010-2011, *Acer circinatum* died predominantly from biotic factors, *P. menziesii* from mechanical factors while *Taxus brevifolia* and *Tsuga heterophylla* had very similar mortality rates from biotic and mechanical factors. Stress was more of a factor overall from 2011-2012 when *Acer circinatum*, *Taxus brevifolia* and *Tsuga heterophylla* all had greater than 0.5% mortality rates. The biotic mortality rate for *P. menziesii* was high at 0.8% in 2011-2012 and for *Taxus brevifolia* at 2.1% in 2011-2012.

Table 6. Proportion of factors associated with death in relation to size class for selected species under the assumption of uniform mortality for 2011-2012.

Species	2010—2011 EASTERN				2011—2012 WESTERN			
	1 ≤ dbh < 10 (cm)	10 ≤ dbh < 50 (cm)	50 ≤ dbh < 100 (cm)	dbh ≥ 100 (cm)	1 ≤ dbh < 10 (cm)	10 ≤ dbh < 50 (cm)	50 ≤ dbh < 100 (cm)	dbh ≥ 100 (cm)
	<i>Acer circinatum</i>							
Biotic	66.7%	100.0%	--	--	47.4%	--	--	--
Mechanical	23.3%	0.0%	--	--	25.1%	--	--	--
Stress	7.8%	0.0%	--	--	25.1%	--	--	--
Unknown	2.2%	0.0%	--	--	2.3%	--	--	--
<i>Pseudotsuga menziesii</i>								
Biotic	--	--	--	0.0%	--	--	--	100.0%
Mechanical	--	--	--	100.0%	--	--	--	0.0%
Stress	--	--	--	0.0%	--	--	--	0.0%
Unknown	--	--	--	0.0%	--	--	--	0.0%
<i>Taxus brevifolia</i>								
Biotic	62.5%	16.7%	--	--	35.5%	63.6%	--	--
Mechanical	37.5%	83.3%	--	--	35.5%	31.8%	--	--
Stress	0.0%	0.0%	--	--	25.8%	9.1%	--	--
Unknown	0.0%	0.0%	--	--	3.2%	4.5%	--	--
<i>Tsuga heterophylla</i>								
Biotic	50.0%	33.3%	50%	0.0%	22.2%	43.8%	50%	--
Mechanical	15.4%	66.7%	50%	100%	18.5%	43.8%	50%	--
Stress	30.8%	0.0%	0.0%	0.0%	57.4%	12.5%	0.0%	--
Unknown	3.8%	0.0%	0.0%	0.0%	1.9%	0.0%	0.0%	--

The majority of deaths for *Acer circinatum* was from biotic factors, with mechanical and stress playing lesser roles in both years. *P. menziesii* has 100% mechanical death in 2010-2011 and 100% biotic death in 2011-2012, but this is attributed to the small number of mortalities—one mortality in 2010-2011 and three from 2011-2012. *Taxus brevifolia* mortality rates are high before they reach the medium size class, with no mortalities > 44 cm. These smaller trees are mostly being killed by biotic and mechanical factors. *Tsuga heterophylla*, on the other hand, has a higher rate of stress mortalities (30.8% and 57.4%) for the 1 cm ≤ dbh < 10 cm size class than the other species. While biotic factors predominately kill the small *Tsuga heterophylla*, mechanical factors become the principal cause after they reach ≥ 10cm.

Discussion

The hypothesis that forest composition is gradually shifting from shade-intolerant species like *P. menziesii* to shade-tolerant species like *Tsuga heterophylla*, *Taxus brevifolia*, and *Abies amabilis* in WFDP is supported by our findings (North *et al.* 2004). Franklin *et al.* calculated a mortality rate for *P. menziesii*—0.75% in Wind River Experimental Forest—almost double the 0.3% in 2010-2011 and 0.5% from 2010-2012 found in WFDP (1987). The high mortality rate in Franklin *et al.* could be due to the high wind-related mortality (33-46% of total), as only one *P. menziesii* died from mechanical factors during our study period. The low mechanical cause of death could be attributed to no major windstorms occurring over the two years of the study strong enough to uproot a large-diameter *P. menziesii*.

Of the 563 deaths recorded in the eastern and western portions of the plot, 48% of the deaths were from biotic factors, while 26% and 24% were from stress and mechanical factors, respectively. Contrastingly, Das *et al.* recorded suppression in more than half (53%) of the dead trees in the Sierra Nevada of California (2011). The WFDP has a relatively low percentage for stress, likely because competition in old-growth forests ceases to be the primary cause of mortality. In the WFDP, biotic agents are the most dominate cause, attributing for almost half of the deaths and competition plays a lesser role.

Condit *et al.* found a high annual mortality rate of 2-3% in Panama forests. (1995). Mortality rates in tropical forests are much higher than the 1.1-1.6% mortality rate found in the WFDP temperate forest. Tree-diameters in the tropics do not grow as large as trees found in the Pacific Northwest of the United States. Thus, high mortality rates in the small

trees of Panama can be compared to the understory species and smaller stems like *Acer circinatum* in WFDP (Table 4).

Taxus brevifolia grow in forests dominated by shade-intolerant species like *P. menziesii*, as well as shade-intolerant forests dominated by late-successional species like *Tsuga heterophylla* (Busing *et al.* 1995). This would support the low annual mortality rates observed for *Taxus brevifolia* in most forest types, supported by Busing *et al.*'s finding of 0.83% mean annual mortality for *Taxus brevifolia* \geq 5 cm dbh in mature and old-growth forests in Washington and Oregon. However, the results in Table 3 illustrate episodic mortalities for *Taxus brevifolia*. The mortality rate was 4.1% in 2010-2011 and only 1.3% in 2011-2012. There are no tree deaths for dbh > 50 cm, suggesting that *Taxus brevifolia* has low mortality rates when they reach a large diameter-class, but they are especially susceptible to biotic and mechanical factors early on in development.

The ecological services of carbon storage and species habitat identified by Lutz *et al.* is important when considering the large-diameter tree decline in WFDP (2012). Large-diameter *P. menziesii* trees in WFDP are being replaced by smaller, shade-tolerant species. While *P. menziesii* has little mortality relative to other species—0.3% and 0.5% versus 1.1% and 1.6% overall mortality—it is all large-diameter trees dying (Figure 4). It is expected that the amount of woody debris will increase in WFDP as the large-diameter dead trees becoming snags and coarse woody debris when they eventually fall to the ground. If mortality trends continue at the rate they have been for the last two years, there will be less than 10 of the 304 *P. menziesii* \geq 100 cm dbh by the year 2180. Furthermore, with predictions by van Mantgem *et al.* that tree mortality rates will further increase in the western United States across elevations and tree sizes, *P. menziesii* likely will have even

higher mortality rates in future decades (2009). The findings in WFDP follow the trend of large-diameter tree populations around the world dying and being replaced by younger, smaller trees (Lindenmayer *et al.* 2012, Lutz *et al.* 2009). Given these observations, I suggest continuing annual mortality analysis of WFDP and similar plots to monitor regional warming and consequent increases in tree mortality from water deficits, insect outbreaks, and natural disturbances.

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