AN ABSTRACT OF THE THESIS OF

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Abstract approved:

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Windthrow has been studied extensively as a cause of mortality and as a landscape disturbance agent in temperate forests throughout the United States. The effects of windthrow mortality on stand species composition and structure, forest regeneration and seral development have been well described at the site (e.g. single gap) and landscape (e.g. thousands of hectares) scales, predominantly by using field and remote sensing techniques, respectively. Few studies of windthrow have been conducted in small (e.g. hundreds of hectares), topographically confined and ecologically similar forests. This study addresses the spatial and temporal patterns of windthrow mortality in an old-growth Douglas-fir (*Pseudotsuga menziesii*) forest of this understudied spatial extent (*ca.* 150 ha). Coarse woody debris (CWD) data were collected as proxy for mortality along transects in the field and were spatially distributed in a GIS. The causes of mortality and the spatial and temporal distributions of CWD were assessed. Density and volumetric distributions of CWD were compared to those of the live tree population in the study area. Correlations between landscape attributes known to affect mortality susceptibility at the landscape scale, such as topographic exposure and slope steepness, were tested by comparing CWD data to field-collected and GIS-derived landscape attributes. Wind was

found to be the dominant cause of mortality of sampled CWD. The spatial distribution of CWD, and thus mortality susceptibility, was found to be uniform across classes of landscape attributes, and subtle distributional variations that did exist were not related to landscape attributes in a statistically significant manner. These findings suggest that chronic wind disturbance is the dominant cause of mortality in the study area, and that episodic wind mortality is not an active process affecting the study area forest. These findings differ from those of studies conducted at the landscape scale, which have shown a predictable relationship between landscape pattern and chronic and episodic wind-derived tree mortality. The chronic wind disturbance affecting the study area predominantly generates small, single tree gaps that contribute to seral progression rather than alter it.

Patterns of Chronic Wind Mortality in a Small, Old-growth *Pseudotsuga menziesii* Forest in the Western Cascades, Oregon

by
Samuel J. Littlefield

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APPROVED

Major Professor, representing Geography

Chair of the Department of Geosciences

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Samuel J. Littlefield, Author

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INTRODUCTION

Windthrow is the structural failure of living trees, either by uprooting or breakage, caused by wind. Windthrow is an important disturbance process in most temperate forested regions of the United States, including the Pacific Northwest (Sinton et al. 2000, Gray and Spies 1996, Franklin et al. 1987, Harmon et al. 1986), the mid-Atlantic states and New England (Boose et al. 2001, Peterson and Pickett 1990), the northern Midwest (Liechty et al. 1997), and the Rocky Mountain Front Range (Veblen et al. 1991).

Windthrow can be affected by environmental and biotic factors that operate from stand to landform to regional spatial scales, and over temporal scales that range from years to centuries (Sinton et al. 2000). In environments prone to windthrow, the process continually affects the forest through single tree or small patch mortality (Veblen et al. 1991, Harmon et al. 1986). Also, episodic events driven by regional air masses or severe storms can drastically alter forest structure by laying flat extensive swaths of forest (Baker et al. 2002, Boose et al. 2001, Sinton et al. 2000). Both subtle and extensive manifestations of the disturbance process help to shape forest structure at the stand and landscape level, acting as a disruptive or stabilizing force on the landscape.

Windthrow as a Mortality Agent

Tree mortality has many ecological implications, such as alteration of population or community structure, resource release, and creation of habitat (Franklin et al. 1987). As a mortality agent, windthrow has a distinct set of characteristics that make it both unique and important in an ecological context.

Windthrow mortality is unique in that it rapidly shifts biomass to necromass, but it also acts as a significant disturbance process affecting more than the tree(s) killed. Windthrown trees are often large, and their structural failure may lead to subsequent crushing or breakage of other trees and understory vegetation. More than 15 percent of total mortality in mature and old-growth Douglas-fir (*Pseudotsuga menziesii*) stands can be attributed to these chain-reaction failures (Franklin et al. 1987). The rapidity with which windthrow mortality occurs is part of what makes the creation of new resources so important. A standing snag, slowly fragmenting as it decomposes, offers the same nutrient input to a system as would the instantaneous blowdown of the same tree. The speed with which the surrounding community gains access to these resources, however, can affect certain species' ability to capitalize on the resource influx. Western hemlock (*Tsuga heterophylla*), for example, gathers nutrients from organic matter very effectively, even before advanced stages of decay begin (Bormann et al. 1995). Therefore, hemlock, rather than other conifers, is better adapted to realize the benefits of windthrow-derived nurse logs in Pacific Northwest forests.

Probably the most significant unique resource generated by windthrow is the small-scale forest canopy gap. Vegetation growth and regeneration can be significantly enhanced by increased availability of light, water and nutrients in windthrow gaps. Gray and Spies (1996) noted that conifer seedling establishment in western Cascades forests was greater in windthrow gaps than under closed forest canopies, and that growth response increased with increasing gap size. However, enhanced establishment of Douglas-fir, as opposed to western hemlock, was not likely to establish in gaps with a diameter less than the height of the canopy. This *disturbance threshold* (point along a continuum of disturbance extent or severity after which community response is qualitatively different (Romme et al. 1998)) is an example of the scale dependency of windthrow as a disturbance process. Post-windthrow successional trajectories vary depending on whether the gaps created by the disturbance are small or large. Small gap generation may only elicit branch extension of surviving dominant trees, while large gaps may elicit more widespread resource competition, at some point allowing for seed establishment and growth of shade intolerant trees (Romme et al. 1998). Response to windthrow gap generation may also differ between seedlings of overstory species and understory shrubs. Alaback and Tappeiner (1991) noted differing responses to windthrow between western hemlock seedlings and early huckleberry (*Vaccinium ovalifolium*) in the Pacific Northwest. Western hemlock responded to increased light availability by increasing twig growth and branch development for the first growing season following disturbance. Huckleberry allocated additional biomass belowground immediately following disturbance, but its aboveground response lagged several years behind that of western hemlock. Such adaptations to small, infrequent gap generation allow for rapid response to and varied exploitation of disturbance-derived resources.

Pit and mound topography generated by windthrow can have a profound effect on soil structure and composition, and in turn can affect forest community composition. Mounds are usually poorly sorted soils with high organic content, while pits are generally comprised of well sorted mineral soil beds. Bormann et al. (1995) noted that, in the coniferous forests of southeastern Alaska, windthrow periodically homogenizes upper soil horizons. Liechty et al. (1997) added that, in the Great Lakes region of the United States, windthrow-derived soil perturbation may alter soil formation and the decomposition rate of organic matter. These changes may influence the accumulation of C, N, and organic matter, and therefore may alter growing conditions for vegetation (Bormann et al. 1995). The heterogeneous microsite topography associated with pits and mounds can also alter community response to disturbance. Peterson and Pickett (1990) noted higher species richness, biomass and stem density in pits than on mounds in a four year old windthrow in Pennsylvania, a phenomenon attributed to higher moisture maintenance and soil retention in pits.

Windthrow as a Landscape Disturbance Process

Disturbance regimes are the spatial and temporal dynamics of disturbances over extended periods of time (Turner et al. 2001). Characteristics of disturbance regimes include their size, severity, intensity, spatial distribution, frequency, and return interval or rotation period. Stabilizing landscape disturbances are often frequent and small, homogeneous in severity, intensity, and spatial distribution, and they tend to progress seral development. Disruptive landscape disturbances are often infrequent and large, heterogeneous in severity, intensity, and spatial distribution, and they tend to effect successional trajectories or evolutionary responses that are different than those existing prior to the disturbance (Romme et al. 1998, Turner et al. 1998).

Physical and environmental variables influence the critical windspeeds required to cause windthrow, as well as the spatial scale and return interval at which critical windspeeds occur (Mitchell 1995). Over short time periods, spatially distributed variables such as topographic exposure, stand structure and composition, and soil composition combine to affect windthrow susceptibility at the landscape scale. Over long time periods of time, variable susceptibility of a landscape to windthrow may generate forest structural and compositional patterns that are spatially heterogeneous.

Landscape scale patterns of forest structure and composition developed through long-term interactions with a disturbance process both indicate and influence a developing disturbance regime. Baker et al. (2002) provided evidence of this phenomenon during a study of windthrow across elevation gradients on both sides of the Continental Divide in Colorado. Physical variables including topography and distance from the divide were taken into account. Nonetheless, the best predictors of windthrow susceptibility were stand structure and species dominance, which after accounting for elevation and precipitation, were predominantly controlled by previous disturbance regimes (e.g., fire and windthrow). Therefore, a disturbance regime becomes an important force driving landscape modification, where process affects pattern and pattern affects process.

Windthrow also responds to landscape patterns generated by humans. Sinton et al. (2000) noted that clearcut patches exerted a stronger influence on windthrow susceptibility than all physical and environmental variables in a 265 km^2 basin in the northwestern Cascade Mountains of Oregon. At this spatial extent and physiographic setting, stands of old-growth Douglas-fir and western hemlock trees were found to be more susceptible to windthrow than mature stands (greater than *ca.* 80 years old), and this disparity was exacerbated near clearcut edges. In part, this was because trees along clearcut edges, which did not mature in wind prone areas, were found to be less likely to resist windthrow. Thus, the creation of a clearcut edge imposed greater wind exposure on nearby trees. Harvest patterns modified the effects of climate, landforms, and vegetation on windthrow susceptibility, and patch clearcutting may have destabilized the natural disturbance patterns that allowed for old-growth forest structure development.

Similar to artificial edges, the boundaries of windthrow created patches may be more susceptible to future windthrow, and this edge effect may be exacerbated in areas of high wind exposure. Harcombe et al. (2004) noted incremental windthrow patch growth over roughly 50 years in a 500 ha mature coastal spruce (*Picea sitchensis*) – western hemlock forest. The patch was of a size expected from a large, infrequent disturbance event, but was generated by chronic wind mortality that was confined in space by topography. Thus, wind-derived heterogeneity of forest stand structure may exist even at relatively small scales if topography is variable and conducive to wind confinement.

Current Study

Much research has been conducted to quantify and describe windthrow mortality patterns and processes at the landscape scale, generally at a spatial extent of several thousands of hectares (e.g. Harcombe et al. 2004, Kramer et al. 2001, Sinton et al. 2000, Rebertus et al. 1997, Foster et al. 1992, Veblen et al. 1991, Gratkowski 1956). Also, much research has been conducted at the site and microsite scale to quantify and describe the response of understory species and tree regeneration to windthrow disturbance, generally in small gaps or in/on pits and mounds (e.g. Liechty et al. 1997, Gray and Spies 1996, Bormann et al. 1995, Alaback and Tappeiner 1991, Peterson and Pickett 1990). Some work has incorporated stand level data (e.g. Mitchell et al. 2001), but has done so to quantify timber losses for forest clearcut planning purposes in British Columbia.

This study seeks to fill a gap in knowledge by assessing the spatial and temporal distribution of windthrow mortality at the small forest scale (*ca.* 150 ha), and does so by addressing four research questions: ***Does windthrow occur as a chronic or episodic disturbance mechanism in the study area? Do physical and topographic variables affect windthrow disturbance susceptibility? Given the forest composition, structure, and age, what are the key ecological implications of windthrow disturbance in the study area? What commonalities and disparities exist between windthrow patterns at various scales?***

METHODS

Site Description

The study area comprises 145 hectares of old-growth Douglas-fir forest, including a second-order 60 ha gauged basin (Watershed 2), its alluvial fan, and three adjacent first-order basins (Figure 1). These basins drain roughly northwest to Lookout Creek, whose catchment is the H.J. Andrews Experimental forest (Andrews). The Andrews is located approximately 80 km east of Eugene, OR, USA.

The study area is in the southwestern, lower elevation portion of the Andrews. Bedrock is composed of late Oligocene to early Miocene volcaniclastic rocks (Swanson and James 1975). Topography in and near the study area was formed primarily by fluvial and mass movement processes. The area is defined by two high, steep ridges and interspersed by three smaller, more rounded ridges, all of which run roughly northwest. Elevation ranges from 460 to 1070 m. The study area has a north-northwest aspect, but fine scale variation generates more complex topography on the ground. Slope steepness ranges from nearly flat to over 150%, with an average of 50%. Slope lengths range from 50 to 500 m. Soils have loamy surface horizons with aggregate bound by organic matter, and are well drained with a porosity of 60 to 70% (Swanson and Jones, 2002). The study area has a marine temperate climate, with cool wet winters and warm dry summers. Approximately 70% of precipitation occurs from November to March from low-intensity frontal storms from the southwest. The region receives approximately 230 cm of precipitation annually, primarily as rain within the elevation range of the study area. Mean annual temperature is 8.5 °C (Bierlmaier and McKee 1989).

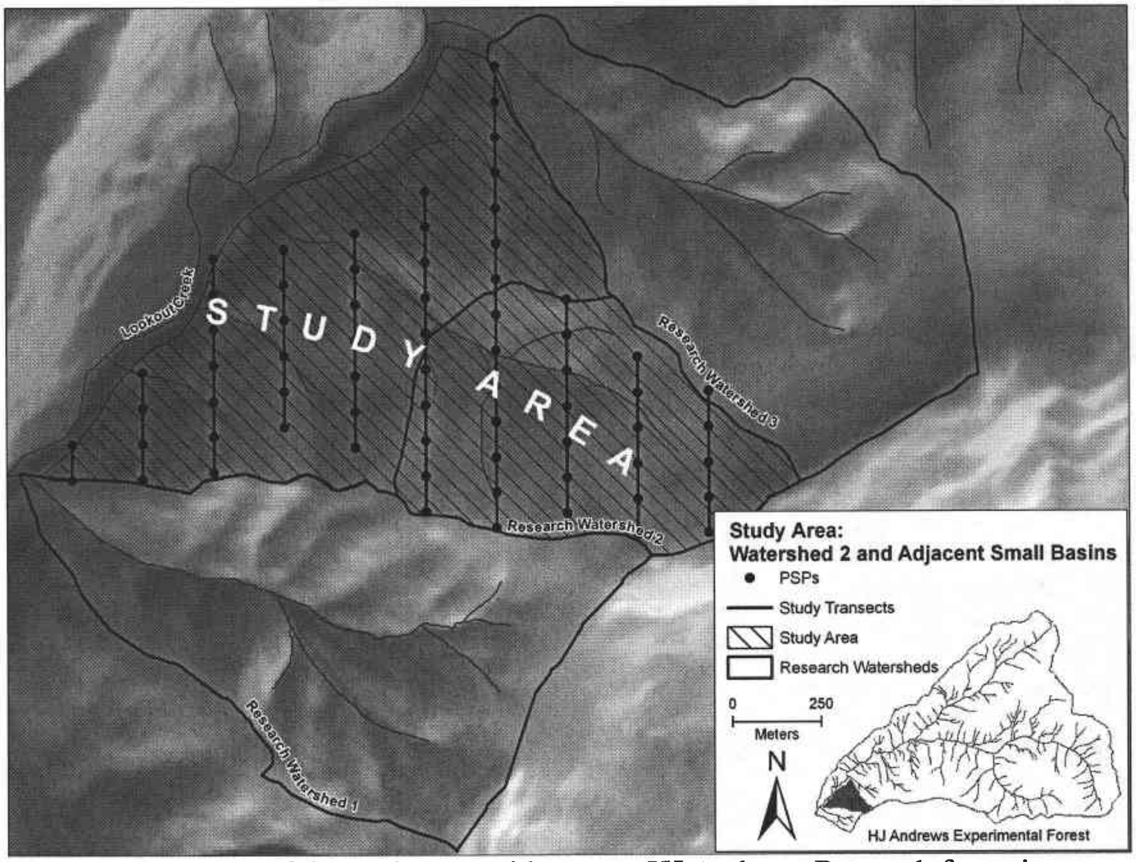


Figure 1: Area map of the study area with greater HJ Andrews Research forest inset. Research Watershed 2 represents the upper 60 ha of the study area. The lower portions are composed of three small drainages and the lower portion of the Watershed 2 mainstem.

The forest of the study area is approximately 480 years old and was initiated by a stand replacing fire (Morrison and Swanson 1990). Primary plant associations in the study area are western hemlock / salal (*Gaultheria shallon*) at upper elevations and western hemlock / Oregon grape (*Mahonia nervosa*) at lower elevations (Bible, 2001). Both associations are typical climax associations in western Oregon. Late seral communities for both of these climax associations typically include Douglas-fir as the dominant overstory species, but Douglas-fir is not the climax species in areas with more than 165 cm of annual precipitation (Franklin and Dyrness, 1973).

A network of 67 non-slope corrected 0.10 ha permanent sample plots (PSPs) was installed in the study area in 1982 for forest inventory purposes (Acker et al. 2002) (Figure 1). Data from the PSP network shows western hemlock to be the dominant tree species by count, while Douglas-fir is the dominant tree species by basal area (Table 1). Stand density of Douglas-fir and western hemlock decreased from 1982 to 2000, but western hemlock basal area increased while Douglas-fir basal area decreased. The shifts in species allocation are attributed to a lack of recruitment of less shade tolerant Douglas-fir and mortality of large Douglas-fir trees (Bible 2001). Also, due to the small size of the sample plots, the death of a single large Douglas-fir within the PSP network can significantly alter estimates of stand basal area. This transition follows known patterns of seral development in forests with western hemlock climax associations, which occur primarily because western hemlock is capable of reproducing itself beneath the forest canopy, while Douglas-fir is not (Franklin and Dyrness, 1973).

Table 1: Basic statistics for the study area forest for 1982 and 2000. Data from 67 Permanent Sample Plots inventoried in 1982 and 2000. TPH is trees ha^{-1}, BA is basal area as $m^2\ ha^{-1}$, DBH is diameter at breast height in cm. 1982 statistics adapted from Bible (2001); 2000 statistics calculated from PSP data (H.J. Andrews, *unpublished PSP data*).

	1982 Average			2000 Average			Change		
	TPH	BA	DBH	TPH	BA	DBH	TPH	BA	DBH
Total (all species)	380.0	57.2	-	397.2	58.7	-	17.2	1.5	-
Western hemlock	221.9	12.9	21.8	215.5	15.3	23.9	-6.4	2.4	2.1
Douglas-fir	89.3	42.3	59.6	76.3	39.3	63.9	-13.0	-3.0	4.3

Several mortality agents are active within the study area. From 1982 to 2004, wind was the third most important cause of mortality of trees in the PSPs, after *unknown* and suppression (H.J. Andrews, *unpublished PSP data*). However, wind may significantly affect forest biomass and species composition because it affects larger trees. Wind caused 16% of mortality from 1982 to 2004, with an average DBH of 37 cm. Suppression constituted 32% of sampled mortality, but it primarily affected small understory trees with an average DBH of 11 cm.

Small portions of the study area endured a low severity fire in the mid-1800s (Morrison and Swanson 1990). None of the study area has been harvested, but neighboring watersheds to the northeast and southwest were harvested in the 1960s (Figure 1). Watershed 1 (WS1), the 96 ha watershed sharing the southeastern bounding ridge of the study area, was completely clearcut between 1962 and 1966 and prescribed burned in 1967. Watershed 3 (WS3), the 101 ha watershed sharing the northwestern bounding ridge of the study area, was 25% patch harvested in 1963. Only a 6.5 ha patch cut from WS3 directly borders the study area, sharing approximately 350 m of ridgeline.

Data Acquisition

Field Methods

A field survey of mortality distribution was conducted at the study area at the H.J. Andrews Experimental Forest in July 2004. Ten transects of varying lengths, spaced 200 m apart, were used to traverse the study area (Figure 1). Transect lengths varied due to their arrangement within the study watershed; that is, transects are oriented north-south, and are only approximately as long as the study area is wide at the longitude at which each transect sits. Transect lengths ranged from 100 to 1,300 m; the total length of all sampling transects was 5,800 m. Transects link the PSPs, which are spaced 100 m apart (Figure 1). The location of the first PSP, and therefore the start of each transect, was originally located a random distance from the ridge bounding the southern edge of the study area (Acker et al. 2002). This placement served to reduce bias while ensuring complete coverage and representation of the several small basins that compose the study area. These transects were selected for use in this study because their prior installation made access easy and distance measurements possible without the use of a GPS. Also, transects were arranged as to capture all combinations of slope and aspect present in the study area, so landscape representation could be adequately achieved. In 1982, 78 PSPs were installed, but 11 of them were either never used or were decommissioned (LTER Terrestrial Vegetation Plots, 1982). Only the transect areas between active PSPs were sampled, except in one case. Transect 1 (Figure 1, far left) only had 1 active PSP, so an inactive PSP was located and the area in between the active and inactive PSP was sampled.

Sampling Framework

Ten, 10-m wide belt transects were laid out along the original PSP transects. The total area inventoried was 58,000 m^2, 5.8 ha, or approximately 4% of the 145 ha study area. Downed and standing dead trees were inventoried as proxy for historical mortality data. The inventory was conducted using the transect-intersect method, whereby all downed and standing dead trees having any material located within a transect were inventoried. Only dead trees with a DBH greater than or equal to 10 cm were inventoried. The following tree-level variables were noted for each inventoried dead tree:

1. Sequential tree number
2. Last PSP encountered and paced distance (m) since that point
3. Species
4. Approximate length (m)
5. Approximate DBH (cm), measured ~1.4m above bole butt flare
6. Tree fall azimuth in degrees (if fallen)
7. Decay class
8. Evident cause of mortality

The sequential tree number was recorded for data management purposes. The number of the last PSP encountered and the paced distance since that PSP were inventoried to allow for relative location calculation. That is, X and Y locations of PSPs are known, so the location of each dead tree could be established in a GIS by calculating the distance relative to a particular PSP. Species was determined by bole, bark, branch, and needle morphology. Length was determined by cloth tape measurement. Diameter was measured using a metal diameter tape. Tree fall azimuth was determined by aligning a compass to the centerline of a fallen bole and recording the azimuth of fall. Decay class was inventoried on a scale of 1 to 5, following Sollins et al. (1987), with class 1 being least decayed and class 5 being most decayed. Cause of mortality was assigned based on the manner of structural failure of an inventoried tree. Specifically, trees were considered to be windthrown if roots were pulled from the ground and windsnapped if the bole had broken above the base.

It should be noted that the manner of structural failure of a tree may not represent the actual cause of tree mortality. Tree death, though sometimes abrupt, is often a gradual process progressed by multiple contributing factors (Franklin et al. 1987). Thus it can be difficult to assess the actual cause of mortality, especially when dead trees are in advanced stages of decay. It is recognized that pathogens contribute to tree susceptibility to both root and bole failure, thus disease was assigned as the cause of mortality, regardless of the structural failure of a tree, if clear evidence of pre-death disease interaction was present.

Site-level variables were also collected at the location of each inventoried dead tree, including percent slope and degrees aspect. Slope was measured using a clinometer and aspect was measured using a compass.

Calculation of Volume of CWD in Transects

The volume of mortality within transects was calculated with field-collected length and diameter data, length data estimated from an allometric relationship, and maximum within-transect bole distance data estimated from mortality fall directions. Missing values for bole length and DBH were estimated using a linear regression between DBH and length for all trees with measurements for both variables (n = 508). The linear model, with associated standard errors, was:

$$\text{Bole length (m)} = \underset{(0.01)}{0.47}\,(\text{DBH (cm)}) + \underset{(0.70)}{9.73}$$

This statistically significant relationship ($p<0.01$; $r^2=0.84$; $F=2695$; 1, 507 d.f.) was used to calculate missing length (n = 85) and DBH (n = 5) values. Lengths were missing primarily due to heavy fragmentation of boles fallen across and into steep stream channels. Diameters were not measured due to advanced decay.

Volume of mortality per unit area was estimated by calculating the maximum length of each sampled tree within the belt transect given its fall direction relative to the transect (Figure 2). For example, as transects run north-south, a 20 m long bole with a fall azimuth of 270° would have a maximum in-transect length of 10 m. Likewise, a 20 m long bole with a fall azimuth of 330° would have a maximum in-transect length of 20 m (Figure 2). Volume for each tree was calculated as a cylinder using the maximum possible in-transect length and the field measured DBH.

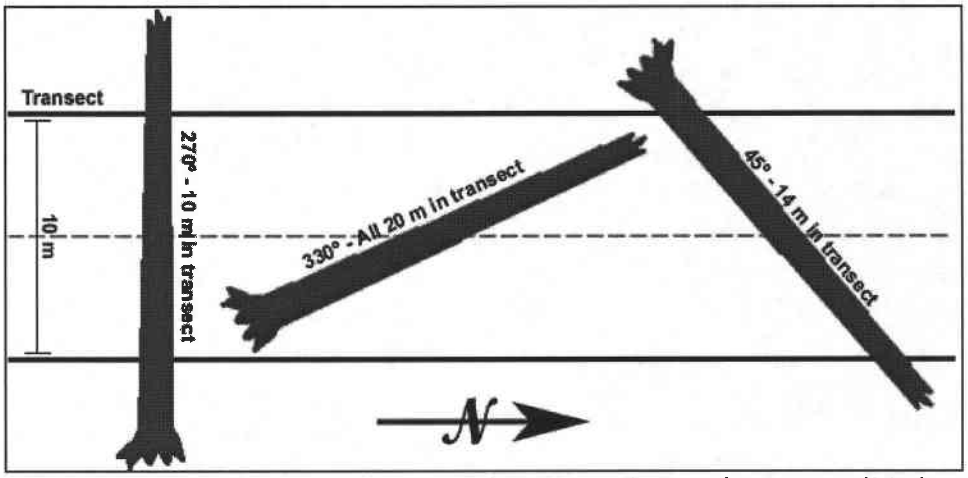


Figure 2: Conceptualization of several scenarios where the maximum possible in-transect length of 3 boles, each 20 m in length, is different due to the orientation of fall relative to the transect.

This method of volume calculation has several deficiencies. Due to the lack of consideration for bole taper, the lack of consideration for decay and associated losses in biomass, as well as the likely overestimation of in-transect length, this method probably overestimates the volume actually present within the transects. However, the purpose of volume calculations was to generate a relative measure of volume that could be assessed for distributional characteristics over variations in the physical landscape. Values produced by this method should not be taken to exactly represent the volume of inventoried mortality, but rather an estimate of the *maximum possible volume* of inventoried mortality.

Data Analysis

Summary Statistics

Basic summary statistics were calculated from field data for a variety of mortality attributes. Attributes of mortality noted during field sampling were binned using common classes, such as 10 cm DBH classes and cardinal directions of aspect, and graphed for preliminary data exploration. Distributions of species, size class, decay class, and cause of mortality were generated and evaluated. Summary statistics such as mean DBH and total volume by species were also calculated. Some distributions calculated by species were further broken down by size class (large or small) relative to species-specific median DBH. Median DBH values were 88 and 30 cm for Douglas-fir and western hemlock, respectively. Species and size distributions of living trees in the study area were calculated from 2000 PSP data and compared to distributions of inventoried mortality.

GIS Methods

Mortality Aggregation

Mortality data from field surveys were converted to a point *feature class* (GIS vector data layer) using the Add X/Y Data function in ArcMap 9.0 (ESRI, 2005). The X and Y values of mortality points were calculated using relative distances from PSPs with known latitude and longitude values. Point based mortality data were converted to estimates of mortality count and volume per unit area using the Point Statistics smoothing algorithm function in the Spatial Analyst extension toolbox of the ArcINFO 9.0 software package (ESRI, 2005). Mortality points, and attributes belonging to these points, were summed and averaged at 3 rectangular window sizes: 25 m vertical (north – south) by 10 m horizontal (east – west), 50 m vertical by 10 m horizontal, and 100 m vertical by 10 m horizontal. Windows were iterated at a 1 m cell size, and each resultant 1 m raster cell was given the value (average, sum, etc.) of the window for which it was the centroid. Mortality summary rasters representing smoothed values of the following point data were generated for each window size:

1. Count of all inventoried mortality
2. Sum of maximum possible volume of all inventoried mortality
3. Count of inventoried Douglas-fir mortality
4. Sum of maximum possible volume of inventoried Douglas-fir mortality
5. Count of downed western hemlock mortality
6. Sum of maximum possible volume of inventoried western hemlock mortality
7. Mean length of all downed trees.
8. Sum of cosine values for fall directions (C below)
9. Sum of sine values for fall directions (S below)
10. Mean length of all downed trees.

The circular distribution of fall directions disallows arithmetic averaging (consider that $\{355° + 5°\}/2 \neq 180°$). Vector addition (detail below) can be used to determine the mean direction of circularly distributed data. Sum of cosine (C) and sum of sine (S) values were calculated for each window to facilitate vector addition during post-GIS data processing.

Per unit area calculation, or smoothing, was performed at 3 window sizes because the appropriate scale of assessment was not known prior to analysis. Windows needed to be small enough as to not smooth out spatial variability and patterns that may have existed in the dataset. However, windows needed to be large enough to yield values that were biologically reasonable. That is, small windows, if situated over a small patch of mortality, might yield per unit area values that are drastically overestimated. Basic statistics were calculated for mortality density and volume for each smoothed dataset and compared (Table 2).

Table 2: Basic statistics for smoothed mortality data for comparison and window size selection.

	25 m Window		50 m Window		100 m Window	
	Count mort ha^{-1}	Volume m^3 ha^{-1}	Count mort ha^{-1}	Volume m^3 ha^{-1}	Count mort ha^{-1}	Volume m^3 ha^{-1}
Maximum	320	6032	260	4659	190	2597
Minimum	0	0	0	0	40	136
Mean	103.10	1041.48	103.10	1041.48	103.10	1041.48
Std Dev	65.67	1085.12	49.53	884.24	31.30	550.23

The 100 m window dataset maintained a range of values and variability of both count and volume that seemed most reasonable, and thus it was selected for analysis and comparison to landscape attributes (Table 2). Personal field observations indicated that patches of no mortality were rare, but sometimes small stretches of transect (10 to 50 m) would not be crossed by fallen trees. However, these areas were often flanked by a small amount of mortality that did not happen to intersect the transect. This was especially common in areas with only small tree mortality. Though these stretches represented a dearth of large tree mortality that existed in the area, a smoothed value showing no mortality would be an underestimation. Thus, the null minimum values shown in Table 2 for 25 and 50 m windows seemed unreasonable. Also, the volume ha^{-1} estimates produced by the 25 and 50 m windows seemed exorbitantly high considering that published values indicate maximum mortality volumes of less than 1000 m^3 ha^{-1} for the study region.

Landscape Aggregation

Mean slope and topographic exposure were calculated for each 100 by 10 m window, and aspect was assessed as was mean fall direction. Rasters of slope, cosine and sine aspect, and topographic exposure were first derived at a 10 m grid cell resolution from a 10 m digital elevation model (DEM) (H.J. Andrews 2005) clipped to a rectangular extent of 2000 m beyond all edges of the Andrews. The extent of 2000 m beyond the Andrews boundary was selected to allow for the proper assessment distance of the Topex-to-distance model (described below) for all areas of the Andrews landscape. Slope and aspect rasters were derived from the clipped DEM using tools from the Spatial Analyst extension of ArcINFO 9.0 (ESRI 2005).

Topographic exposure was calculated from the Topex-to-distance model, which is a measure of the sum of vertical angles to skyline in eight cardinal directions, limited to a specified distance. Topographic exposure is a relative measure of the exposure to wind a given location within a landscape is likely to maintain given that surrounding topography modifies local windspeeds. Several models of topographic exposure have been devised, such as EXPOS (Boose et al. 1994), Topex (Wilson 1984), and Topex-to-distance (Quine and White 1994). EXPOS and Topex take into account the angles from a given landscape location to higher, adjacent topography. The EXPOS model works in a manner similar to a hillshade model, where a given angle of inflection is specified, and areas below that angle of inflection in a specified direction beyond topographic features are not considered exposed, be it from sun or wind. This method does not take into account distances between high and low elevation features, which play a significant role in windspeed modification. EXPOS has been successful in explaining historical hurricane windspeeds in the northeastern United States, where topography undulates smoothly and distances between hilltops are fairly great (Boose et al. 2001). However, EXPOS was not found to correlate well with wind damage in the deeply-incised topography common in the western Cascade Range (Sinton 1996).

The Topex-to-distance model accounts for angles to higher, adjacent topography, as well as the maximum distance at which such topography is likely to be influential. The model has been shown to correlate well with windspeed in complex, deeply-incised terrain on Vancouver Island, British Columbia (Mitchell et al. 2001, Ruel et al. 2002). Topex-to-distance scores are output from a GIS script written by Arnold Moy of The University of British Columbia (UBC): Centre for Applied Conservation Research. The script was developed for Dr. Stephen J. Mitchell's Windthrow Research Group at UBC. The limited distance specification was set at 2000 m, as good results had been ascertained in topography similar to that of the study area using the same value. The topex-to-distance script outputs a raster image with the same cell size as the input DEM (10 m).

Slope and topographic exposure scores were averaged arithmetically over each moving window area using the Focal Statistics function in the Spatial Analyst extension toolbox of ArcINFO 9.0 (ESRI 2005). This function produced landscape aggregation raster datasets representing smoothed slope and topographic exposure values. Rasters representing the sum of cosine (C) aspect and sum of sine (S) aspect values were also generated to allow for the calculation of mean aspect per window using vector addition during post-GIS data processing.

Point Sampling and Post-GIS Data Processing

Smoothed mortality, slope, aspect, and topographic exposure rasters generated by the moving window analysis were sampled with a point feature class with points spaced

100 m apart along the belt transects. The first point along each transect was located 50 m from the transect initiation point, i.e. the transect bounding PSP. Points were attributed with the raster cell values for which they were the centroid, yielding a point feature class with smoothed slope, topographic exposure, and mortality attributes, as well as smoothed angular data values.

Distance in meters from each point to the nearest stream channel and the clearcut ridge separating the study area from WS1 were calculated and attributed to the point feature class using the Near tool from the Analysis tools available in ArcINFO 9.0 (ESRI 2005). The attribute table of the 100 m sample point feature class was then exported to database file format for spreadsheet manipulation. The database file included the latitude and longitude values for each sample point.

The mean directions of tree fall and aspect attributed to each sample point were calculated in spreadsheet software from smoothed sum cosine (C) and sine (S) fall azimuth and aspect angle values using vector addition methods. Mean circular direction was determined by:

$$C = \sum_{i=1}^{n} \cos\theta_i \,, \quad S = \sum_{i=1}^{n} \sin\theta_i \,, \quad R^2 = C^2 + S^2 \quad (\mathrm{R} \geq 0)$$

where the direction of $\overline{\theta}$ of the vector resulting from the addition of summed cosine (C) and sine (S) values ($\theta_{1,\ldots,}\theta_n$) is given by:

$$\overline{\theta} = \begin{cases} \tan^{-1}(S/C) & when\ S > 0, C > 0 \\ \tan^{-1}(S/C) + \pi & when\ C > 0 \\ \tan^{-1}(S/C) + 2\pi & when\ S < 0, C > 0 \end{cases}$$

and $\bar{\theta}$ is known as the *mean direction* (Fisher 1993). The *circular standard deviation* of tree fall direction, a measure of uniformity of fall direction, was computed by the following equations (Fisher 1993):

$\bar{R} = R/n$, where $\bar{R}$ is the *mean resultant length*
$V = 1 - \bar{R}$, where V is the *sample circular variance*
$v = \{-2\log(1-V)\}^{\frac{1}{2}}$, where v is the *circular standard deviation.*

After the calculation of mean fall direction and mean aspect, the processed database files were converted to GIS point feature classes using the Add X/Y Data function in ArcMap (ESRI 2005) and the smoothed values were used to make maps for spatial assessment.

Wind Assessment

Wind records from 5 meteorological stations (met stations) located at the Andrews were examined to determine dominant wind directions and magnitudes. Concurrent daily wind data for 1 January 1997 through 31 December 2002 were gathered from the HJ Andrews online database (HJ Andrews, 2005). Data included maximum daily windspeed and mean wind direction for the PRIMET, CENMET, UPLMET, H15MET, and VANMET stations. Mean wind directions were converted to flow vectors (direction wind flows to) for comparison to tree fall directions. The directional distributions of all windspeeds and of the top 5% of maximum daily windspeeds by cardinal flow vectors were determined and graphed for each meteorological station. The high magnitude and general wind direction distributions from each station were then compared to one another, as well as to the distributions of other meteorological stations. The distributions of the top 5% of windspeeds were compared to windspeed data from early January 1990, a time period during which windthrow is known to have taken place at the Andrews.

Hypotheses and Hypothesis Tests

Hypotheses pertaining to distributions of inventoried mortality, their association with landscape attributes, and their association with forcing factors were devised prior to analysis. Null hypotheses are presented below:

1. Mortality distributions:
   a. The size distribution of Douglas-fir and western hemlock CWD does not differ from that of trees living in the study area.
   b. Mortality rates of key species do not vary through time.
   c. Mortality is not caused by episodic wind disturbance.
2. Mortality and the landscape:
   a. CWD distribution does not vary across slopes, aspects, and levels of topographic exposure.
   b. CWD distribution is not related to distance from the clearcut edge of the study area.
   c. Mortality is not more likely on hydric soils, i.e. near stream channels.
3. Forcing factors:
   a. Mortality fall directions are not unevenly circularly distributed
   b. Strong winds are not unevenly circularly distributed
   c. Fall directions of mortality are not associated with wind directions.

Distributions of mortality by species and size class were compared to size and species distributions from PSP data to address hypothesis 1a. Hypothesis 1b was addressed by comparing the decay class distributions for Douglas-fir and western hemlock mortality to expected distributions from the literature. Distributions of cause of mortality by species were assessed to address hypothesis 1c. Linear regression and comparison of distributions using chi-square tests were used to evaluate hypotheses 2a, 2b, and 2c. Hypotheses 3a, 3b, and 3c were addressed by comparing the mean fall direction, as well as the distribution of mortality by cardinal tree fall direction, to aspect and wind direction histograms.

RESULTS

Detailed results are presented below. In short, most of the null hypotheses could not be rejected for the study area. Size distributions of CWD differed from live tree PSP data for the principle tree species in the study area. Mortality rates differed by species, with western hemlock mortality having increased in recent time. CWD was evenly distributed across landscape classes, and the distribution was not related to distances from the clearcut margin of the study area or stream channels. The fall direction distribution of CWD was unimodal, and was well correlated with aspect (i.e. the downhill direction).

Mortality Summary Statistics

Size and Volume Distributions

Transect sampling resulted in the inventory of 598 dead trees over the total transect length of 5800 m or 10.3 dead trees per 100 linear m. Approximately 99.5% of found dead trees had fallen prior to sampling. Thus, the dead trees inventoried during sampling are hereafter referred to as coarse woody debris (CWD). The *maximum possible volume* (volume) of CWD that could have existed within the transect areas was estimated to be 6040.6 m^3 over the 5.8 ha (non-slope corrected) sampling area or 1041.5 m^3 ha^{-1} (Table 3). The spatial distribution of CWD is shown in Figure 3.

Roughly 75% of CWD by count and greater than 95% of CWD volume was Douglas-fir; western hemlock made up roughly 25% of CWD by count, but less than 5% of CWD volume (Table 3). Other species found were western red cedar, Pacific yew (*Taxus brevifolia*), big leaf maple (*Acer macrophyllum*) and chinquapin (*Castanopsis chrysophylla*). Only Douglas-fir and western hemlock are considered further.

Table 3: Allocations of transect-inventoried downed dead trees and of trees living in PSP plots in 2000 by counts, volumes, and percent of total measurement. Data for live trees less than 10 cm DBH were excluded from live tree statistics, as were species composing <= 1% of stems.

	Count				Volume or Basal Area			
	Trees ha^{-1}		% of Total		Dead: $m^3\ ha^{-1}$ Live: $m^2\ ha^{-1}$		% of Total	
Species	Dead	Live	Dead	Live	Dead	Live	Dead	Live
Douglas-fir	74.8	69.7	72.6	23.7	999.1	39.3	95.9	67.5
Western hemlock	22.8	156.0	22.1	52.9	38.4	15.0	3.7	25.8
Western red cedar	2.1	13.1	2.0	4.5	2.6	1.4	0.3	2.5
Pacific yew	2.1	24.3	2.0	8.3	0.7	0.6	0.1	1.0
Big leaf maple	1.0	11.3	1.0	3.9	0.7	0.8	0.1	1.4
Chinquapin	0.3	15.4	0.3	5.2	0.1	0.6	0.0	1.0
TOTALS	103.1	289.9	-	-	1041.5	57.7	-	-

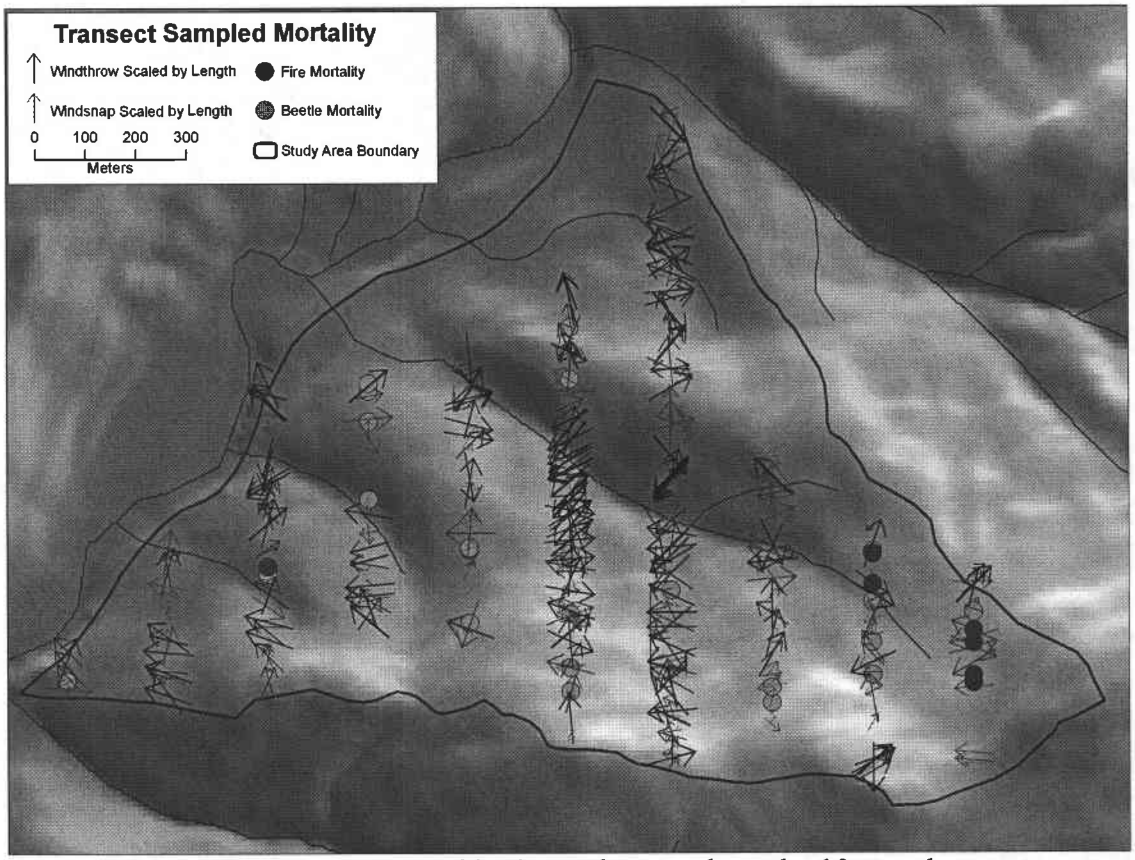
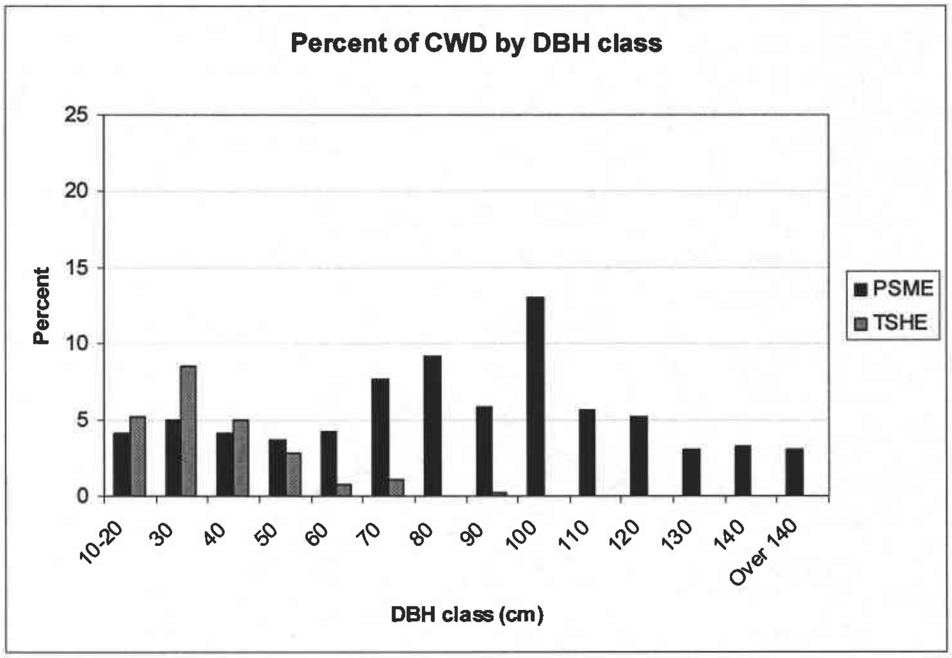


Figure 3: Map of CWD as surveyed in the study area along the 10 sample transects. Mortality points are scaled by bole length and are oriented by direction of tree fall. CWD is scaled by relative length values, not to the map scale.

The disparity between percent of CWD by count and percent of CWD by volume for Douglas-fir and western hemlock is due to the different species-specific size distributions of inventoried CWD. The majority of inventoried Douglas-fir CWD was approximately equal to or greater than the size of the largest inventoried western hemlock (Figure 4a). The mean DBH of inventoried CWD was 84 cm for Douglas-fir and 33 cm for western hemlock. No western hemlock CWD with a DBH greater than 90 cm was found, while the maximum DBH of Douglas-fir CWD was 220 cm. The size distribution of Douglas-fir mortality was somewhat bell shaped, with the largest percentage of mortality from the 90 to 100 cm DBH class, and concentration tapering to smaller and larger size classes. This size distribution of Douglas-fir CWD is somewhat inversely related to that of the size distribution of the living tree population of the study area, but percentages of Douglas-fir CWD in the smallest and largest size classes were similar to those of living trees (Figure 4b).



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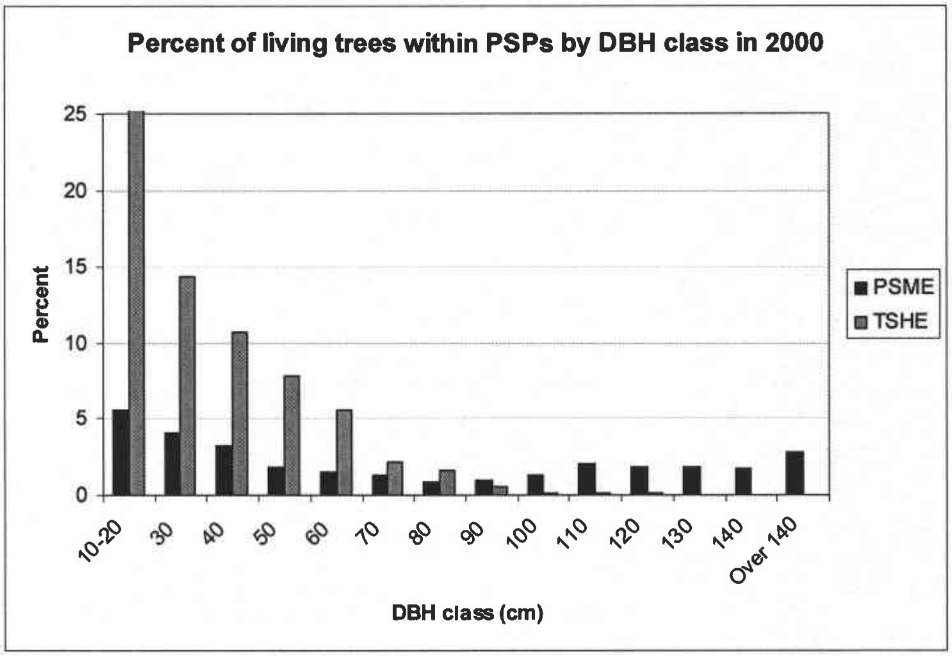


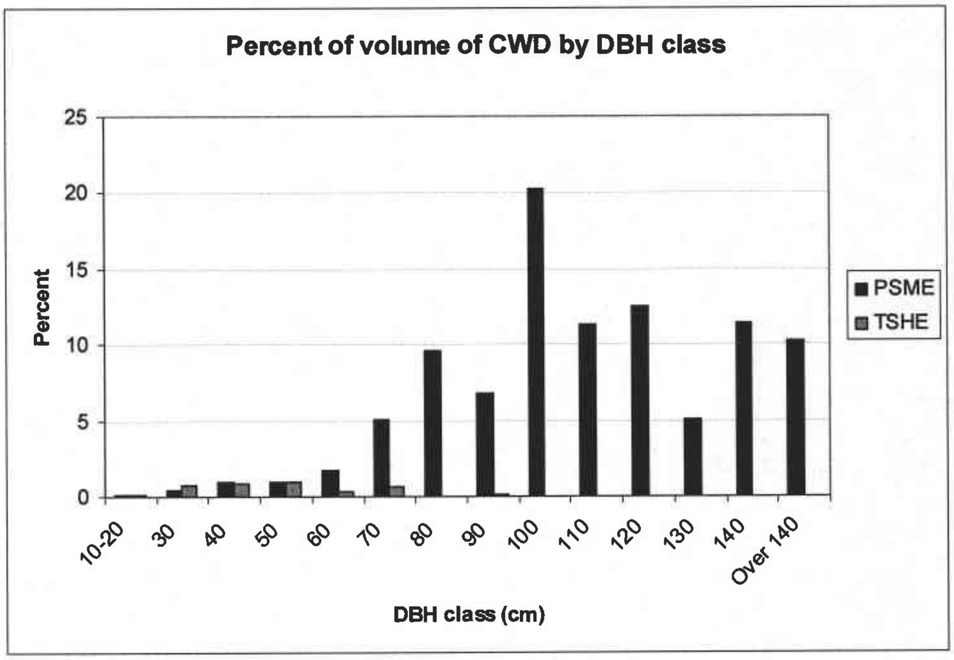
b)

Figure 4: Histograms of percent of CWD and living trees by species in 10 cm DBH bins. Live tree data from 2000 PSP measurements. PSME is Douglas-fir and TSHE is western hemlock. These acronyms are used throughout. Note the somewhat inversely related size distributions of Douglas-fir CWD and live Douglas-fir, as well as the disparity between the distributions of western hemlock CWD and live western hemlocks.

The living tree population, in terms of density and basal area, was not evenly distributed by species (Figures 4b, 5b). Based on calculations of PSP data, western hemlock was the most common species of living trees by density, followed by Douglas-fir and several other species. Taking basal area as a proxy for volume, the majority of live volume present in the study area is Douglas-fir, followed by western hemlock and several other species (Table 3).

The size distribution of live western hemlocks was heavily skewed towards smaller size classes; in 2000, over 25% of all PSP inventoried stems, of any species, were western hemlocks between 10 and 20 cm DBH (Figure 4b). Live Douglas-fir trees were more evenly distributed across size classes (Figure 4b). Tree volume increases geometrically with diameter (Harmon et al. 1986). Thus, western hemlock maintained far less volume per unit area than Douglas-fir due to its left-skewed size distribution, and the majority of the volume of Douglas-fir exists as large trees despite the relatively even size distribution of the species (Figure 5b).

Several differences exist between the distributions of CWD found in the study area and those of the trees living in the study area. The proportion of the living tree population composed of small live western hemlock trees, by density (Figure 4) and by volume (Figure 5), was far greater than the percent of CWD composed of similarly sized western hemlock trees. The proportion of the living tree population density composed of large Douglas-fir trees was less than that of CWD composed of similarly sized Douglas-fir trees (Figure 4). However, the proportion of stand basal area composed of large live Douglas-fir trees was similar to the proportion of CWD volume composed of similarly sized Douglas-fir (Figure 5).



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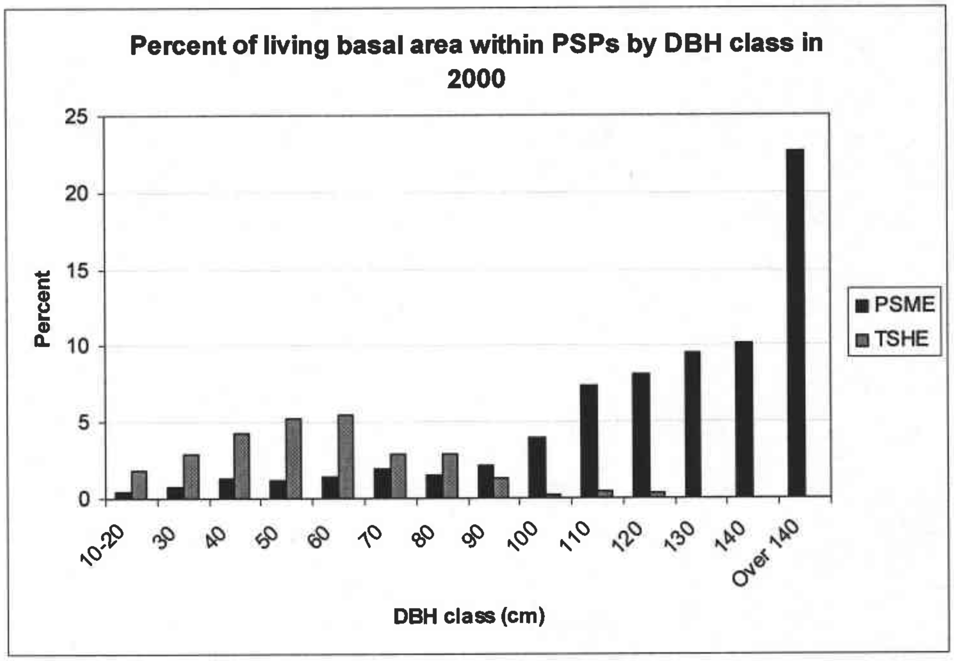


b)

Figure 5: Histograms of percent of a) volume of CWD and b) basal area of living trees by species in 10 cm DBH bins. Live tree data from 2000 PSP measurements. Note that a more live tree volume is composed of western hemlock that CWD volume, and that much of the total CWD volume is composed of Douglas-fir that is near 100 cm DBH.

Decay Class Distributions

The decay class distributions of CWD indicate that Douglas-fir mortality occurred at a relatively constant rate through time, while western hemlock mortality has increased in the recent past. Mean decay class, while not a representation of the mean time since mortality, may show a disparity of the temporal distribution of mortality between species. The mean decay class for Douglas-fir CWD was 3.1, while it was 1.9 for western hemlock CWD (Figure 6). Western hemlock CWD was most commonly found in decay classes 2 and 1, with comparatively little found in higher decay classes. Douglas-fir CWD was most commonly found in decay class 3, with frequency decreasing to lower and higher decay classes.

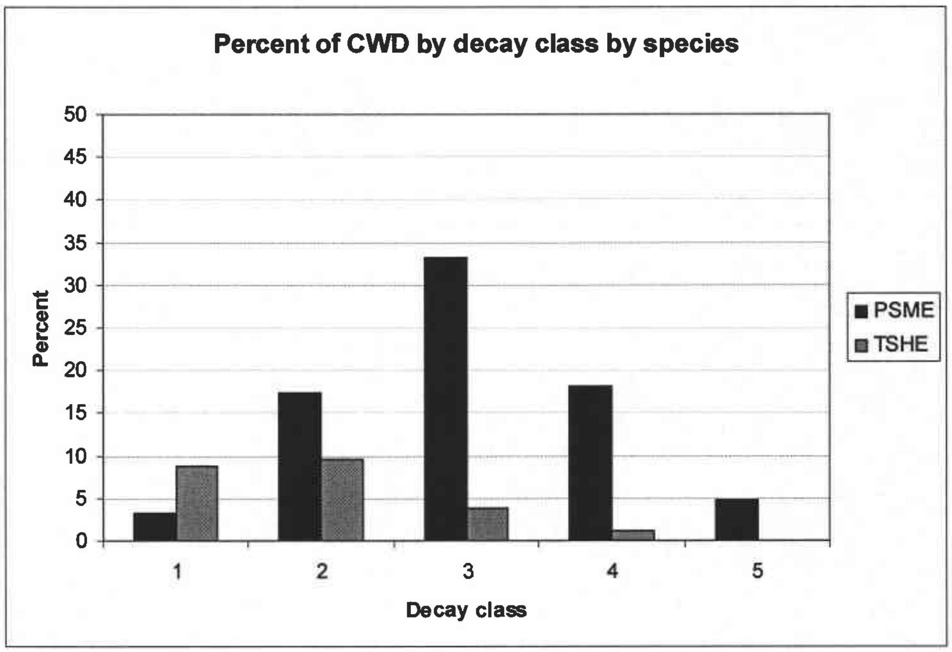


Figure 6: Histogram of percent of CWD, by count, by decay class by species. Note that western hemlock has been shown to decay faster than Douglas-fir (Sollins et al., 1987).

Western hemlock CWD represents an increasing proportion of CWD, by count, with decreasing decay class (Figure 6). However, in terms of volume of CWD, western hemlock represents little of the overall CWD in each decay class except for decay class 1.

In decay class 1, western hemlock CWD is dominant in terms of count and volume (Figure 7).

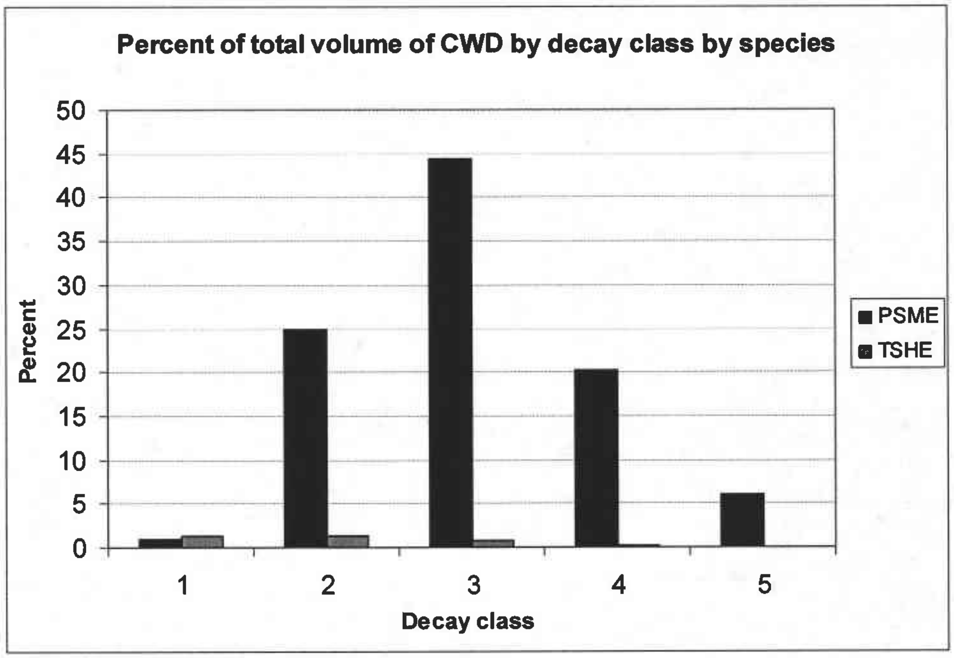
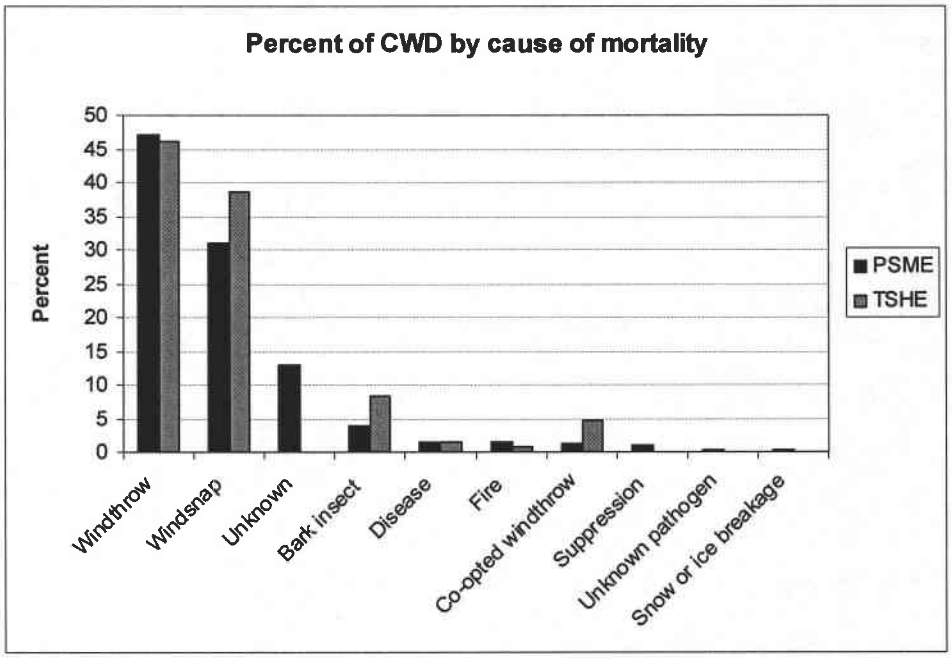


Figure 7: Histogram of percent of CWD, by volume, by decay class by species. Note that western hemlock makes up very little CWD volume in decay classes greater than 1, but that the species makes up the majority of CWD volume in decay class 1.

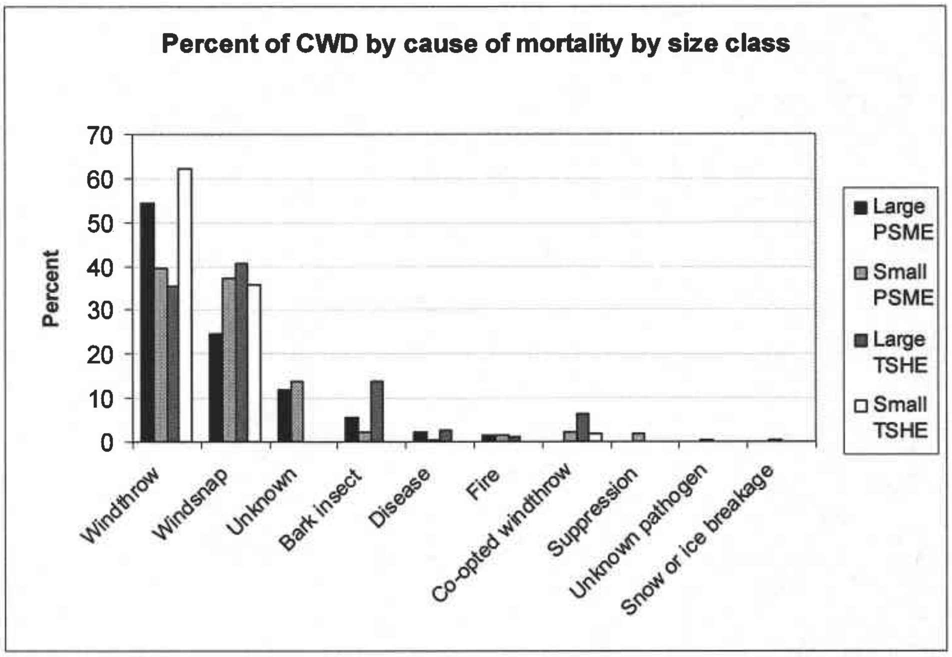
Causes of Mortality

The dominant cause of mortality of sampled CWD was wind. Because CWD was only sampled if it was greater than 10 cm DBH, suppression-induced mortality is largely underrepresented. Approximately 75% of Douglas-fir and western hemlock CWD was killed by wind damage as windthrow, windsnap, or *co-opted* windthrow (trees crushed by falling windthrow or windsnap) (Figure 8a). Douglas-fir and western hemlock responded similarly to mortality agents, which included wind-related agents, bark insects, disease, fire, suppression, unknown pathogens, and snow and ice breakage. The manner of structural failure of wind-derived CWD, i.e. windthrow or windsnap, was independent of species (p:0.27, X^2: 1.21, 1 d.f.) (Figure 8a). However, the manner of structural failure was not independent of species by size class (p:0.002, X^2: 15.15, 3 d.f.) (Figure 8b). Windthrow was the dominant cause of mortality for large Douglas-fir and small western hemlock CWD, where windsnap was the dominant cause of mortality for small Douglas-fir and large western hemlock CWD. For Douglas-fir CWD, the third most common cause of mortality was *unknown*. The lack of determination of cause of mortality was primarily due to extensive decay, evidenced by the average decay class of 4.04 for trees with an undeterminable cause of mortality.

The spatial distribution of some non-wind-derived CWD is of note. Fire-derived CWD was concentrated in the upper elevation portion of the study area. Bark insect-derived CWD was scattered throughout the study area, but generally as small patches rather than single trees (Figure 3). Though the total number of bark insect killed CWD was low, the mortality agent killed a disproportionately high number of large western hemlock trees.



a)



b)

Figure 8: Histograms of a) causes of mortality by CWD species and b) causes of mortality by CWD species by size class. Note that large Douglas-fir and small western hemlock were most commonly windthrown, while small Douglas-fir and large western hemlock were most commonly windsnapped.

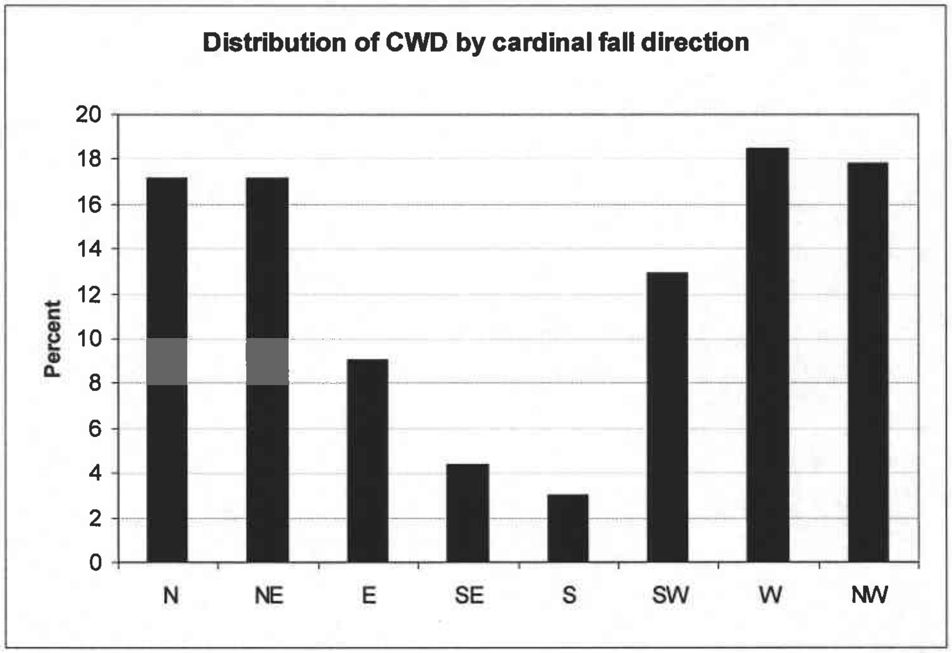
Fall Direction Distributions

The fall distribution of sampled CWD was unimodal, with a mean fall direction of 328.5° (NW) and a circular standard deviation (CSD) of 55.8° (Figure 9a). The fall distribution of wind-derived CWD differed slightly from that of all CWD. Additionally, the fall distribution of wind-derived CWD differed slightly but not significantly by species and size (p:0.42, X^2: 21.7, 21 d.f.) (Figure 9b). However, approximately 80% of CWD fell within 90° of the mean fall direction (generally to the NW) regardless of species or size.

The majority of CWD (87%) was oriented in line with aspect, i.e. downhill, and this pattern occurred regardless of aspect (Figure 10). The mean field sampled aspect of all points at which CWD was found was 320.7°, with a circular standard deviation of 36.8°. The difference between the mean aspect and mean fall direction was 7.8°. This pattern is quite evident when moving window averaged fall directions and averaged aspect directions are mapped as vectors at 100 m sample window centroids (Figure 11). One anomaly existed in CWD fall direction. By field sampled aspect, only 1% of inventoried CWD fell on an east aspect. Based on the 100 m smoothed values for aspect, none of the inventoried CWD was located on an east aspect (Figure 13). However, 9% of inventoried CWD fell to the east. That is, most CWD was oriented downhill, and very little area was of an east aspect, so more CWD was oriented east than expected. The directional distribution of CWD that fell on an east aspect was skewed slightly north, and fall directions were slightly more variable on south aspects than on other aspects. However, these anomalies are likely a function of the small sample size of CWD found on east and south aspects. Slope was found to have a statistically significant linear relationship with the departure of fall direction from the downhill direction ($p<0.01$;

$r2=0.03$; $F=20.3$; 1, 593 d.f.), with departure from downhill decreasing with increasing slope steepness. However, the linear model only explains 3% of the variance in departure, and likely has little biological significance.

Mean fall direction differed slightly by decay class, and Douglas-fir and western hemlock CWD followed a similar trend in changes to mean direction by decay class. However, mean fall directions for all decay classes for both species were within one standard deviation of each other and the total mean fall direction (Figure 12).



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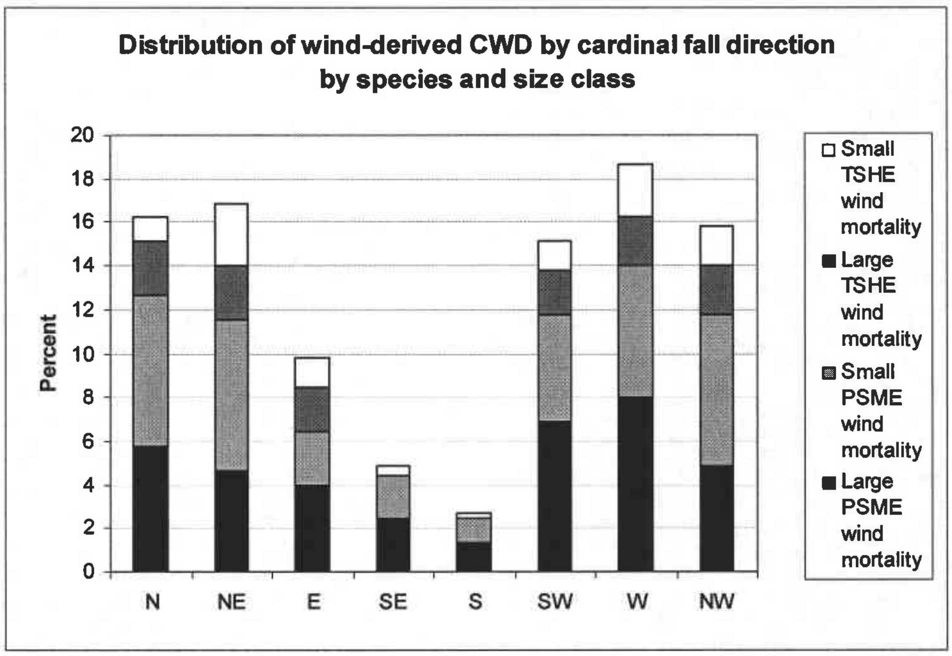


b)

Figure 9: Histograms of a) all sampled mortality by fall direction and b) sampled wind mortality by species and size class.

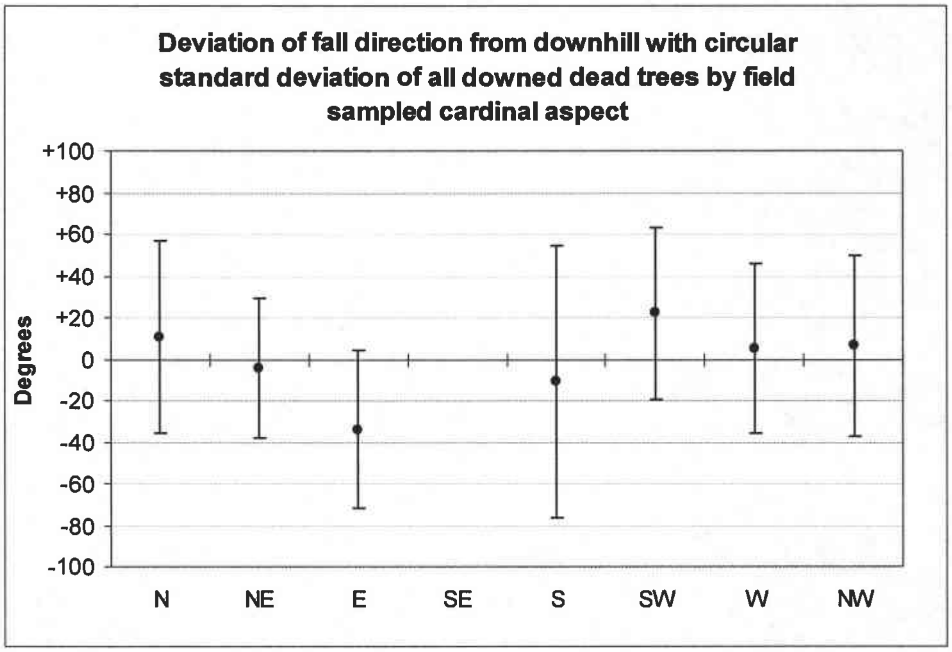


Figure 10: Deviation of fall directions from downhill direction of downed dead trees by cardinal field sampled aspect with CSD as Y-error bars. (n: N=174, NE=51, E=8, SE=0, S=19, SW=52, W=115, NW=176)

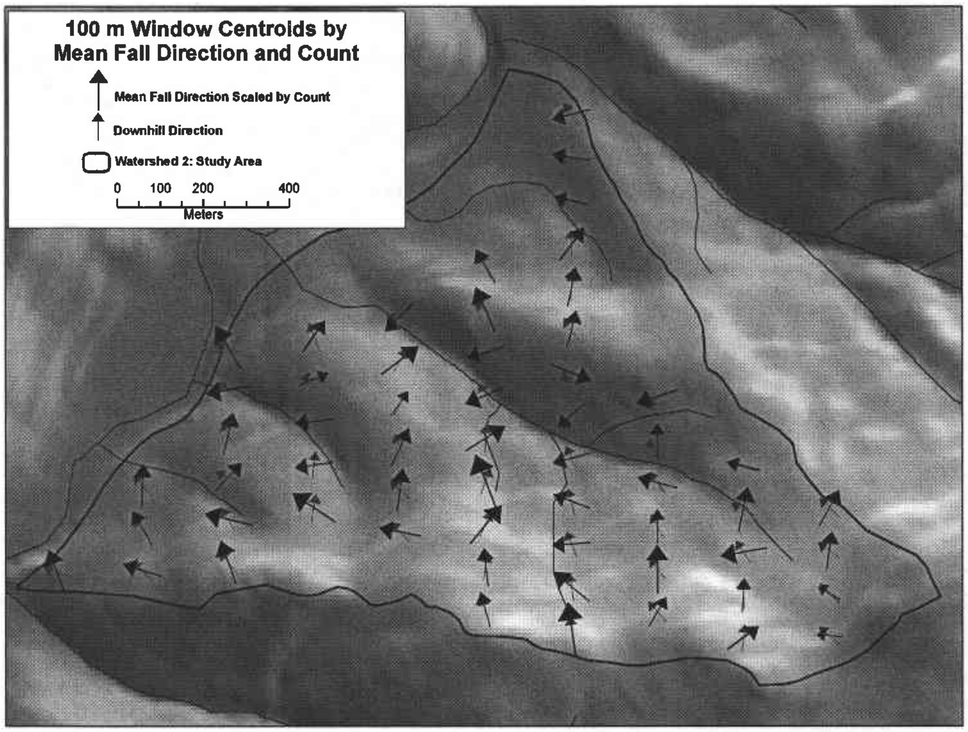


Figure 11: Map of mean fall directions and downhill directions for centroids of 100 m smoothed sampling windows. Note correlation between downhill and fall directions.

Figure 12: Deviation from mean fall direction of downed dead trees (328.5°) by decay class by species with CSD as Y-error bars. Species follow similar trend, but mean fall directions of all decay classes are within 1 CSD of the mean fall direction of all downed dead trees. (n: PSME: 1=18, 2=98, 3=188, 4=103, 5=27; TSHE: 1=50, 2=54, 3=22, 4=6)

Mortality Response to Landscape Attributes

Mortality by Aspect

The study area is of a roughly northwest aspect. Though fine scale variation generates a variety of aspects on the ground, only 5 cardinal aspects were identified on the 100 m window smoothed DEM (Figure 13). The DEM calculations show the sampled landscape to be of a northwest-north aspect, with some areas facing west, southwest, and northeast. The distribution of landscape area by aspect, as calculated from the DEM, is quite similar to the distribution of aspect as inventoried in the field at sites with CWD present. The distribution of aspect areas of sampling transects did not statistically differ from the distribution of the aspect areas of PSPs (p:0.63, X^2: 2.6, 4 d.f.) (Figure 13). Thus, distributions of live tree and CWD data are comparable by aspect.

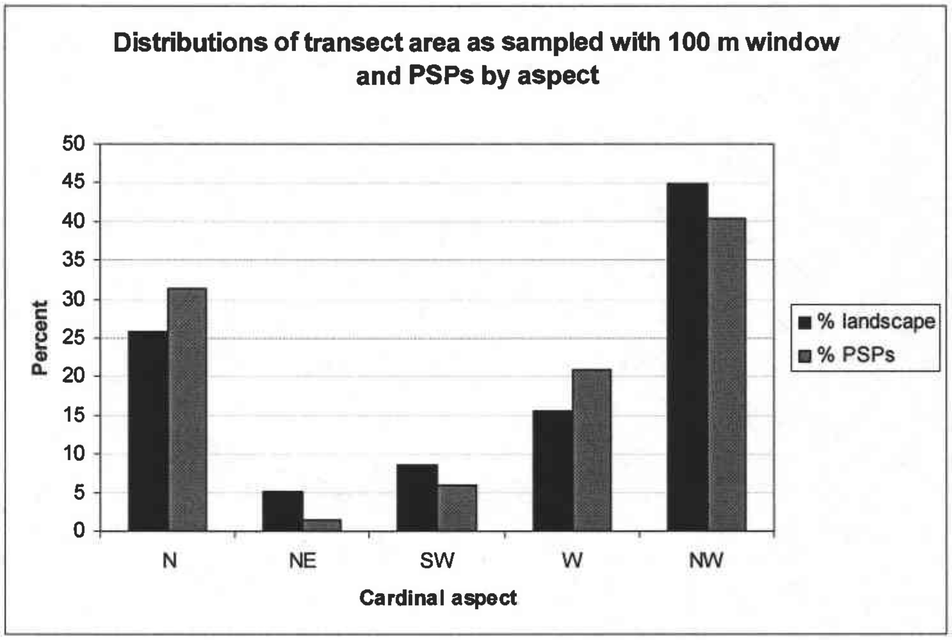


Figure 13: Distributions of transect areas as sampled with 100 m window and PSPs by cardinal aspect. Distributions do not vary in a statistically significant manner.

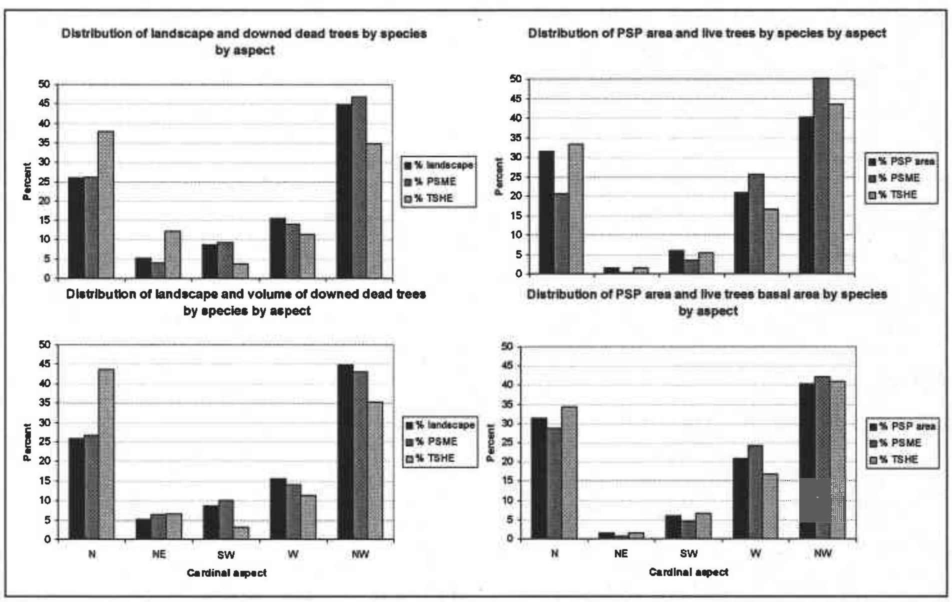
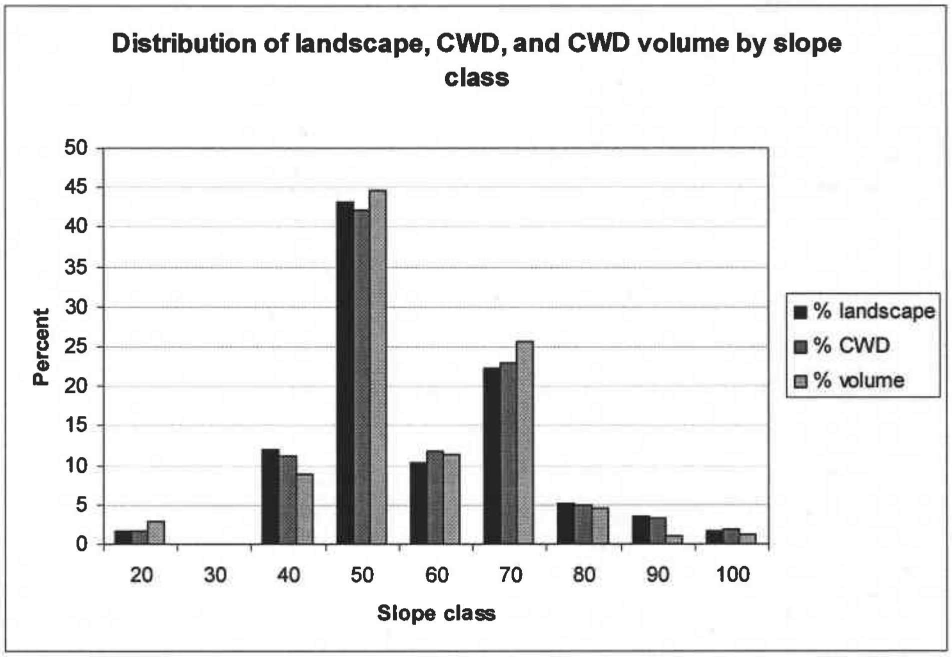


Figure 14: Distributions of CWD and live trees in the study area by density and volume. Downed dead trees refers to CWD. Basal area and volume are not directly comparable, but may serve as proxy for one another.

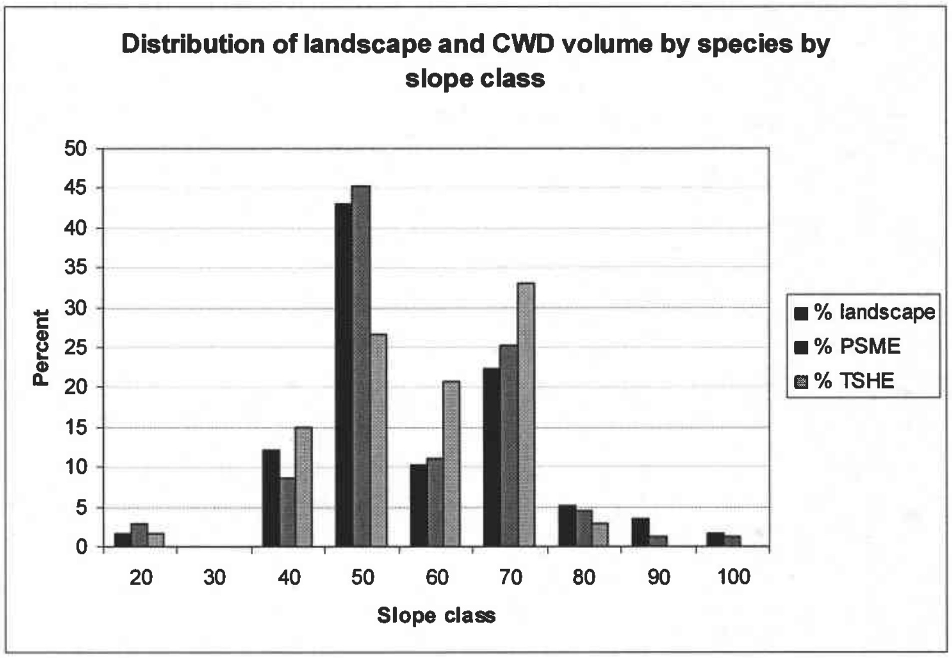
CWD and live trees were evenly distributed across cardinal aspect area by density, volume, and species classes (Figure 14). There is some evidence of uneven distributions of live Douglas-fir density (p:0.07, X^2: 8.7, 4 d.f.) and western hemlock CWD volume (p:0.07, X^2: 8.8, 4 d.f.) across aspect classes (Figure 14), however it is not statistically significant at an alpha level of 0.05.

Mortality by Slope

CWD was evenly distributed across slopes found within the study area (Figure 15a). Little discrepancy exists between the distributions of sampled area by slope class and CWD or volume (CWD: p:~1.0, X^2: 0.5, 7 d.f.) (volume: p:0.34, X^2: 7.8, 7 d.f.). Distributions of mortality across slope differed slightly by species, with western hemlock CWD volume not being evenly distributed among slope classes ($p<0.001$, X^2: 24.7, 7 d.f.) (Figure 15b). However, there was no linear response between slope and CWD density (p:0.83; r^2:~0; F:0.05; 1, 56 d.f.).



a)

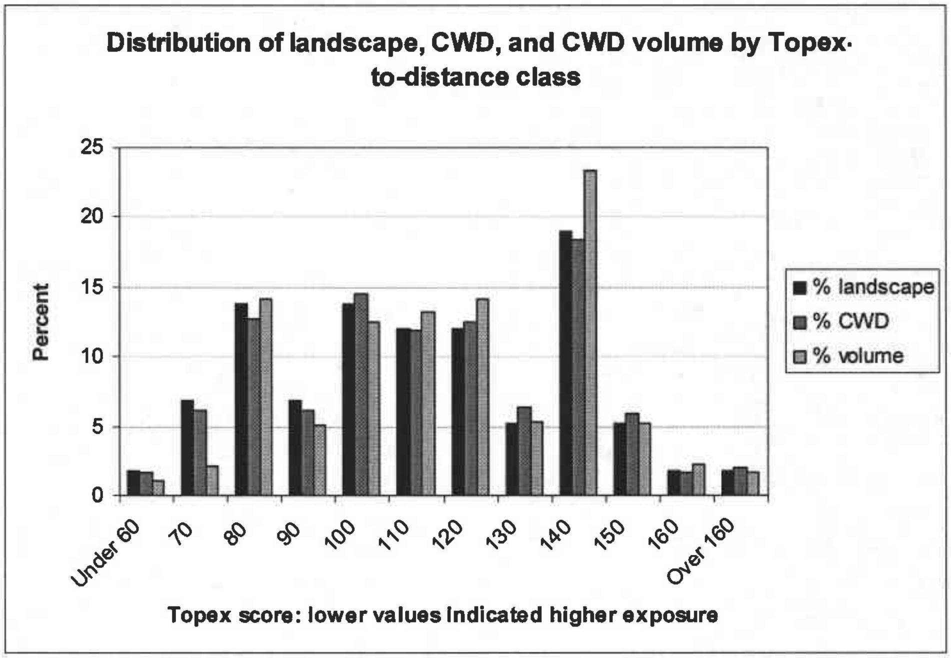


b)

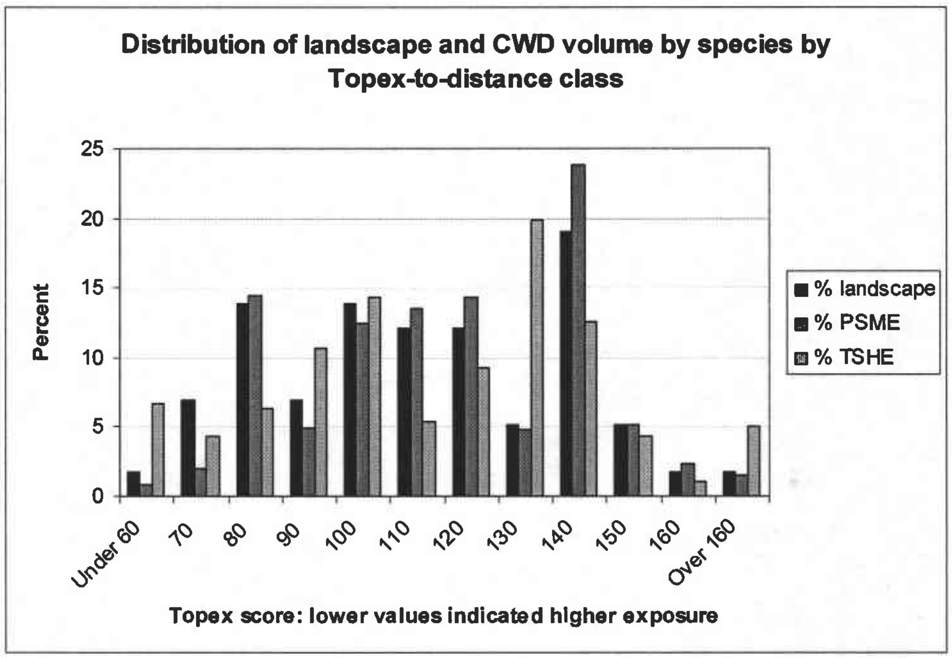
Figure 15: Histograms of a) CWD by 10% slope classes and b) CWD volume by species by 10% slope classes. The distribution of slope classes identified with the moving window analysis of the 10 m DEM was similar to that of values measured on the ground.

Mortality by Levels of Topographic Exposure

CWD, by count and by volume, was evenly distributed across levels of topographic exposure within the study area (CWD: p:~1, X^2: 0.6, 11 d.f.) (volume: p:0.28, X^2: 13.2, 11 d.f.) (Figure 16a). Thus, the majority of mortality occurred in relatively unexposed locations. As such, volume was found to increase with decreasing topographic exposure (p=0.01; r^2=0.11; F=6.62; 1, 56 d.f.), but only 11% of the variance of volume was described by topographic exposure. Distribution of CWD by species by topographic exposure class showed western hemlock volume to be somewhat unevenly distributed across levels of topographic exposure (p:0.003, X^2: 28.1, 11 d.f.) (Figure 16b), but as with slope, the response was not linear (p:0.62; r^2:~0; F:0.24; 1, 56 d.f.).



a)

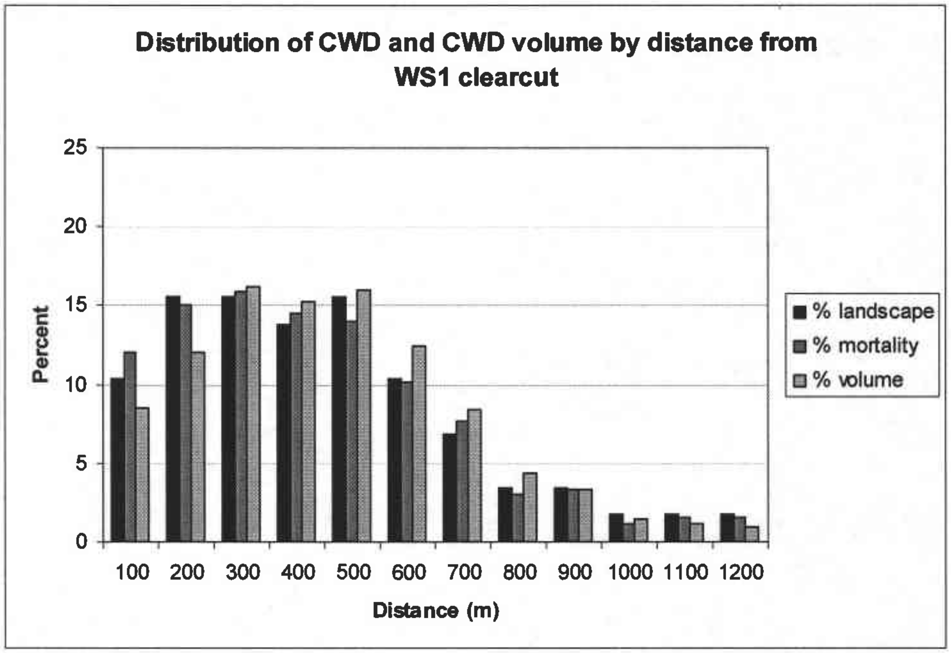


b)

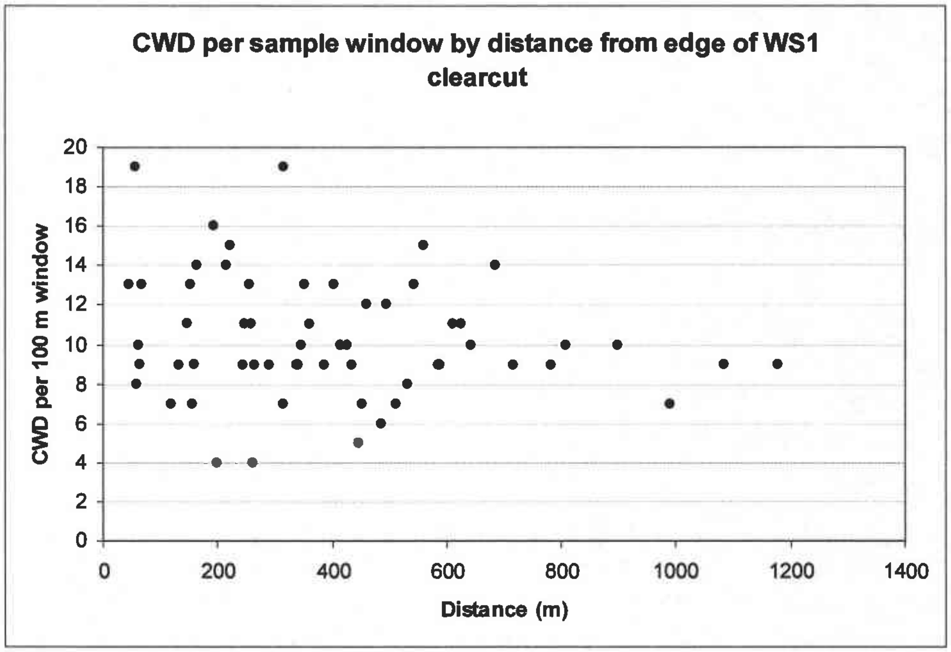
Figure 16: Histograms of a) CWD and CWD volume by topographic exposure classes and b) CWD volume by species by topographic exposure classes.

Mortality by Distance from Clearcut Edge

CWD was evenly distributed across 100 m classes of distance from the clearcut edge separating the study area and Watershed 1 (CWD: p:~1, X 2: 0.8, 11 d.f.) (volume: p:0.98, X 2: 3.4, 11 d.f.) (Figure 17a). This distribution did not vary by species. It seemed possible that the edge effect being tested could decrease with increasing distance from the clearcut edge. However, CWD density is quite variable regardless of proximity to the clearcut edge, with no linear response between distance from the clearcut edge and CWD density ($p=0.19$; $r^2=0.03$; $F=1.78$; 1, 56 d.f.) (Figure 17b). It appears that CWD density decreases at approximately 700 m from the clearcut ridge, but this is likely due to there being few smoothed window sample points located more than 700 m from the clearcut ridge.



a)

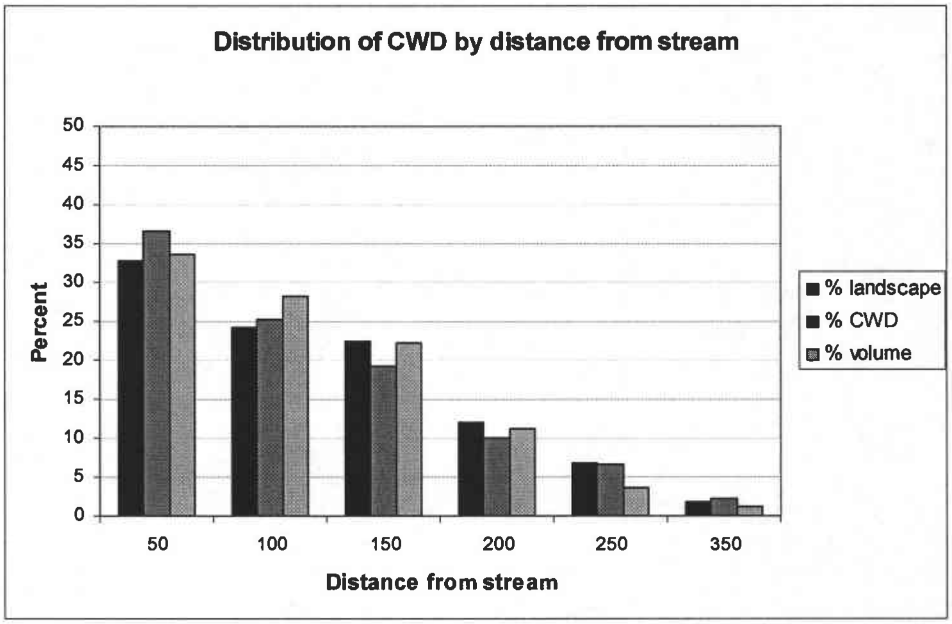


b)

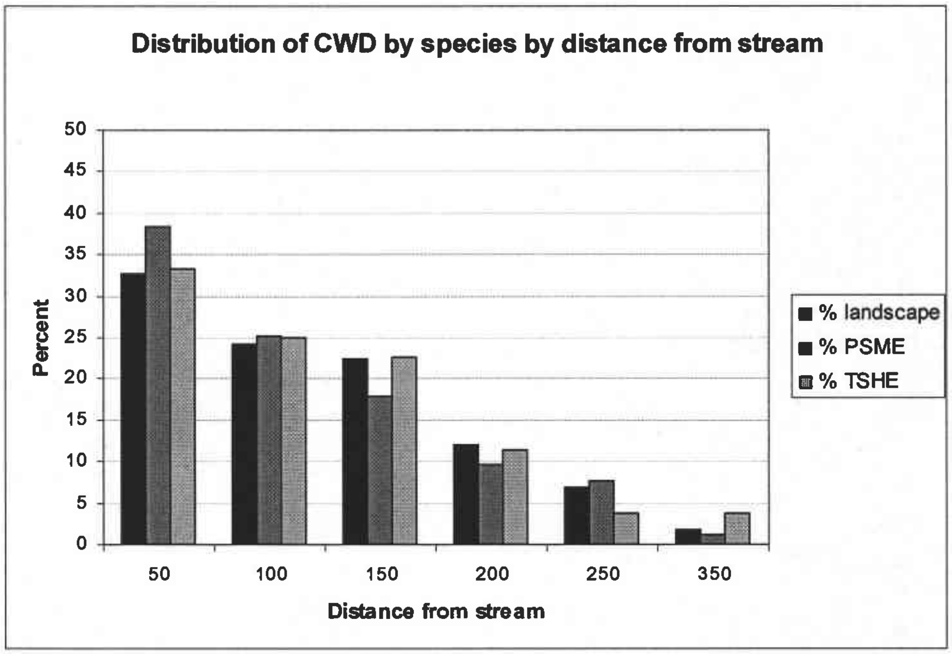
Figure 17: Histogram (a) and b) scatter plot of 100 m window sampled CWD by distance from clearcut edge. Note even distribution across distance classes (a) and variability of CWD density even in close proximity to the clearcut edge (b).

Mortality by Distance from Nearest Stream Channel

CWD, by density and volume, was evenly distributed across 50 m classes of distance from sampling points to the nearest stream channel (CWD: p:0.98, X^2: 0.7, 5 d.f.) (volume: p:0.93, X^2: 1.4, 5 d.f.) (Figure 18a). The distribution of CWD density by distance from the nearest stream channel did not differ by species (Douglas-fir: p:0.93, X^2: 1.4, 5 d.f.) (hemlock: p:0.89, X^2: 1.7, 5 d.f.). However, western hemlock volume was not evenly distributed by distance classes (p:0.05, X^2: 11.3, 5 d.f.), with 50% of total hemlock volume being located within the 50 meter distance class.



a)



b)

Figure 18: Histograms of a) CWD density and volume and percent of landscape area by distance from nearest stream channel and b) CWD density by species and percent of landscape area by distance from nearest stream channel.

Wind Directionality

Wind directions and magnitudes were found to be temporally and spatially variable across the Andrews landscape during the period of assessment (January 1, 1997 through December 31, 2002). The meteorological (met) station closest to the study area is PRIMET (Figure 19). All other met stations are located in more eastern, higher elevation portions of the Andrews. The H15MET station anemometer is fixed at a height of 500 cm; the gauges of the other met stations for which data were assessed are fixed at a height of 1000 cm. The three higher elevation stations with anemometer heights of 1000 cm (VANMET, CENMET, UPLMET) recorded windspeeds that were categorically higher than those recorded at PRIMET (Table 4), but they were less directional (Figures 19, 20).

Table 4: Mean daily maximum windspeeds (m s^{-1}) and mean daily maximum of top 5% of windspeeds by cardinal flow direction (direction wind flows to). Data from 1997 through 2002 from 5 meteorological stations at the Andrews. Gauge height 1000 cm (H15MET gauge height 500 cm).

	PRIMET		CENMET		UPLMET		H15MET		VANMET	
Flow Direction	All Days	Top 5%	All Days	Top 5%	All Days	Top 5%	All Days	Top 5%	All Days	Top 5%
N	3.41	**none**	6.53	10.83	5.52	9.10	3.50	6.85	8.50	13.13
NE	4.87	7.44	6.36	10.37	4.49	11.38	4.11	5.56	7.11	12.94
E	3.46	9.70	9.00	10.95	4.85	10.40	2.94	5.09	5.76	13.06
SE	2.20	7.80	8.13	13.05	5.43	10.28	2.40	5.13	4.73	**none**
S	2.71	7.55	7.28	10.73	6.00	10.30	2.47	5.40	4.37	**none**
SW	1.81	7.53	4.90	10.88	5.84	10.48	3.29	5.48	6.52	12.56
W	2.03	**none**	4.94	10.29	6.19	10.23	3.42	5.77	9.07	12.71
NW	2.74	**none**	5.84	10.78	6.11	10.22	2.48	**none**	9.47	13.22
Total Mean	3.85	7.49	5.30	10.67	5.28	10.34	2.70	5.44	6.25	12.86

About 62% of all winds and 90% of strong winds (top 5% of winds by magnitude during the period of record) recorded at PRIMET flowed northeast (Figure 20), but the fastest winds recorded at PRIMET flowed east. Despite their high degree of magnitude, winds flowing east were quite rare, composing only about 1% of all winds and the top

5% of winds recorded at PRIMET. Wind magnitudes and directionality also differed among the high elevation sites. The H15MET station recorded the lowest windspeeds, but this is likely due to its lower anemometer position. The CENMET station recorded winds of a similar magnitude from all 8 cardinal directions (Table 4), but the majority of winds flowed southwest and west (Figure 20). Winds recorded at UPLMET were similar in magnitude to those recorded at CENMET, but the distribution of winds across cardinal aspects was much more even at UPLMET (Figure 20). Winds recorded at VANMET flowed predominantly east. However, the top 5% of winds recorded at VANMET, which were the fastest of any winds recorded (Table 4), flowed predominantly northeast and west (Figures 19, 20).

The means of all windspeeds and the top 5% of windspeeds from the 4 met stations with equal anemometer heights were well correlated with Topex-to-distance scores (all: $p<0.01$; $r^2=0.986$; $F=141.0$; 1, 2 d.f.) (top 5%: $p<0.01$; $r^2=0.997$; $F=736.1$; 1, 2 d.f). However, the correlation should be regarded cautiously due to the small sample size.

Winds also differed by season. The majority of strong winds at upper elevation met stations occurred during the winter, primarily from December to February. However, winds at PRIMET showed an opposite trend, with the majority of the top 5% of winds by magnitude occurring between May and August (Figure 21).

A windstorm known to have caused windthrow throughout the Andrews occurred in early January 1990. Records for PRIMET from two days (January 7-8, 1990) show windspeeds that exceed the top windspeeds recorded from 1997 through 2002 by at least 2 m s^{-1}. These fast winds flowed to the northeast.

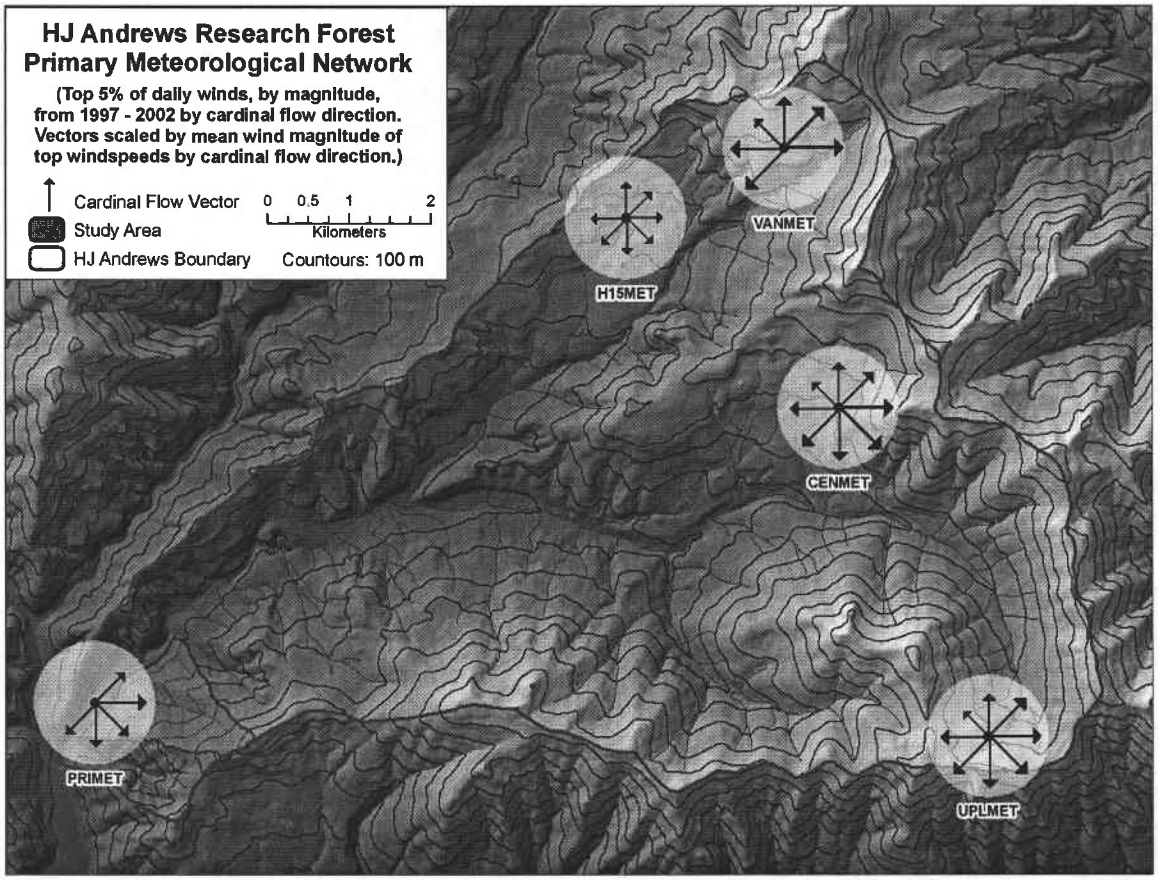


Figure 19: Map of HJ Andrews primary meteorological network. Wind flow vectors, by cardinal direction (to), are scaled by mean magnitude of windspeeds of top 5% of winds from 1997 – 2002 for all met stations.

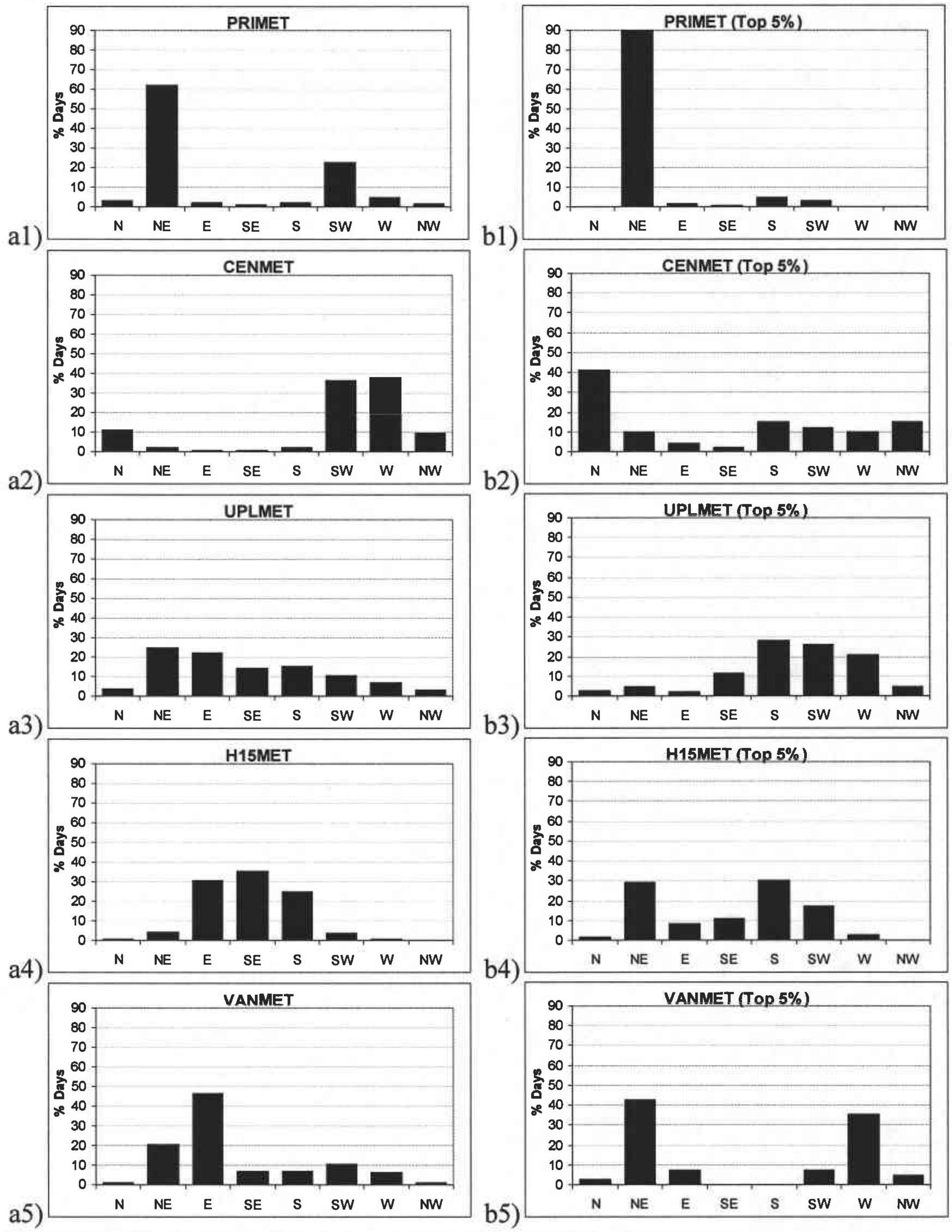


Figure 20: Histograms of a) daily winds and b) top 5% of winds by magnitude by cardinal direction for 1997 through 2002 for 5 HJ Andrews met stations.

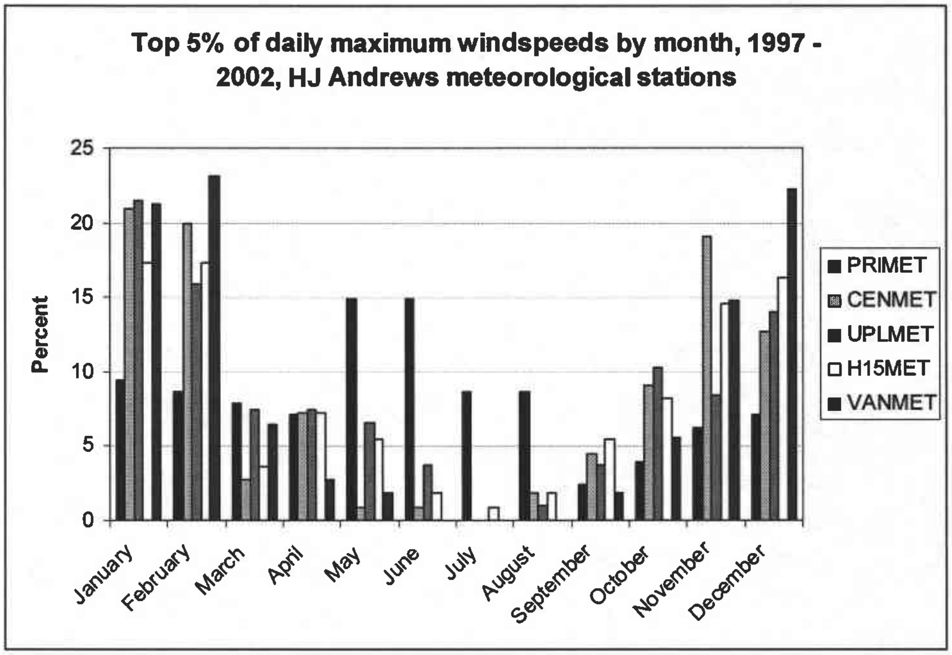


Figure 21: Distribution of the top 5% of daily maximum windspeeds from 1997 through 2002 by month for 5 HJ Andrews met stations. Note that fast winds from PRIMET occur primarily during the summer months, which is abnormal as compared to the distributions of the other 4 met stations.

DISCUSSION

Chronic or episodic mortality?

Results from this study show wind to have been the dominant cause of mortality of trees sampled in the study area. Evidence suggests that wind mortality in the study area was the result of chronic disturbance (unable to reject null hypothesis 1c). This finding is supported by relatively even temporal distributions of mortality (as decay class of CWD), as well as by CWD fall directions and wind distribution characteristics.

The distribution of Douglas-fir CWD was skewed towards larger size classes. However, the somewhat inverse relationship between size distribution of Douglas-fir CWD and that of living Douglas-fir trees suggests that, in the study area, Douglas-fir becomes increasingly susceptible to mortality at nearly 100 cm DBH, and that live

Douglas-fir trees of approximately 100 cm DBH are not being replenished fast enough to keep pace with mortality. The likely outcome of such a scenario is the gradual decline of the presence of Douglas-fir as a species in the study area, a fate expected of even a long enduring seral species given a lack of broad scale forest disturbance or localized species maintenance (Franklin and Dyrness, 1973). In the near future, however, it appears that the largest of living Douglas-fir trees may maintain their position of prominence within the study area forest. Much of the found Douglas-fir CWD was between 70 and 100 cm DBH, but Douglas-fir CWD was evenly distributed among size classes over 100 cm DBH. This pattern is inversely related to the size distribution of live trees in PSPs, which suggests that the rate of Douglas-fir mortality may decline after a peak in mortality susceptibility around 100 cm DBH, and that the survivorship of old-growth Douglas-fir trees may increase with size after a period of heavy mortality. This agrees with Bible's (2001) finding of increased survival of large, old Douglas-fir trees.

Western hemlock mortality appears to have increased in recent time compared to Douglas-fir mortality, thus null hypothesis 1b is rejected. The residence time of logs in each decay class increases geometrically with increasing decay class (Harmon et al. 1986). Therefore, the error associated with each decay class, in terms of standard error about the mean time since mortality of sampled logs, increases with increasing decay class (Sollins et al. 1987). Also, downed logs lose volume with increasing decay, and small logs become difficult to identify in advanced stages of decay. Thus, a bell shaped distribution is expected with a constant rate of mortality, as a small amount of CWD is expected in low decay classes due to their short residence times, and a small amount of CWD is expected in decay class 5 due to the volume loss and small tree disappearance. In

Douglas-fir stands older than approximately 130 years, the majority of CWD has been found to be divided between decay classes 3 and 4 (Harmon et al. 1986). Therefore, the decay class distribution found for Douglas-fir CWD represents a relatively even distribution of mortality through time. The roughly equal amounts of CWD found in decay classes 2 and 4, in terms of count and volume, suggest a possible spike in Douglas-fir mortality during the last 50 years that could be related to an episodic disturbance. Due to the coarse temporal resolution of decay classes, a particular causal event cannot be determined. The decay class distribution found for downed dead western hemlock represents a recently increased rate of mortality. Additionally, western hemlock has been found to progress through decay classes at a faster rate than Douglas-fir. For western hemlock, Sollins et al. (1987) found mean times since mortality of 4, 9, 25, and 81 years for decay classes 1, 2, 3 and 4, respectively. Mean times since mortality for Douglas-fir were 3, 11, 50, and 87 years for the same classes. Thus, the decidedly left-skewed distribution of decay classes of western hemlock CWD suggests that western hemlock mortality is significantly more concentrated in recent time than Douglas-fir mortality.

The recent increase in western hemlock mortality may be due mostly to the species' recent attainment of large size classes that are susceptible to wind damage. Therefore, the rejection of hypothesis 1b should be regarded carefully. Western hemlock CWD, by percent of all CWD inventoried, was far less common than its presence as a living species in the study area would suggest. Thus, fewer western hemlocks appear to be dying than are living. Therefore, barring a drastically increased rate of western hemlock mortality in the future, the species will likely gain increasing dominance in the study area through time.

Based on the decay class distribution of CWD, Douglas-fir has historically inputted far more CWD, in terms of count and volume, than western hemlock. However, for decay class 1, western hemlock is the principal contributor of CWD by count and volume. This suggests that western hemlock is now the primary contributor of CWD in the study area, and that an increasing proportion of CWD will be western hemlock. As western hemlock CWD decays faster than Douglas-fir CWD, the residence time of CWD in the study area may decrease as a whole.

Sobota (2004) noted that trees most often fell downhill in riparian areas of several forest types. Results from this study show a similar trend, as the mean fall direction of downed dead trees varied consistently by aspect. The disproportionate amount of CWD oriented to the east may be explained by the distribution of fast winds. Given that most CWD was found to be in line with aspect, trees falling east likely endured an additional, directional pressure. This pressure may have come in the form of the fastest winds affecting the study area which, according to the PRIMET data assessed, flowed east. Strong winds from abnormal directions are more likely to blow down trees than strong winds from prevailing directions (Sinton 1996) because tree physiology adapts to the surrounding environment. Reaction wood and rooting structure develop to resist constant environmental pressures, which can include dominant wind and storm directions (Telewski 1995). Thus, the fast, east flowing winds may have been abnormal enough to cause a level of mortality disproportionate to the concentration of such winds. Though the dissimilar percentages of east flowing winds and east falling mortality may serve as a basis for a relationship between winds and mortality in the study area, the relationship cannot be quantified with the data gathered for this study.

Several possible reasons exist for the CWD fall direction distribution not being better aligned with the fast wind distribution recorded at PRIMET. Winds in complex terrain are heavily modified by that terrain (Sinton 1996, Hannah et al. 1995), and wind directionality and magnitude can vary significantly over short distances. Thus, the PRIMET wind distribution may not be fully representative of the distribution of winds actually affecting the study area. Almost all strong winds recorded at PRIMET flowed northeast. As the dominant aspect of the study area is north-northwest, the direction of strong winds may have simply pushed trees in their downhill direction. Also, strong winds recorded at PRIMET occurred most often during summer months. Windthrow morality has been found to occur most often during abnormally cold temperatures, where snow and ice loading, as well as decreased wood elasticity, can contribute to root throw and bole breakage (Sinton and Jones 2002, Sinton 1996). These conditions are not likely during the summer months. Finally, the study area is situated on a lee slope respective to the high magnitude winds affecting the study area. Thus, the entire study area may be protected against strong winds likely to cause episodic windthrow.

Topographic Modification of Mortality Susceptibility?

The spatial distribution of CWD was not found to be associated with any of the topographic variables assessed, thus hypothesis 2a is rejected. Slope has been found to affect mortality susceptibility, with steep slopes inputting more CWD to riparian ecosystems in coniferous forests similar to the forest in the study area (Sobota 2004). The lack of such a finding in the study area could be because slope may only affect tree fall susceptibility in soils with high moisture content, hence the relationship in riparian areas.

However, the sample size of trees in riparian areas in this study was not high enough to evaluate such a relationship.

Topographic exposure has been found to be well correlated with windthrow mortality at the landscape scale (Boose et al. 2001, Mitchell et al. 2001). Given the low degree of association between local fast wind directions and tree fall directions, a strong relationship between topographic exposure and the density of windthrow-derived CWD was not expected. No relationship between exposure and CWD density was found in terms of count, but a weak linear association existed between CWD volume and exposure, with volume increasing with decreasing exposure. This inverse relationship seems somewhat counterintuitive, but western hemlock CWD volume was found to increase near stream channels. Topographic exposure, as quantified using the Topex-to-distance model, is lowest in deep topographic incisions (e.g. in stream channels). Thus, the weak, inverse relationship between topographic exposure and CWD volume is likely due only to high levels of western hemlock CWD volume being present in stream channels.

Clearcuts made adjacent to unmanaged (Sinton et al. 2000) and managed (Mitchell et al. 2001) forests can yield additional and excessive wind exposure that can cause abnormally high levels of windthrow mortality. The increased exposure related to clearcuts occurs for the same physiological reason described above in a rare winds context. Trees at the clearcut margin develop under stand mitigated winds, but uncut trees become exposed to unmitigated winds after the harvest of adjacent trees. No association between CWD density and the distance from the clearcut boundary was found for any combination of decay class, size class, and species. The lack of association between clearcut distance and CWD density existed even within the first hundred meters from the clearcut margin. Thus, hypothesis 2b is rejected. The clearcut margin runs along the ridgeline defining the study area and its basins. As such, the trees that mark the clearcut margin were under high levels of topographic exposure even before the adjacent forest area was harvested. Therefore, an increase in topographic exposure caused by the installation of the clearcut may not have been significant enough to cause increased mortality and associated CWD density.

The lack of any findings supporting topographic modification of windthrow susceptibility may be due to several factors. Most importantly, the study area may not be physically variable enough to result in areas of increased mortality susceptibility. That is, the majority of the study area is of one general aspect (northwest-north), and there are few areas of extreme topographic exposure or slope, so mortality susceptibility may be relatively even across the study area.

Ecological Implications of Chronic Wind Disturbance?

The forest of the study area is changing. Stand density of western hemlock and Douglas-fir is decreasing, but is decreasing at a faster rate for Douglas-fir. Different mortality rates for Douglas-fir and western hemlock suggest that progression to climax, western hemlock dominated plant associations is occurring. At the stand level, biomass of Douglas-fir trees in the study area has remained relatively constant since 1982, but only because net primary production has offset mortality (Acker et al. 2002). Western hemlock maintains a far greater percentage of regeneration than Douglas-fir. Additionally, the percent of stand basal area or biomass composed of western hemlock has increased steadily since 1982. Mortality of western hemlock has increased in recent time, but not likely to an extent that would reverse the species ascension to dominance.

Chronic wind disturbance and associated tree mortality is playing an important role in the development of the study area forest. The rapid generation and release of an abundance of resources caused by windthrow mortality affects growth and regeneration of vegetation surrounding single tree and small patch mortality. Western hemlock maintains a regenerative advantage over Douglas-fir in single tree and small patch gaps (Gray and Spies 1996) due to limited light availability. Also, western hemlock trees are more capable of exploiting nurse log resources than Douglas-fir. Thus, the single tree and small patch wind mortality that is dominant in the study area provides both a growth medium and light conditions that favor the climax species.

Localized pockets of concentrated mortality, and resultant CWD, may occur even under chronic disturbance regimes, as can be seen in the study area on the mortality distribution map (Figure 3). However, unless these pockets developed due to elevated disturbance susceptibility caused by landscape structure, rather than by chance, then they are not likely to remain after a single generation of forest development. No associations between landscape attributes and mortality concentration were found in this study. Therefore, no sites within the study area will be likely to continually sustain Douglas-fir regeneration due to large mortality patch maintenance. Even if regeneration favors Douglas-fir in larger patches of concentrated mortality identified during this inventory, the areas will eventually by succeeded by the climax species.

Douglas-fir logs can take more than 200 years to decompose (Sollins et al. 1987), and carbon sequestration benefits are maintained during this period. Meanwhile, regeneration of shade tolerant species in canopy gaps yields additional sequestration. Thus, a period of high carbon storage may follow broadly distributed small patch and single tree mortality. Estimates of volume made in this study (1041 m^3 ha^{-1}) are higher than published values for similar forests (650 – 850 m^3 ha^{-1}, Harmon et al. 1986), but this was expected given the method of calculation.

How Do Patterns in the Study Area Differ from Patterns at Greater Spatial Extents?

Chronic windthrow appears to be the dominant cause of mortality in the small, forested study area. No evidence of historical episodic windthrow mortality was found. This finding differs from that of researches conducted at much larger spatial extents, most of which show episodic windthrow to be a significant landscape disturbance process affecting stand structure and composition, including in forests of the type inventoried in this study (Harcombe et al. 2004, Kramer et al. 2001, Sinton et al. 2000, Rebertus et al. 1997, Foster et al. 1992, Veblen et al. 1991). The lack of a finding of episodic mortality in this study does not mean that a discrete, severe windthrow disturbance event has not affected or will not affect the study area. However, it appears that at the spatial extent of inventory (145 ha), the return interval for catastrophic wind disturbance can be at least as long as the residence time of CWD (>200 yrs). It is also possible that episodic mortality events have occurred in the study area and that evidence for such events may exist, but that the sampling design employed for this study was not able to identify such events. The temporal resolution afforded by inventorying decay class may be too coarse to identify major wind events. That is, fine scale variation of mortality in time (year to year, storm to storm) and space could essentially average out within the residence time of each decay class.

Rampant fire suppression through the 20th century has yielded a departure from historical fire disturbance return intervals (Baker 1992). The lack of fire disturbance elevates the importance of roles played by other disturbance agents in the successional development of forests. Landscape scale catastrophic windthrow can be a dominant disturbance process that drastically alters seral development (Veblen et al. 1991). Such severe manifestations of the disturbance process are known to generate forest heterogeneity at the landscape scale (Boose et al. 2001). This research suggests that chronic windthrow mortality operating in small forests will actually aid in the progression of seral development, rather than alter it. Thus, small, topographically similar and protected forests similar to the study area may more commonly realize climax associations.

CONCLUSIONS

This study provides insight into the disturbance processes affecting small, old-growth forests in the western Cascades. The study is novel in that little windthrow research had been conducted at a spatial extent between that of the site and the landscape. Findings show chronic windthrow disturbance to be the dominant cause of mortality, which was found to be unaffected by topographic variability that exists within the study area. Tree susceptibility to windthrow mortality was found to be unaffected by proximity to a clearcut edge bordering the study area, a finding that differs from studies conducted at greater spatial extents. Sampling was not replicated in multiple small forests or in forests of different age classes and species composition, thus the scope of inference of this study is limited to the actual study area. However, findings still suggest that small, topographically protected, old-growth Douglas-fir forests in the western Cascades may be likely more to reach climax plant associations (i.e. western hemlock dominated) without additional, severe disturbances such as fire or forest harvest when chronic windthrow is the only active disturbance process. More research needs to be conducted to address the role of wind disturbance at small and intermediate spatial extents (greater than 20 ha, less than 1,000 ha).

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