The tree mortality regime in temperate old-growth coniferous forests: the role of physical damage

Andrew J. Larson and Jerry F. Franklin

Abstract: Aspects of the tree mortality regime were characterized for old-growth conifer forests in Mount Rainier National Park, Washington, USA, using individual tree (stems ≥5 cm diameter at breast height (dbh)) records from a network of permanent forest research plots. Average annual forest-wide mortality rates of trees ≥15 cm dbh never exceeded 1% on a stem-density or basal-area basis; mortality was slightly higher for stems <15 cm dbh. Physical agents of mortality (uprooting, stem breakage, and crushing by falling debris) accounted for approximately 40% and 45% of mortality events in trees <15 and ≥15 cm dbh, respectively. These physical processes were chronic sources of mortality: they were not associated with a single or few disturbance events. Preexisting decay fungi were associated with trees that died proximately due to stem breakage (41%) and uprooting (22%), consistent with a predisposing role of decay fungi in trees that die due to mechanical damage. Given the importance of physical processes in the tree mortality regime, we suggest that a richer mechanistic understanding of the causes and consequences of tree mortality in natural forests will be achieved with models that consider the physical, as well as the physiological, attributes of trees and forests.

Résumé : Le régime de mortalité des arbres dans les vieilles forêts de conifères du Parc national du mont Rainier dans l'État de Washington a été caractérisé à l'aide de données d'arbres individuels (tronc ≥ 5 cm au dhp) provenant d'un réseau de parcelles expérimentales permanentes. Dans l'ensemble des forêts, le taux annuel moyen de mortalité des arbres ≥ 15 cm au dhp n'a jamais dépassé 1 % sur la base du nombre de tiges ou de la surface terrière; la mortalité était légèrement plus élevée chez les arbres < 15 cm au dhp. Les causes abiotiques de mortalité (déracinage, bris du tronc et écrasement dû à la chute de débris) représentaient respectivement environ 40 et 45 % des cas de mortalité chez les arbres < 15 cm et ≥ 15 cm au dhp. Ces processus abiotiques étaient des sources chroniques de mortalité : ils n'étaient pas associés à un ou quelques épisodes de perturbation. Des champignons de carie préexistants étaient associés aux arbres qui sont finalement morts à cause du bris du tronc (41 %) et du déracinage (22 %); ce qui est cohérent avec le rôle prédisposant des champignons de carie chez les arbres qui meurent à la suite de dommages mécaniques. Étant donné l'importance des processus abiotiques dans le régime de mortalité des arbres, nous croyons que nous parviendrons à une meilleure compréhension des mécanismes associés aux causes et aux conséquences de la mortalité des arbres dans les forêts naturelles avec des modèles qui tiennent compte des attributs physiques, aussi bien que physiologiques, des arbres et des forêts.

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Introduction

Tree mortality directly regulates tree populations and forest community composition and structure. Mortality determines the upper bounds of tree size and age and influences the form of tree size distributions (Lorimer et al. 2001). Dendroecological studies (e.g., Winter et al. 2002) and manipulative experiments (e.g., Van Pelt and Franklin 1999) demonstrate that tree mortality indirectly influences subsequent forest structural dynamics: understory tree establishment, growth, and survival respond to overstory tree mortality.

Only direct long-term observations can reveal rates and causes of tree mortality in natural forests. Several otherwise comprehensive studies of tree mortality have emphasized correlates while eschewing causes (e.g., Condit et al. 1995; van Mantgem et al. 2009). Consequently, despite the fundamental ecological importance, rates and especially causes of tree mortality in natural forests remain poorly understood.

Physical processes constitute a tractable baseline from which to characterize the tree mortality regime in natural forests (Clark and Clark 1991). Trees dying due to physical processes can be clearly distinguished from the trees dying proximately due to biotic factors or competition, i.e., trees that die intact and standing (Clark and Clark 1991; van Mantgem and Stephenson 2007). Here, "physical processes" is used as an inclusive term that subsumes mechanical mortality (uprooting or stem breakage) due to direct interactions with environmental phenomena such as wind and snow and crushing mortality caused when trees are damaged by falling trees or tree parts (Fig. 1). These respective physical agents of tree mortality are readily differentiated (Putz et al. 1983; Gale and Barford 1999).

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Fig. 1. An example of a ~25 cm dbh *Tsuga heterophylla* crushed and killed by a larger falling tree (the bole of which is visible in the lower left corner of the image). The stem of the crushed tree was sound — with no evidence of preexisting decay fungi or rotten wood — which is characteristic of most trees killed by crushing in this study (Fig. 6). The tree tag visible near the center of the image measures 3.7 cm long.

Physical processes provide a means to partition the multiple interacting factors (sensu Franklin et al. 1987) leading up to tree mortality. Decay fungi reduce the resistance of trees to physical damage (Fig. 2): the stems and structural roots of infected trees fail under smaller external loads relative to uninfected trees (Quine and Gardiner 2007). However, the incidence of preexisting decay in trees killed by different physical processes is poorly described. Tree mortality due to physical damage alters the local resource environment (e.g., through the formation of canopy gaps), leading necessarily to altered competitive interactions and residual tree performance (Van Pelt and Franklin 1999). Consequently, understanding the contribution of physical processes to the tree mortality regime is a necessary prerequisite to evaluating theoretical predictions for competitive tree mortality and forest dynamics (e.g., Enquist et al. 2009).

Aspects of the tree mortality regime in temperate old-growth coniferous forests of northwestern North America, including rates and causes of tree mortality, are reported in this paper. A 30-year record of tree mortality in a series of 12 permanent forest research plots provides the empirical basis for this analysis, which has three objectives: (*i*) improving the empirical knowledge base regarding natural forest dynamics by quantifying overall rates of tree mortality in natural forest stands, including variation among species and tree size classes; (*ii*) assessing the relative importance in the tree mortality regime of different modes of physical damage and in contrast to the combined effects of biological agents and competition; and (*iii*) assessing the incidence of decay fungi in trees dying from different physical mortality agents. Portions of the tree demography data set analyzed here have been used in earlier analyses of forest structure and dynamics (Franklin et al. 1988; Spies et al. 1990; van Mantgem et al. 2009); the analysis presented here extends the period of

Fig. 2. An example of an uprooted *Pseudotsuga menziesii* with preexisting structural root rot, which predisposed this tree to mechanical failure. Note the characteristic root ball: structural roots failed at ground level and remain buried in the soil matrix.

study to 30 years and is the first comprehensive analysis of the mortality cause portion of the data set.

Study forests

Study sites are in old-growth conifer forests on the western slope of the Cascade Range within Mount Rainier National Park, Washington, USA. This park incorporates a variety of forest associations (Table 1), which reflect a range of environmental conditions (Franklin et al. 1988). The two forest zones present — the *Tsuga heterophylla* and *Abies amabilis* zones — are characteristic of the western Cascade Range and represent a sequence from low to high elevations (Franklin and Dyrness 1988; Acker et al. 2006). Descriptions of plant community composition and environmental characteristics typical of the plant associations are provided by Franklin et al. (1988).

The study forests are dominated by seven tree species (Table 2). *Tsuga heterophylla* (Raf.) Sarg. is the shade-tolerant, late-successional dominant on warmer low-elevation sites. *Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes is another shade-tolerant species that becomes increasingly dominant with increasing elevation and annual snowfall (Franklin and Dyrness 1988). Other common tree species are *Thuja plicata* Donn ex D. Don, *Pseudotsuga menziesii* (Mirbel) Franco, *Taxus brevifolia* Nutt., *Chamaecyparis nootkatensis* (D. Don) Spach, and *Tsuga mertensiana* (Bong.) Carr. *Pseudotsuga* is distinctive among this group in being a shade-intolerant pioneer species; the other six species are all moderately to very shade tolerant and able to regenerate in the absence of fire or other severe disturbances. *Thuja plicata*, *P. menziesii*, and *T. brevifolia* are characteristic of the *Tsuga heterophylla* Zone, but also occur in lower-elevation *Abies amabilis* Zone forests (Franklin and Dyrness 1988; Franklin et al. 1988). *Chamaecyparis nootkatensis* and *T. mertensiana* are associated with the coolest and wettest *Abies amabilis* Zone forests,

Table 1. Site characteristics and sample intervals.

				January		July		
Site	Elevation (m)	Age class (years)	Plant association	$T_{\min}$ (°C)	$T_{\max}$ (°C)	$T_{\min}$ (°C)	$T_{\max}$ (°C)	Annual precipitation (mm)
TO11	604	550	TSHE/OPHO	–2.4	4.0	8.2	21.7	1867
TO04	668	750	TSHE/OPHO	–2.6	3.9	8.2	23.4	1928
TA01	671	300	TSHE/ACTR	–2.8	3.8	8.2	26.2	1919
AV02	841	1000	ABAM/VAAL	–4.1	2.2	7.5	24.1	1688
AO03	866	1000	ABAM/OPHO	–5.4	1.2	7.2	22.8	1710
AG05	951	650	ABAM/GASH	–4.3	2.0	7.4	22.3	2239
AB08	1055	750	ABAM/BENE	–5.9	0.6	7.0	21.8	1429
AV06	1061	750	ABAM/VAAL	–4.9	1.4	7.1	21.5	2518
AV14	1067	1200	ABAM/VAAL	–5.3	2.5	8.2	19.8	2119
AM16	1183	600	ABAM/MEFE	–6.0	0.9	7.7	20.3	2776
AR07	1451	330	ABAM/RHAL	–5.8	0.8	6.6	18.9	2874
AE10	1451	300	ABAM/ERMO	–5.8	0.8	6.6	18.8	2961

Note: Plant associations are *Tsuga heterophylla – Oplopanax horridum* (TSHE/OPHO), *Tsuga heterophylla – Achlys triphylla* (TSHE/ACTR), *Abies am-*
– Gaultheria shallon (ABAM/GASH), *Abies amabilis – Menziesia ferruginea* (ABAM/MEFE), *Abies amabilis – Oplopanax horridum* (ABAM/OPHO),
VAAL). Detailed descriptions of the plant associations are provided in Franklin et al. (1988). Climate data are derived from PRISM (Daly et al. 2002,

as well as other subalpine forest types (Franklin and Dyrness 1988; Franklin et al. 1988). *Taxus brevifolia* is a small tree that generally does not exceed 10 m in height; the other remaining species are capable of growing into the upper canopy.

The dominant stand-replacing disturbance agent in the forests of Mount Rainier National Park is infrequent high-severity fire (Hemstrom and Franklin 1982; Franklin et al. 1988). Avalanches are also common in steep mountainous topography occupied by montane and subalpine forests (Hemstrom and Franklin 1982). Mature and old forests in this region also experience chronic, low- to moderate-severity wind disturbances and occasional bark beetle outbreaks and host various fungal pathogens (Franklin and DeBell 1988; Edmonds et al. 1993). More than 300 years have passed since the most recent high-severity disturbance (wildfire) at all of the study sites.

Study sites span a range of climatic conditions (Table 1). Summers are relatively warm and dry, whereas winters are cool and wet. Mean monthly minimum and maximum temperatures decrease with elevation, whereas mean monthly precipitation increases with elevation. The *Abies amabilis* Zone is characterized by a persistent winter snowpack, the depth and duration of which generally increase with elevation. The proportion of total precipitation falling as snow is smaller and winter snowpacks are less persistent in the lower-elevation *Tsuga heterophylla* Zone (Franklin and Dyrness 1988).

Local physiography and geology are dominated by Mount Rainier, an active volcano (Pringle 2008). Soil parent materials in the vicinity of Mount Rainier are of Holocene age and reflect the recent eruptive history; the most common soil parent materials are depositions of tephra (Franklin et al. 1988), including materials from eruptions of Mount St. Helens, as well as Mount Rainier. Additional detailed information about the physical and biological characteristics of the study sites is available in Acker et al. (2006) and online (http://andrewsforest.oregonstate.edu/pubs/webdocs/reports/permplot.cfm?topnav=55).

Methods

Field procedures

In 1977 and 1978, twelve 1 ha permanent plots were established in old-growth forests in Mount Rainier National Park spanning elevations from 604 to 1451 m above sea level (asl) (Table 1). Plots were haphazardly located within stands representing characteristic forest communities identified during the Mount Rainier National Park forest vegetation classification project (Franklin et al. 1988). Plots were established to study the long-term dynamics of old-growth conifer forests, including rates and causes of tree mortality. In each plot, all trees ≥15 cm dbh (diameter at breast height, 1.4 m above ground level) were measured for diameter to the nearest 0.1 cm, identified to species, and individually tagged. In three plots (TA01, AV02, AO03), all trees ≥5 cm dbh were also measured and tagged. In the remaining plots, trees ≥5 cm dbh and <15 cm dbh were subsampled in a 0.25 ha area (0.188 ha at site AR07). These two size classes are hereafter referred to as <15 cm dbh and ≥15 cm dbh, respectively.

Plots were censused every 4 to 10 years (mean = 5.7 years), with the most recent census in 2007 or 2008. Field workers were supplied with information about tree attributes (species, size, and approximate location) to facilitate relocation and measurement during repeat censuses. At each census, new trees that exceeded the minimum diameter at breast height threshold (in-growth) were measured, tagged, and identified to species.

Data reduction and analysis

Fates of individual tagged trees were tracked. Detailed information about tree position, condition, and cause of mortality was recorded for newly dead trees during each census. Field observations were used to categorize mortality into one of three classes of proximate cause: biological agents and competition (i.e., intact, standing dead trees), direct mechanical causes (uprooting and stem breakage), and crushing by falling trees or tree parts. Direct mechanical mortality can be differentiated from crushing with a high de-

Density (no. of trees·ha^{-1})		Basal area (m^2·ha^{-1})		
Initial	Final	Initial	Final	Census years
249	224	89.4	91.1	1978, 1984, 1990, 1995, 2000, 2008
424	474	68.1	72.7	1978, 1983, 1988, 1993, 1998, 2008
399	375	105.9	111.3	1977, 1982, 1987, 1991, 1995, 2001, 2007
1032	1086	76.5	80.9	1977, 1982, 1987, 1991, 1996, 2001, 2008
381	252	97.6	100.9	1977, 1982, 1987, 1991, 1996, 2001, 2008
870	1097	82.6	88.5	1978, 1983, 1988, 1993, 1998, 2008
422	486	75.1	76.2	1978, 1984, 1990, 1995, 2002, 2008
1191	1274	51.3	55.6	1978, 1983, 1988, 1993, 1998, 2007
491	417	73.3	64.4	1978, 1984, 1990, 1995, 2000, 2008
841	1086	63.8	66.2	1978, 1983, 1989, 1994, 1999, 2007
487	473	78.5	79.0	1978, 1983, 1988, 1993, 1998, 2007
781	704	93.8	98.7	1978, 1983, 1988, 1993, 1998, 2007

abilis – Berberis nervosa (ABAM/BENE), *Abies amabilis – Erthonium montanum* (ABAM/ERMO), *Abies amabilis*
Abies amabilis – Rhododendron albiflorum (ABAM/RHAL), and *Abies amabilis – Vaccinium alaskanse* (ABAM/
2008).

Table 2. Tree species, family, total number of sites, and number of stems in which individual species occurred during the study period.

Species	Family	No. of sites	No. of stems	No. of mortalities
Abies amabilis (Dougl. ex Loud.) Dougl. ex J. Forbes	Pinaceae	11	3453	657
Tsuga heterophylla (Raf.) Sarg.	Pinaceae	10	2065	333
Chamaecyparis nootkatensis (D. Don) Spach	Cupressaceae	6	625	58
Thuja plicata Donn ex D. Don	Cupressaceae	8	226	13
Tsuga mertensiana (Bong.) Carr	Pinaceae	3	214	14
Pseudotsuga menziesii (Mirbel) Franco	Pinaceae	8	210	25
Taxus brevifolia Nutt.	Taxaceae	5	84	15
Abies grandis (Dougl. ex D. Don) Lindl.	Pinaceae	1	9	4
Abies lasiocarpa (Hook.) Nutt.	Pinaceae	1	5	4
Abies procera Rehd.	Pinaceae	3	4	3
Alnus rubra Bong.	Betulaceae	2	2	2
Pinus monticola Dougl. ex D. Don	Pinaceae	1	2	2
Picea sitchensis (Bong.) Carr.	Pinaceae	1	1	0
Totals	4	12	6900	1130

gree of certainty (van der Meer and Bongers 1996; Gale and Barford 1999). Trees were only classified as crushed when the debris — fallen green and dead trees, or parts thereof — causing the damage was observed in situ. Most crushed trees of the sizes studied here (≥5 cm dbh) have partially or completely snapped stems (Fig. 1). Other damage due to crushing includes bole injuries, pinning (where the stem deflects to the ground but does not snap), and partial uprooting. The definition of crushing used in this study is conservative: trees uprooted in groups (i.e., "domino effect" sensu van der Meer and Bongers 1996) were categorized as direct mechanical mortality. Presence of preexisting decay fungi and rotted wood at the location of structural failure was recorded for trees dying proximately due to physical causes, including structural root rot in uprooted trees (Edman et al. 2007). Individual fungal species were not consistently recorded by the field crews, thus only presence or absence of fungi and rotted wood is reported here.

Annual rates of stem mortality for all trees and by species and size class were calculated for each site by census combination in which at least 15 trees were present at the first census of the interval (cf. Condit et al. 1995). The annual mortality rate, m, was calculated as

$$[1] \qquad m = 1 - [1 - (M_1/N_0)]^{1/t}$$

where N_0 is the number of trees alive at the previous census, M_1 is the number of trees dying between the previous and current census, and t is the time between censuses in years (Lutz and Halpern 2006). A similar equation was used to calculate mortality on a basal-area basis. Basal-area mortality provides an estimate of the amount of resources made available by mortality events (Harcombe et al. 2002).

Incidence (presence or absence) of preexisting decay fungi in trees killed by mechanical causes was modeled using generalized linear mixed models with a binomial error distribution and a logit link (Crawley 2007). Study site was treated as a normal random effect and modeled as random intercepts. Analyses were carried out in the statistical program R and made use of functions in the lme4 library (R Development Core Team 2008).

Table 3. Average annual mortality rates for all species pooled.

	Basal area		Stems	
Site	<15 cm dbh	≥15 cm dbh	<15 cm dbh	≥15 cm dbh
TO11	0.019 (0.007–0.038)	0.004 (0.001–0.010)	0.024 (0.012–0.044)	0.008 (0.005–0.013)
TO04	0.010 (0.002–0.220)	0.006 (0.002–0.008)	0.012 (0.002–0.028)	0.007 (0.005–0.011)
TA01	0.003 (0.001–0.006)	0.002 (0.001–0.003)	0.004 (0.003–0.005)	0.003 (0.001–0.004)
AV02	0.005 (0.002–0.013)	0.005 (0.001–0.008)	0.006 (0.003–0.015)	0.003 (0.002–0.008)
AO03	0.007 (0.002–0.014)	0.005 (0.001–0.011)	0.008 (0.003–0.014)	0.005 (0.003–0.007)
AG05	0.005 (0.001–0.010)	0.003 (<0.001–0.006)	0.005 (0.001–0.011)	0.004 (<0.001–0.007)
AB08	0.004 (0–0.013)	0.004 (0.002–0.009)	0.003 (0–0.009)	0.004 (0.002–0.007)
AV06	0.007 (0.002–0.024)	0.006 (0.001–0.018)	0.005 (0.002–0.018)	0.005 (0.002–0.010)
AV14	0.011 (0–0.024)	0.008 (0.004–0.017)	0.011 (0–0.023)	0.006 (0.004–0.013)
AM16	0.001 (0–0.005)	0.003 (0.001–0.006)	0.001 (0–0.004)	0.003 (0.001–0.004)
AR07	0.006 (0–0.014)	0.003 (0.002–0.003)	0.008 (0–0.017)	0.003 (0.002–0.004)
AE10	0.014 (0.010–0.025)	0.002 (0.001–0.004)	0.011 (0.006–0.017)	0.003 (0.001–0.005)

Note: Minimum diameter at breast height (dbh) sampled was 5 cm. Basal area was measured in square metres. Rates are averages across all census intervals with ranges (minimum–maximum) in parentheses.

Results

Species composition, tree abundance, and stand structure

The fates of 6900 individual live trees were followed during the study, which collectively represented 13 species and four families (Table 2). Seven species accounted for 99.7% of the stems recorded (Table 2); *A. amabilis* and *T. heterophylla* were the two most common species. During the 30-year study period, 1130 trees died, with the seven most common tree species comprising 98.7% of mortality events (Table 2). Only two stems of a single hardwood species (*Alnus rubra*) were encountered; both individuals died during the study.

Changes in total stem density over the three-decade study period varied among plots: half experienced a net decline in stem density, whereas the other half experienced an increase in stem density during the study (Table 1). In contrast, basal area increased in 11 of the 12 plots (Table 1). In plot AV14, basal area declined 11.3%, primarily due to the death of four large stems (>100 cm dbh) during the penultimate census interval.

Forest-wide mortality rates

Average annualized mortality of all tagged stems (all species pooled) expressed as percentage loss of basal area did not exceed $0.8\%\cdot\text{year}^{-1}$ for trees ≥15 cm in any plot. Average annualized basal-area mortality was slightly higher for the small diameter class (trees <15 cm dbh) and was greatest ($1.9\%\cdot\text{year}^{-1}$) in the low-elevation plot, TO11.

Average annualized mortality expressed as percentage of all tagged stems (all species pooled) did not exceed $0.8\%\cdot\text{year}^{-1}$ for trees ≥15 cm dbh and was as low as $0.3\%\cdot\text{year}^{-1}$ at some sites (Table 3). For the trees ≥15 cm, average annual mortality rate never exceeded $1.3\%\cdot\text{year}^{-1}$ in any interval and was as low as $0.02\%\cdot\text{year}^{-1}$ for one census interval in plot AG05. Smaller stems (<15 cm dbh) died at a higher average rate than did larger trees (Table 3). Small diameter tree mortality rates were highest on plots TO11 and TO04, where maximum annualized rates for an individual census interval were 4.4% and 2.8%, respectively.

Species-specific mortality rates

Among individual species, sample sizes were large enough to calculate demographic rates for *A. amabilis* and *T. heterophylla* in the <15 cm size class at multiple sites (Fig. 3). The average mortality rate of small *A. amabilis* was generally <1.0% at individual sites. Average annual mortality rates of small *T. heterophylla* ranged from about 0.5% to 1.0%, except at the two low-elevation plots (TO04 and TO11) where average annual mortality rates were 1.5% and 2.4%, respectively.

Individual species' mean annual mortality rates for stems ≥15 cm dbh were always <1.0% (Fig. 4). During a few census intervals, annualized stem mortality rates for *T. heterophylla* and *A. amabilis* exceeded 1.0%. Mortality rates of *T. plicata* and *C. nootkatensis* were exceptionally low, with average annual rates of <0.1% to 0.2% and 0.2%, respectively. Average annual mortality of *P. menziesii* was as high as 0.9% in plot AB08 and as low as 0.0% in plot AG05. Annual mortality of *T. heterophylla* ≥15 cm dbh was highest on the two low-elevation plots (TO11 and TO04), similar to the pattern observed for stems <15 cm dbh. Average annualized *T. mertensiana* mortality was 0.5% at plot AM16 and <0.1% at plot AR07.

Taxus brevifolia was present in sufficient numbers to allow calculation of mortality rates only at plot AG05, where mean annual mortality of *Taxus* stems was 0.3% for both <15 cm dbh and ≥15 cm dbh size classes.

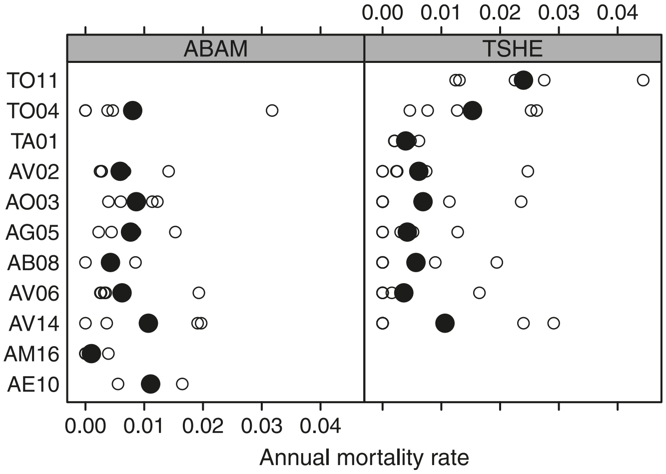
Size-specific mortality rates

The relationship between mortality rate and tree size was highly variable across the individual study sites (Fig. 5). The most consistent trend was decreasing mortality rates over the size range of 5 to 30 cm dbh (10 of 12 sites). In some cases, there were too few trees in a particular size class to calculate mortality rates, especially for large diameter trees (e.g., AV06, TO11, and TO04); consequently, the form of the mortality rate – tree size relationships in Fig. 5 should be interpreted cautiously.

Proximate causes of mortality

Physical processes (uprooting, stem breakage, and crushing by falling trees or litter) were important causes of tree mortality (Table 4). Physical processes accounted for 39.7% of tree mortalities in the <15 cm dbh size class (range for

Fig. 3. Variation in annual stem mortality rates for *Abies amabilis* (ABAM) and *Tsuga heterophylla* (TSHE) stems <15 cm dbh in old-growth forests of Mount Rainier National Park, Washington, USA. Each panel corresponds to a different tree species. Each row represents an individual study site, with site names listed along the left side of the figure; see Table 1 for study site characteristics. Site AR07 did not have enough dying stems of this size class during any census interval to calculate an annual rate (see Methods) and thus does not appear in the figure. Open symbols are annual stem mortality rates calculated for individual census intervals. Solid symbols are the arithmetic mean of the annual rates for individual census intervals.



individual sites: 11.8% to 75.0%). Physical processes were slightly more important as causes of mortality in the larger (≥15 cm dbh) size class, with 44.4% of mortality events caused by some form of physical damage (range for individual sites: 22.2% to 59.0%).

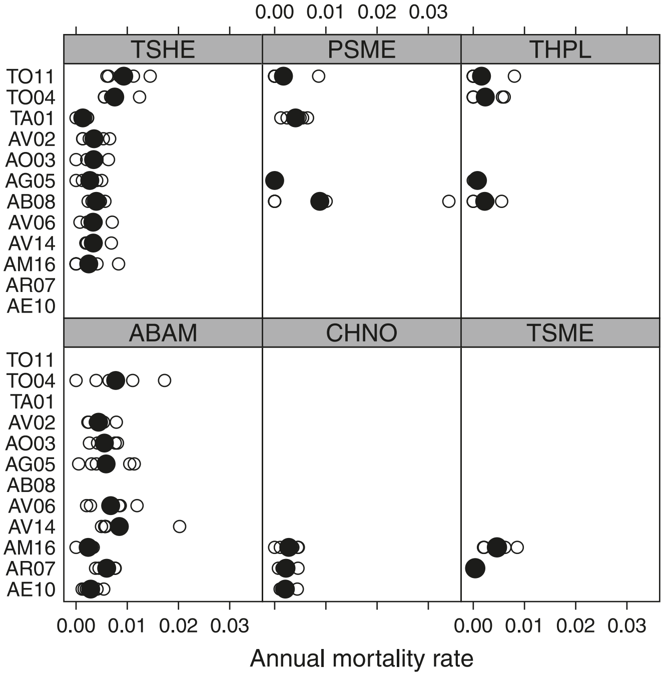
Crushing by falling green and standing dead trees contributed substantially to the tree mortality regime (Table 4). Crushing was most important in the smaller size class: 25.3% (range 5.9% to 60.0%) of all mortality events were due to crushing by falling trees or tree parts (e.g., limbs, branches, bole segments). A smaller proportion of large tree mortality was caused by crushing: averaged across study sites, 7.9% (range 0% to 17.1%) of all mortality events in the ≥15 cm class were attributed to crushing. Falling green trees caused more mortality than falling dead trees; the magnitude of the difference was larger in the ≥15 cm dbh class (Table 4).

Stem breakage and uprooting were relatively uncommon in the smaller size class (Table 4), collectively accounting for only 15% of the cumulative mortalities of 5–15 cm dbh trees. These same mortality agents were more important for larger trees (Table 4), indicating that trees become increasingly susceptible to direct mechanical damage with increasing size.

Tsuga heterophylla and *A. amabilis* exhibited striking differences with respect to the relative importance of uprooting. Fully 23.4% of *T. heterophylla* in the <15 cm dbh size class were uprooted (Table 5).

Family-level differences were apparent in the relative importance of different mortality causes (Table 5). *Thuja plicata* and *C. nootkatensis* were much more likely be killed by stem breakage than species belonging to Pineaceae. This difference was complemented by a relatively lower proportion of standing deaths for *Thuja* and *Chamaecyparis* relative to Pineaceae.

Fig. 4. Variation in annual stem mortality rates for stems ≥15 cm dbh. Each panel corresponds to a different tree species. Each row represents an individual study site, with site names listed along the left side of the figure; see Table 1 for study site characteristics. Open symbols are annual mortality rates for individual census intervals. Solid symbols are the arithmetic mean of the annual rates for individual census intervals. Abbreviations: TSHE, *Tsuga heterophylla*; PSME, *Pseudotsuga menziesii*; THPL, *Thuja plicata*; ABAM, *Abies amabilis*; CHNO, *Chamaecyparis nootkatensis*; TSME, *Tsuga mertensiana*.



Association of decay fungi with mechanical and crushing mortalities

Evidence of decay fungi at the location of structural failure in trees dying from physical processes was more common in the larger trees: depending on the study plot, wood at the location of structural failure was rotten in as many as 80% of trees dying from mechanical causes. In contrast, in half of the plots, no evidence of decay fungi was observed in the smaller trees killed by physical processes.

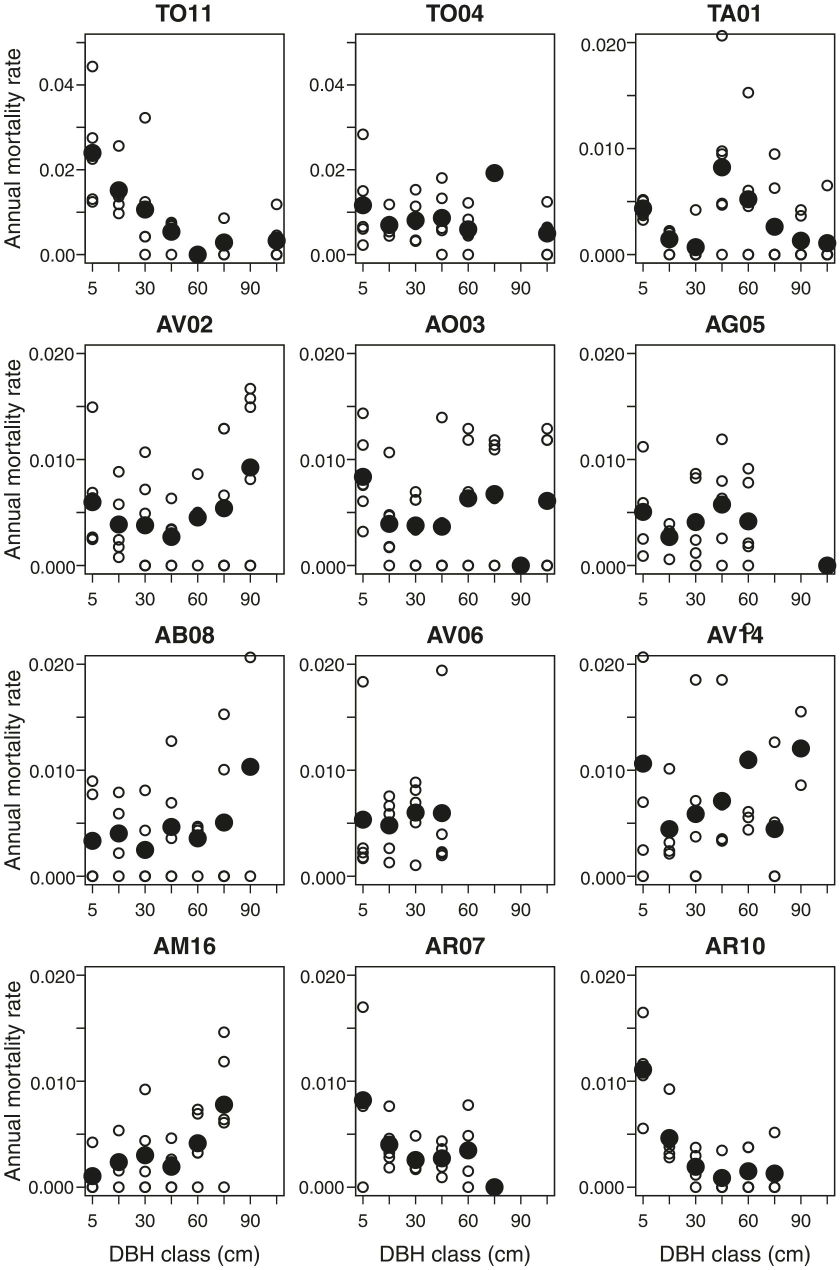
The incidence of preexisting decay fungi differed strongly between trees killed by direct mechanical damage and crushing (Fig. 6). Parameter estimates for generalized linear mixed models confirm that trees crushed by falling green or dead trees were less likely to be infected with decay fungi at the location of structural failure than trees killed by stem breakage or uprooting (Table 6).

Discussion

Forest-wide, species- and size-specific mortality rates

Overall mortality rates in these old-growth forests were exceptionally low on the basis of both stem density and basal area. Mortality rates are consistently higher in tropical

Fig. 5. Variation of stem mortality rate across the tree size spectrum for all species pooled. Each panel corresponds to an individual study site (see Table 1 for study site characteristics). Open symbols are annual mortality rates for individual census intervals. Solid symbols are the arithmetic mean of the annual rates for individual census intervals. DBH, diameter at breast height.



(e.g., Condit et al. 1995) and temperate hardwood (Runkle 2000; Harcombe et al. 2002) forests compared with those observed here. Stem mortality rates (for trees ≥15 cm dbh) are within the range — but clustered at the low end — of turnover rates (average of recruitment and mortality) reported in a review of studies in 27 conifer forests (Stephenson and van Mantgem 2005). Mortality rates in the present study were similar to, but generally slightly lower than, those reported for other old-growth conifer forests (van Mantgem et al. 2009) in western North American and old-growth mixed hemlock (*T. canadensis*) – hardwood forests in eastern North America (Lorimer et al. 2001; Busing 2005).

Based on the few other studies available for comparison, stem mortality rates in old-growth conifer forests of the Pacific Northwest appear to be consistently low, generally below 1.0%·year^{-1}. Franklin and DeBell (1988) documented an annual mortality rate of 0.75%·year^{-1} in a 500-year-old *Pseudotsuga–Tsuga* forest in the southwestern Washington Cascades. Edmonds et al. (1993) observed annual mortality rates of 0.8%–0.9%·year^{-1} in old-growth forests in the western Olympic Mountains of Washington State. Reconstructed mortality stem rates (0.3%–0.5%·year^{-1}) in temperate coniferous rain forests of Southeast Alaska (Hennon and McClellan 2003) are within the range of mortality rates observed in this study. Here, the three sites with the lowest annual mor-

Table 4. Total number of trees dying and proportion of tree mortality attributable to different causes during the three-decade study period.

Site (no. of mortalities)	Crushed by falling green tree (%)	Crushed by falling dead tree (%)	Uprooting (%)	Stem breakage (%)	Biotic and stress (%)
Trees <15 cm dbh					
TO11 (*n* = 19)	5.3	10.5	42.1	5.3	36.8
TO04 (*n* = 30)	16.7	—	16.7	3.3	63.3
TA01 (*n* = 15)	6.7	13.3	6.7	—	73.3
AV02 (*n* = 181)	14.4	13.3	8.3	4.4	59.7
AO03 (*n* = 44)	15.9	15.9	4.5	—	63.6
AG05 (*n* = 31)	6.5	16.1	6.5	6.5	64.5
AB08 (*n* = 4)	25.0	25.0	—	25.0	25.0
AV06 (*n* = 48)	20.8	6.3	16.7	4.2	52.1
AV14 (*n* = 21)	4.8	4.8	9.5	4.8	66.7
AM16 (*n* = 6)	—	16.7	—	16.7	66.7
AR07 (*n* = 5)	—	60.0	—	—	40.0
AE10 (*n* = 17)	5.9	—	—	5.9	88.2
All sites (*n* = 421)	13.1	11.6	10.2	4.8	60.3
Trees ≥15 cm dbh					
TO11 (*n* = 46)	—	—	26.1	21.7	52.2
TO04 (*n* = 83)	9.6	1.2	36.1	12.0	41.0
TA01 (*n* = 27)	3.7	—	—	18.5	77.8
AV02 (*n* = 64)	7.8	3.1	9.4	23.4	56.3
AO03 (*n* = 49)	10.2	4.1	6.1	22.4	57.1
AG05 (*n* = 74)	2.7	1.4	28.4	17.6	50.0
AB08 (*n* = 35)	8.6	—	8.6	25.7	57.1
AV06 (*n* = 109)	2.8	4.6	20.2	9.2	63.3
AV14 (*n* = 61)	8.2	1.6	34.4	11.5	44.3
AM16 (*n* = 41)	9.8	7.3	7.3	19.5	56.1
AR07 (*n* = 52)	1.9	1.9	9.6	25.0	61.5
AE10 (*n* = 68)	2.9	1.5	10.3	22.1	63.2
All sites (*n* = 709)	5.5	2.4	18.8	17.8	55.6

Note: See Table 1 for study site characteristics.

Table 5. Cumulative number of trees dying and proportion of mortality attributable to different causes for the most abundant species studied.

Species (no. of mortalities)	Crushed by falling green tree (%)	Crushed by falling dead tree (%)	Uprooting (%)	Stem breakage (%)	Biotic and stress (%)
Trees <15 cm dbh					
Abies amabilis (*n* = 304)	13.5	12.2	5.9	4.3	64.1
Tsuga heterophylla (*n* = 107)	11.2	8.4	23.4	5.6	51.4
Trees ≥15 cm dbh					
Abies amabilis (*n* = 353)	4.8	2.3	17.8	15.6	59.5
Chamaecyparis nootkatensis (*n* = 58)	5.2	1.7	15.5	31.0	46.6
Thuja plicata (*n* = 13)	7.7	—	23.1	38.5	30.8
Tsuga heterophylla (*n* = 226)	6.2	3.1	24.8	15.9	50.0
Tsuga mertensiana (*n* = 13)	7.7	—	—	23.1	69.2
Pseudotsuga menziesii (*n* = 25)	4.0	—	—	28.0	68.0

tality rates (0.25%–0.29%) had rates similar to that observed for a 1100-year-old *Sequoia sempervirens* (Lamb. ex D. Don) Endl. forest (0.29%) in northern California (Busing and Fujimori 2002).

At Mount Rainier, the cool higher-elevation sites tended to have lower annual mortality rates (Table 3) than lower-elevation plots. This is consistent with the trend observed by Edmonds et al. (1993) in the Olympic Mountains and the reconstructed dynamics of montane *Abies–Tsuga–Chamaecyparis* forests in coastal British Columbia, Canada (Parish and Antos 2006).

Mortality rates were consistently low across species. The two members of Cupressaceae, *T. plicata* and *C. nootkatensis*, were particularly notable, with average annual mortality rates ≤0.2% for trees in the ≥15 cm dbh class, lower even than the 0.29%·year^{-1} reported for *S. sempervirens* ≥10 cm dbh (Busing and Fujimori 2002). These results, together

Fig. 6. The proportion of trees dying (all sites pooled) due to different mechanical agents with preexisting decay fungi (see also Table 6).

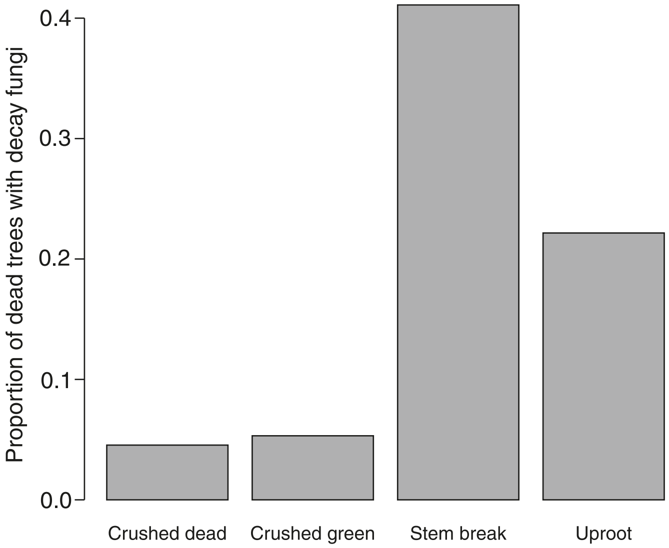


Table 6. Estimated generalized linear mixed model fixed effect coefficients for the incidence of preexisting decay fungi in trees dying due physical damage.

Fixed effect	β	SE	P value
Intercept	–3.11	0.65	<0.001
Crushed by falling green tree	0.11	0.77	0.880
Stem breakage	2.81	0.63	<0.001
Uprooting	1.90	0.64	0.003

Note: Crushed by falling dead tree is used as the reference cause for mortality cause effects.

with the limited other data for *Thuja* and *Chamaecyparis*, indicate that very low mortality rates may be characteristic of these species. Franklin and DeBell (1988) reported mortality of 0.52%·year^{-1} for *Thuja* during a 36-year period in the southwestern Washington Cascades; no *Thuja* died and *Chamaecyparis* died at a rate of 0.68%·year^{-1} in the western Olympics (Edmonds et al. 1993). The distinctively low mortality rates of *Thuja* and *Chamaecyparis*, complimented by their capacity for vegetative regeneration (Parish and Antos 2006), likely facilitate long-term coexistence with their more fecund associates, *T. heterophylla* and *A. amabilis*.

Field notes and observations from the most recent census indicate that the difference in the relative importance of uprooting for *T. heterophylla* and *A. amabilis* in the <15 cm dbh size class is likely due to the tendency for *T. heterophylla* regeneration to be concentrated on rotten woody substrates (Christy and Mack 1984), especially at the low-elevation sites TO11 and TO04 (Table 4). *Tsuga heterophylla* in the <15 cm dbh class appear to experience high rates of uprooting on this substrate.

Goff and West (1975) introduced an important hypothesis about tree mortality in old-growth forests. They reasoned that overstory trees enjoy dominant positions with access to abundant resources and consequently lower mortality rates, whereas understory trees exist in a marginal environment and consequently experience elevated mortality rates due to competitive stress. Goff and West (1975) further posited that the largest (and presumably oldest) trees experience elevated mortality rates due to senescence and increased exposure to disturbance (e.g., wind) and pathogens. This logic culminated in the prediction that in old-growth forests, a U-shaped curve would describe the relationship of tree mortality rate to tree diameter at breast height. Since then, several investigators have searched for the U-shaped mortality curve, with varying degrees of support (e.g., Runkle 2000; Lorimer et al. 2001; Coomes et al. 2003).

Our data do not support Goff and West's (1975) prediction. However, a clear trend of decreasing mortality rate with size was apparent over the small end of the size spectrum. This result does support the notion that the understory is a "high risk" location, where small trees experience elevated mortality rates (Harcombe and Marks 1983; Clark and Clark 1991). Furthermore, our data for mortality cause reveal that the rationale for elevated mortality rates in the small size classes — competitive interactions with larger trees (Goff and West 1975; Coomes et al. 2003) — is incomplete: in fact, crushing by falling trees and litter is a significant mortality agent in the smaller size classes.

Physical processes and interactions with decay fungi

Physical processes were important sources of tree mortality in this study, similar to findings from other studies in tropical (van der Meer and Bongers 1996; Gale and Barford 1999) and temperate (Hennon and McClellan 2003) forests. Averaged across the study sites, approximately 40% of the mortality events occurring during the 30-year study were attributable, proximately, to physical agents. Uprooting and stem breakage were ubiquitous, as was crushing by both green and dead trees (Table 4). Notably, mechanical mortality was not associated with a few intermediate or catastrophic wind disturbances. Here, annualized mortality rates (all causes pooled) did not exceed 1.3%·year^{-1} in any census interval-by-plot combination for the large trees, indicating that mechanical processes were a chronic "background" source of mortality. This contrasts with some forests of eastern North America that are subject to hurricanes (e.g., Harcombe et al. 2002) and strong convective storms (e.g., Matlack et al. 1993). It also contrasts with patterns of mortality in coastal *Picea–Tsuga* forests in the Pacific Northwest. These coastal forests are characterized by a mixed-severity wind disturbance regime, including chronic wind-related mortality (~3% stems·year^{-1}; Greene et al. 1992), localized blowdown patches (Taylor 1990), and widespread high-severity blowdown events (Henderson et al. 1989).

Mechanical interactions between trees — crushing by falling trees and tree parts — were an important cause of mortality. Damage and mortality due to falling trees and litter has seen remarkably little scientific study; most studies of this topic have been limited to damage and burial of seedlings by litterfall (Clark and Clark 1991). Although crushing preferentially affects small trees (Table 4), it is in no way limited to seedlings in the forests studied here; stems >20 cm dbh are susceptible (Fig. 2) and crushing mortality of trees >70 cm dbh was observed. Crushing was a minor source of canopy gap formation in a New England old-growth *Picea–Abies* forest (Worrall et al. 2005). Crushing has been recognized as an important cause of mortality, accounting for about 5%–75% of mortality events in the few tree demography studies in mature and old-growth forests that have resolved mode of mortality to this level of detail (e.g., Harcombe and Marks 1983; Lieberman et al. 1985; van der Meer and Bongers 1996). The lower end of this range is probably conservative because those studies considered only strict crushing and not the domino effect or "pushed" trees (Lieberman et al. 1985). The fraction of mortality due to crushing observed here is similar to values previously reported for other old-growth conifer forests in the Pacific Northwest (Franklin and DeBell 1988; Edmonds et al. 1993).

The degree to which decay fungi increased the risk of stem failure or uprooting by either direct mechanical processes or crushing could not be quantified in the present study. However, the difference in infection rates in trees killed by crushing and direct mechanical processes provides some insight: infection with decay fungi should have little influence on the likelihood of a tree being crushed. Trees killed by crushing were much less likely to be infected with decay fungi than trees killed by direct mechanical processes (Table 6; Fig. 6), consistent with a predisposing role of decay fungi in direct mechanical tree mortality (Fig. 2) but little or no direct effect on the likelihood of crushing mortality.

The contribution of decay fungi to mechanical tree mortalities and the tree mortality regime in general is probably underestimated in many forests: few studies have recorded the presence or absence of decay fungi or rotted wood in trees dying proximately due to mechanical failure. Here, 41% of snapped stems and 22% of uprooted stems had evidence of preexisting decay fungi. Edman et al. (2007) reported that up to 70% of recently fallen trees in an old-growth *Picea abies* forest were colonized by heart-rot fungi. In the forest studied by Edman et al. (2007), approximately 40% of logs originating from stem snap were infected with decay fungi, whereas 22% and 15% of logs originating from butt breakage and uprooting contained heart-rot fungi, respectively; these proportions are remarkably similar to those observed in the old-growth conifer forests studied here (Fig. 6). In a New England old-growth *Picea–Abies* forest, physical agents were responsible, proximately, for approximately 29% of tree mortality events (n = 312) leading to canopy gap formation or expansion (Worrall et al. 2005). Of this total, stem, butt, and root rots collectively were present in 50% (n = 157) of the canopy trees killed by physical processes (Worrall et al. 2005). Matlack et al. (1993) found that the vulnerability of *Quercus* stems to wind damage was strongly linked to preexisting decay in a New Jersey pine–oak forest: 56% of wind-damaged and 0% of standing (undamaged) *Quercus prinus* stems and 70% of wind-damaged and 12.5% of standing *Quercus velutina* stems were rotted. Future studies will likely confirm the importance of decay fungi as drivers of tree mortality and forest dynamics in a wide variety of forests.

Mortality rates and causes in relation to successional status

In contrast to the collective observations of tree mortality in old-growth Pacific Northwest conifer forests presented here and elsewhere (Franklin and DeBell 1988; Edmonds et al. 1993), early successional forests on similar sites experience much higher rates of tree mortality. Young (<80-year-old) *Pseudotsuga–Tsuga* forests in the Cascade Range are characterized by high annual mortality rates: 1.1%–5.3% (Bible 2001; Lutz and Halpern 2006). A similar trend is apparent for *A. amabilis* dominated forests; an average annual mortality rate of 4.6% was observed during a long-term study in what is now an approximately 60-year-old *A. amabilis* stand located in the central Washington Cascade Range (D. Sprugel and A.J. Larson, unpublished data). The dynamics of Pacific Northwest conifer forests — as measured by annualized stem mortality rates — appear to become increasingly stable as succession advances, consistent with the proposal that slow internal dynamics are broadly characteristic of late-successional plant communities.

The importance of mechanical mortality appears to increase through succession. In the young forests studied by Lutz and Halpern (2006), only 18% of tree mortalities were due to mechanical causes, with just a trace amount attributable to crushing. In contrast, mechanical causes of tree mortality were twice as important in the old-growth forests studied here, accounting for approximately 40% of tree mortalities. Perhaps the most dramatic difference is the relative importance of crushing, with only a trace amount apparent in young forests (Lutz and Halpern 2006), whereas in the old-growth forests studied here, fully 25% of mortalities in the 5–15 cm dbh size class were due to crushing. However, the young forests studied by Lutz and Halpern (2006) originated from clearcut harvesting; crushing mortality is likely more important in young forests originating from natural disturbances, especially fire, which have abundant legacies of standing dead trees.

Revising the competition paradigm

Current theory does not accommodate the diversity of mortality processes occurring in natural forests. Quantitative theoretical treatments of forest dynamics emphasize competitive mortality (e.g., Pacala et al. 1996; Strigul et al. 2008), sometimes to the exclusion of all other causes (Enquist et al. 2009). The empirical results of this long-term study highlight the substantial contributions of physical processes to the tree mortality regime in old-growth conifer forests, extending the generality of earlier observations in similar forests (Franklin and DeBell 1988; Edmonds et al. 1993; Hennon and McClellan 2003). Many empirical studies in boreal (e.g., Edman et al. 2007), temperate (e.g., Worrall et al. 2005), and tropical (e.g., Lieberman et al. 1985) forests provide further support for physical processes as important drivers of the tree mortality regime.

Current theory reflects the belief that forest structure and dynamics can be understood as the outcome of the acquisition and utilization of resources essential for the maintenance of physiological processes (Pacala et al. 1996; Strigul et al. 2008; Enquist et al. 2009). This perspective views trees as organisms that interact with the physical environment and each other only as consumers of and competitors for scarce resources. Setting aside, for simplicity, trophic interactions, this view of how trees interact with the physical environment and each other is still incomplete.

Trees are physical entities with structural properties that govern a suite of tree–environment and tree–tree interactions

(King 1986). Trees interact with the vicissitudes of the physical environment through mechanical pathways: trees are constantly subject to dynamic loading due to atmospheric processes such as wind and snow and ice deposition, leading to damage and mortality (Greene et al. 2007; Quine and Gardiner 2007). Trees also interact with each other through mechanical pathways. As physical entities, trees have the potential to originate mechanical work — through the forest canopy debris rain — resulting in tree population regulation through crushing mortality (Harcombe and Marks 1983; Franklin et al. 1987; Clark and Clark 1991). Given these observations, we suggest that a richer mechanistic understanding of the causes and consequences of tree mortality in natural forests, leading to greater predictive ability, will be achieved with models that consider the physical, as well as the physiological, attributes of trees and forests, including traits that confer resistance and resilience to physical damage.

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