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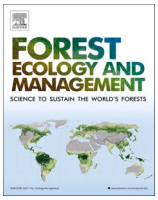

Context matters: Natural tree mortality can lead to neighbor growth release or suppression

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ABSTRACT

Where competition suppresses tree growth, mortality of adjacent trees can release the surviving individuals, leading to a growth increase. However, primary forests are complicated systems, where trees interact in both competitive and facilitative ways mediated by their size, species, and the broad ecological context in which they grow. Thus, the magnitude and even direction of growth responses to the mortality of nearby trees may vary, which has implications for our understanding of community- and ecosystem-level dynamics following mortality events. Unfortunately, although many studies focus on the impacts of light availability and general crowding on tree growth, we know relatively little about the effects of naturally occurring mortality events on the growth of neighboring trees. To address this issue, we used 40 years of data from 15 permanent forest-monitoring plots in Mt Rainier old-growth forests, comparing observed to expected radial growth of individual trees following the death of their nearest neighbor. Although we found evidence of a general growth-release response, this was not universal among all trees, with small trees in particular exhibiting growth suppression (rather than release) following neighboring tree mortality. In addition to small size, growth-suppression was more likely if the dead neighbor was the same species, consistent with facilitative effects as mediated through belowground networks. At the stand level, the average growth release after nearest neighbor mortality was greatest in low-density stands with large trees, with elevation and community composition also playing a role. Decades more monitoring could reveal how long growth release (or suppression) is sustained by individual trees following neighboring mortality events, as well as potential response lags and the role of species identity in determining whether interactions with neighbors are competitive or facilitative. Nonetheless, our results suggest that although mature trees have competitive effects on their larger neighbors, they also have an important role in supporting the ingrowth of small trees. More broadly, we demonstrate that the nature of interactions between individual neighboring trees is highly context dependent.

1. Introduction

Primary coniferous forests with long-lived tree species have dynamically shifting patterns of light availability as trees die and others grow to replace them (Franklin & Van Pelt 2004). Loss of a dominant or co-dominant tree creates a gap in the canopy, increasing light availability and generally allowing suppressed neighbors to rapidly fill this open space (Lutz 1928; Staebler, 1956; Williams 1964). Termed growth release, this process gives shade-tolerant light opportunists the chance to greatly increase their growth rate and potentially become dominant members of the canopy (Frothingham 1915; Lutz 1928; Plice & Hedden 1931; Sinton et al. 2000; York et al. 2004). Shade-tolerant species sometimes also benefit from large gaps, although they are generally more likely to establish in understory positions where they can persist in a suppressed state until an opportunity for growth arises (Franklin and DeBell, 1988; Sinton et al. 2000). The mortality of individual trees is thus important to the dynamics of species turnover and the continuity of carbon stocks as forests age. Growth release, however, may depend on species, their growth stage, the size of the gap created, management history, damage caused to neighbors by crushing or litter-fall, loss of facilitative interactions such as wind-sheltering, biotic mortality agents, and carbon costs incurred due to source-sink dynamics in interconnected root systems (Staebler, 1956; Sinton et al. 2000; Franklin & Van Pelt 2004; York et al. 2004; Renninger et al. 2006).

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The impact of tree mortality events on neighboring tree growth and thus the interaction of mortality with long-term carbon sequestration, may depend on ecological context such as stand age, density, cause of mortality, and individual-scale interactions. For example, as coniferous forests age, pathogens, insect attacks, and wind become increasingly important sources of mortality creating large gaps for seedling establishment. These mortality cycles eventually result in a heterogeneous patchwork of tree species with different ages and shade tolerances that collectively establish massive blocks of vertically continuous foliage, made up of both suppressed and dominant individuals (Franklin et al. 2002; Van Pelt & Nadkarni 2004). This patchwork is capable of harvesting nearly all photosynthetically active light before it reaches the forest floor thereby building vast aboveground carbon stores (Franklin & Van Pelt 2004, Van Pelt & Nadkarni 2004; Van Pelt et al. 2016). Gaps initiated through rot-related mortality can increase in size over time as neighboring trees are infected through grafted root systems (Graham & Bormann 1966; Eis 1972; Slaughter & Parmeter 1995). These gaps may allow more useable light to penetrate than gaps created by beetle-killed trees, which can remain standing for many years (Larson & Franklin 2010) potentially influencing neighbor growth-response due to variation in the amount of released light. Experimental gap creation in primary forests has also initiated growth release. These gaps are larger than those that would likely be formed following the death of an individual tree, but similar to the gaps created by biotic agents (Van Pelt & Franklin 1999). In young, managed forests, removal of a single individual can increase neighbor growth, sometimes as much as the creation of a larger gap (Staebler, 1956). However, the shorter stature of young trees allows more light to penetrate for a given removal-event and competition is more likely to be greater in single-age stands with higher density than would exist in a natural forest hundreds of years post-establishment.

In our study system, the montane forests of Mt. Rainier (traditionally called taqwuma in the Puyallup language) in Washington state (USA), many lines of evidence suggest the strength and even direction of growth responses to nearest neighbor mortality will be context dependent. In these forests, multi-tree gaps have formed driven by the combined effects of drought, *Armillaria* fungal infection, and bark beetle attack (Acker et al. 2006). However, most trees in these forests die without an apparent disruption to the forest structure, that is, no lasting gaps are formed, especially in the understory, where dead trees are over 3X more likely to remain standing (Spies et al. 1990). When the nearest neighbor to a lost tree has been suppressed (*i.e.*, small/subdominate), the surviving tree is not necessarily more prone to growth release than a fellow dominant tree would be, sometimes showing little growth response (Staebler, 1956; He et al. 2022). Mortality itself may be related to neighboring-tree size and condition, particularly in the case of biotic agents (Slaughter & Parmeter 1995; Das et al. 2011; He et al. 2022) suggesting that the individual-scale response to neighbor mortality is not always increased growth.

Competition-driven density-dependent mortality, while present, appears to be a minor factor in older primary forests like these, where trees are both more distant from their nearest neighbor and more likely to have similar competitive abilities. However, mortality due to biotic agents such as bark beetles may have density dependence too (Das et al. 2011; Lutz et al. 2014; Clyatt et al. 2016), making individual-level growth impacts difficult to generalize based on neighborhood competition. Instead of the competition seen during stand initiation, the established root and mycorrhizal networks in old forests may support a variety of growth-promoting facilitative interactions. Potential facilitative interactions include resistance to windthrow and the exchange of carbohydrates, nutrients, and water (Stone & Stone 1975; Graham & Bormann 1966; Ekblad & Huss-Danell 1995; Simard et al. 1997; Fraser et al. 2006; Bader & Leuzinger 2019). Protection from windthrow may be especially important on Mt. Rainier, where this is a frequent source of mortality (Larson & Franklin 2010). This and other effects of exposure-stress, may only be apparent among closely neighboring trees.

Facilitative interactions between individual trees may have positive effects on growth, but this may depend on species identity and the dynamics of inter- and intra-specific interactions (Tarroux and DesRochers, 2011; Graham et al. 2021). Though forest managers have been aware of growth release for well over a century, nearly all research on the subject has involved silvicultural thinning practices aimed at reducing competition or removing overstory hardwoods to promote conifers, usually in young, dense, heavily managed forests where released trees can increase growth up to fivefold (Frothingham 1915; Lutz 1928; Plice & Hedden 1931; Chapman & Bulchis 1940; Staebler, 1956). In these cases the positive effects of thinning may persist for $>$ 50 years post-treatment and even increase over time as trees acclimate to increased light availability (Schlesinger, 1978; Tappeiner et al. 2021).

Growth release following gap formation and density-dependent mortality has been observed in primary forests with similar species composition to Mt. Rainier (Van Pelt & Franklin 1999; Das et al. 2011). In our Mt Rainier study plots, proximity to certain neighboring species, especially the long-lived, shade-intolerant pioneer, Douglas Fir (*Pseudotsuga menziesii*), reduces tree growth rates (Graham et al. 2021). Trees growing in uncrowded stands on Mt. Rainier are more capable of increasing growth as temperatures rise than are trees in crowded stands, suggesting localized competition in dense plots (Ford et al. 2017). Nevertheless, facilitative interactions are predicted to be more frequent under harsh ecological conditions, including the presence of high consumer pressure (Bertness & Callaway 1994; Maestre et al. 2009; Smit et al. 2009). In the case of Mt. Rainier, consumer pressure may take the form of a proliferation of tree-consuming fungal pathogens. Moreover, the presence of some local tree species can have positive impacts on heterospecific neighbor growth, for example Pacific Silver Fir (*Abies amablis*), can enhance growth of Western red cedar (*Thuja plicata*), and in turn, *T. plicata* can promote the growth of Western hemlock (*Tsuga heterophylla*) (Graham et al. 2021, supplemental information). The sometimes positive effects of proximity to *A. amabilis* may be because its roots graft frequently to those of other species (Graham & Bormann 1966). Previous work on mortality and competition in these permanent plots has focused on stand and neighborhood-level processes (Acker et al. 2006; Larson & Franklin 2010; Ford et al. 2017; Graham et al. 2021). Analyses of growth-response to crowding may neglect the growth-enhancing conditions that supported the establishment of dense stands, and miss the potential variety of pairwise individual-level tree interactions, such as neighbor facilitation, that may only be detectable at a finer scale.

Collectively, previous studies suggest that we still have a lot to learn about context-dependent responses of individual trees in old-growth forests to neighboring mortality events. In this study, we address this topic by asking, "How does the natural death of single trees in older, unmanaged forests influence the growth of their nearest neighbors?" Using 40 years of data from 15, 1-ha permanent plots on Mt. Rainier, we track the growth of 9155 trees, and evaluate neighbor-growth response following the death of 1700 of these individuals over this time period. Our objectives in this study are to assess the impacts of single mortality events on the nearest neighboring tree, considering species identity, tree size, neighbor distance, and stand features. If the mortality of a tree locally increases net resource availability, then its neighbor should be released and grow faster than expected based on its individual growth history. However, if facilitative interactions exist between pairs of neighboring trees, or if the mortality of one tree creates a carbon-sink for the other (Lanner 1961; Bader & Leuzinger 2019), then growth may slow in the surviving individual. The intimate interactions of individual trees may influence tree growth-response to neighbor mortality in ways that might not be apparent at the neighborhood-level or following selective tree removal. Long-term monitoring of primary forests can help unravel patterns of tree mortality and neighbor growth. Exploring the potentially dynamic influences of individual tree interactions on growth release in natural forest systems may inform silvicultural decisions in older, secondary forests being managed to promote old-growth characteristics.

2. Methods

Study Site and Plots - Forest measurements took place in 15 coordinate-mapped, 1 ha primary- forest stands on Mt. Rainier, originally established in 1977 as part of the Pacific Northwest Permanent Plot Network (Acker et al. 1998). Mt. Rainier, traditionally called taqwuma in the Puyallup language, is a volcanic mountain located in Mount Rainier National Park, WA, USA (stands in Table 1, species in Table 2). The permanent plots range from 581 to 1454 m a.s.l., and are located in relatively low-diversity, montane coniferous forest stands ranging in age from 150 to 1200 years. While the older stands have a wide range of tree size classes, younger stands have a more recent disturbance history, higher recruitment, and a more even-age structure (Table 1). Stand re-measurements have occurred in ~ 5-year increments (up to 7 censuses) and data collected include dbh (tree diameter at 1.37 m above ground), tree status as healthy (a multi-component metric), declining, or dead, and species, ingrowth of new trees (measured starting at 5-cm dbh), as well as other features not used here. Importantly, tree classified as "healthy", and used as focal trees in this study, had complete crowns, were fully rooted, no signs of mechanical damage from falling neighbors or dropped branches, full, non– broken trunks, and an absence of visible fungal conks. In these Mt. Rainier plots ~ 45 % of tree mortality is a result of mechanical damage in the form of windthrow, uprooting, or crushing (Larson & Franklin 2010). With the exception of crushing damage by falling or decomposing neighbors, most dead trees in these wet forests are predisposed to mechanical damage by chronic infection with root, butt, or heart rots (Larson & Franklin 2010). Plant associations on Mt. Rainier have been classified (Franklin 1988), and Acker et al. (2006) used these classifications to rank each stand in this study from most to least "warm and dry", allowing us to incorporate ecological-community context into the analysis of growth release following neighbor death.

Determination of Nearest Neighbor - We located the nearest neighbor of each of the 9155 trees > 5 cm in diameter in the Mt Rainier permanent plots from their coordinates within each plot. We used the R packages sp (Bivand et al. 2013)and rgeos (Bivand and Rundel, 2021) to generate spatial data frames and calculate the distances between all trees > 5 cm in diameter within each individual plot using sub-setting features in the R package data.table (Dowle & Srinivasan 2021). Tree coordinates within plots were determined during the initial census by laying out a physical grid, subsequently, ingrowth was assigned coordinates based on their distance and azimuth to existing trees. Because the mean distance between neighboring trees was 2.2 m, and never > 5.5 m, we did not correct variation in slope. The nearest neighboring tree to each individual was then selected to create a matrix containing focal-tree data alongside corresponding data describing the nearest neighbor to each focal tree. Of the 9155 trees, 1700 died over the 40- year measurement period, but only 1256 dead trees had living neighbors that met our criteria to be used as focal trees (N = 6900 healthy focal trees with sufficient measuring periods to model).

Tree Growth Models - Frist, we created simple linear models of individual-tree radial growth in order to generate expected values for tree diameter based on growth history in the years prior to the mortality event. Our modeling process began with selection of focal trees, individuals were included in modeling if they were reported to be healthy, with accurately measured dbh, and had a minimum of 3 measurement periods before the final "prediction year" (N = 6900 healthy focal-trees with 3–6 measurement-increments to model). For focal trees with live neighbors, we used 2017, the most recent measurement increment, as the prediction-year. For focal trees with dead neighbors, the year where neighbor death was recorded was used as the prediction-year. It is worth noting, that 18.4 % of living small (<15-cm dbh) trees were excluded as "not healthy", usually due to mechanical damage resulting from neighbor death such as partial crown loss, this was ~ 1.8X the fraction of "regular" sized living trees excluded as "not healthy" (10.3 %).

Linear models, based on 3 or more ~ 5-year incremental diameter measurements, were made to estimate radial growth over time (prior to neighboring tree mortality). We used these models to generate expected values for diameter in the prediction-year (2017 or after neighboring tree mortality) based on model-predicted growth for that year. We used this time-predicted approach, rather than multiple regression, to keep our growth models as simple as possible and avoid additional noise from measurement error in this large 40-year data set. We chose a linear model form because we were viewing a relatively short period of the trees long-term growth trajectory. For each focal tree, we excluded the final year of neighbor measurement from the model, that is, we modeled (a minimum of) 3-years before neighbor death and used the measurement year in which neighbor death was first recorded to compare predicted *vs* observed radial growth. For trees with healthy neighbors, the final year was 2017 when stands were last visited, but 2017 was not used in the growth model resulting in a maximum of 6 measurement-increments available for each model. For example, for trees with surviving neighbors the individual growth model included at minimum the 2001, 2007, and 2012 measurement increments, and predicted growth for the 2017 increment. It is worth noting that the 5-year death window for loss of neighbors could very well cause us to miss a growth response, for example, if the neighbor died just before re-measurement. However, we do not expect this limitation to be different among any of our data sub-sets making our general interpretations still valid.

The growth models (N = 6900) were widely variable in their

Table 1
Characteristics of monitored stands on Mt. Rainier. Corrected growth response (mean stand response/mean stand dbh) shows the magnitude of tree growth following the death of the nearest neighbor, stands are shown ranked by this value. The "warm and dry" ranking is from Acker et al. (2006) where 1 = most "warm and dry", PET is potential evapotranspiration, and Deficit refers to climatic water deficit, an index of aridity. Tree density is on a per ha basis. The three stands with negative growth response (in italic) were excluded from the stand-level analyses.

Stand	Corrected Growth-Response	Elevation (m)	Stand Age (y)	Tree Density	Mean dbh	"Warm & Dry" Rank	PET	Deficit
TO11	0.442	581	550	243	74.9	5	497	73
AO03	0.362	866	1000	372	54.4	11	437	107
TA01	0.202	647	250	375	48.8	3	554	141
AB08	0.149	1061	750	453	47.9	7	439	121
AX15	0.149	1074	150	818	35.5	12	396	69
AV14	0.149	1101	1200	465	40.5	10	323	27
AR07	0.148	1454	330	498	50.7	15	241	18
TB13	0.119	825	150	455	49.2	2	516	99
AE10	0.099	1449	300	724	38.7	13	338	39
AM16	0.034	1185	600	936	31.8	14	416	66
AV02	0.032	857	1000	1153	21.2	8	441	109
AG05	0.010	925	650	975	33.4	6	493	89
TO04	−0.004	659	750	471	49.8	4	514	98
AV06	−0.086	1051	750	1326	27.5	9	437	76
PP17	−0.893	1147	550	947	24.4	1	391	94

Table 2
The species-level response to neighbor mortality. Growth response was only generally observed when the dead nearest neighbor was of a different species, for conspecifics with the exception of *Pseudostuga*, neighbor loss was neutral. The loss of facilitative interactions can be in individual species where growth decreased following neighbor death. Grey dots indicate that data was insufficient for analysis. Paired Wilcoxon Signed-Rank testswere used for comparison of observed and expected growth. To account for family-wise error, *p*-values should be considered significant below the Bonferroni corrected α of 0.003.

	Dead Neighboring Species							
	Same				Different			
Focal Tree Species	Growth Response	*N*	V	*p*-value	Growth Response	*N*	V	*p*-value
All species pooled	none	429	47,867	0.4962	increased	827	190,092	0.006
Abies amabilis	none	264	17,487	0.998	none	223	12,409	0.935
Tsuga heterophylla	none	135	4566	0.959	none	272	17,506	0.415
Chamaecyparis nootkatensis	none	13	50	0.787	increased	88	2785	0.0006
Pseudotsuga menziesii	increased	10	55	0.002	increased	105	4317	<0.0001
Thuja plicata	•	•	•	•	increased	43	759	0.0003
Tsuga mertensiana	•	•	•	•	increased	37	490	0.036
Abies lasiocarpa	•	•	•	•	decreased	12	12	0.034
Picea engelmannii	•	•	•	•	decreased	6	1	0.063
Pinus contorta	•	•	•	•	decreased	17	11	0.0008
Taxus brevifolia	•	•	•	•	none	10	17	0.322
Abies grandis	•	•	•	•	•	•	•	•
Abies procera	•	•	•	•	•	•	•	•
Pinus monticola	•	•	•	•	•	•	•	•
Picea stichensis§	•	•	•	•	•	•	•	•
*Alnus rubra**§	•	•	•	•	•	•	•	•
*Alnus viridis**§	•	•	•	•	•	•	•	•
*Populus balsamifera**	•	•	•	•	•	•	•	•

• = not analyzed (<5 data points per class), § = occurs in plots, no dead nearest-neighbors recorded, * = angiosperm tree.

predictive quality, in some cases greatly over or under predicting tree growth (Fig. 1. $N = 5644$ live-neighbor and $N = 1256$ dead-neighbor models). We suspect that many of the very anomalous predictions came from DBH mismeasurements and short time series. Alternatively, it is equally possible that including climate, plot, and tree diameter variables into our growth models would have overcome much of the spread we observed. We highly recommend re-analysis of this dataset after 3–4 additional measurement increments using more complex growth

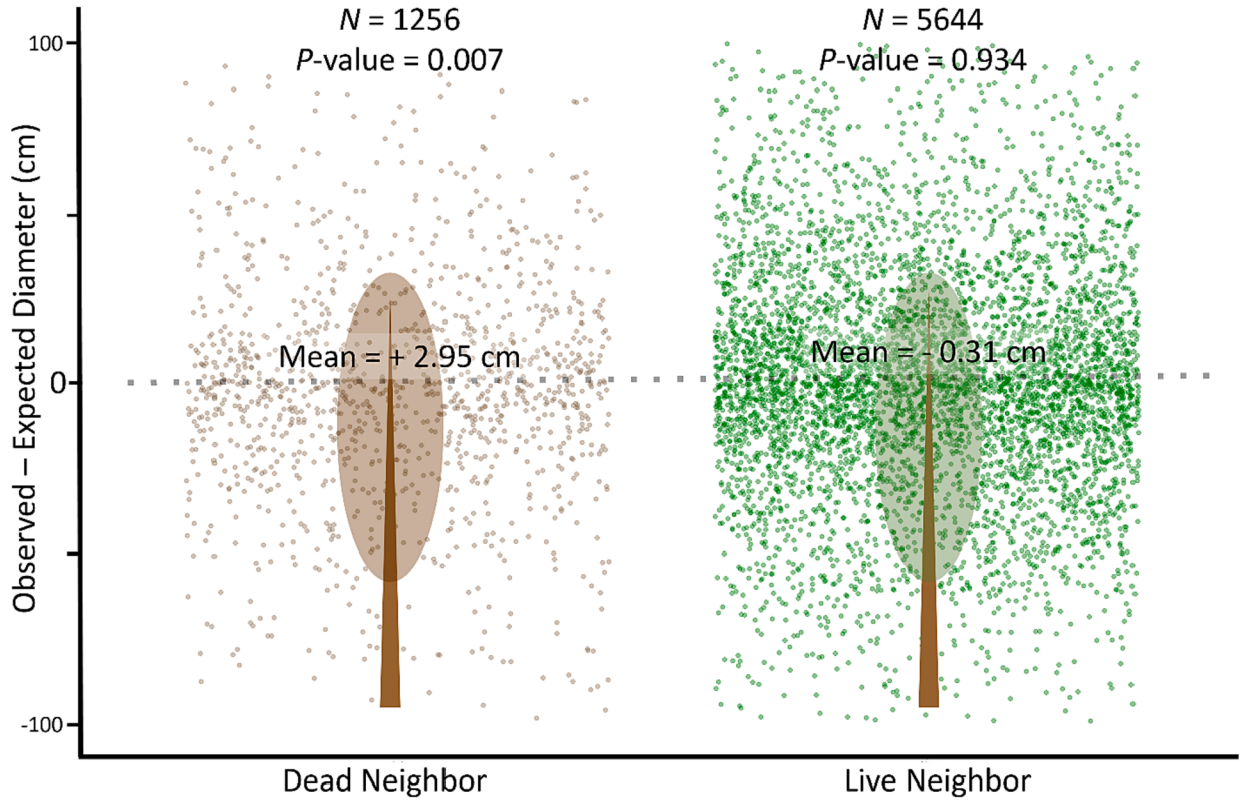

Fig. 1. Raw differences between observed dimeter measurements and expected diameter as predicted by individual growth-models. Although our growth models in some cases wildly over or underestimated tree growth, likely due to measurement errors, in aggregate they provide a valuable approximation of the direction of growth response following neighbor death as evidenced by the reasonable means and further validated by the relationships in Fig. 3. To avoid relying on the magnitude of the difference between observed and expected values, we compared these values with a pair-wise rank test (*p*-values shown), only using this difference magnitude in the form of stand-level means (see Fig. 3). To account for family-wise error, *p*-values should be considered significant below the Bonferroni corrected α of 0.025.

models. Regardless, for the purposes of the present study, we hoped to avoid introducing bias through arbitrary cutoffs in model selection by retaining all successfully-fit individual growth models regardless of the reliability of their parameter estimates or predicted values (eg. highly implausible positive or negative growth trajectories, visible in Fig. 1). That is, because we were interested in overall (aggregate) growth responses, we did not remove any focal trees from our model set due to improbable model fits. The strong trends in stand-level responses and a consistent lack of deviation from mean expected values in trees with living neighbors (see Fig. 1) suggests that this approach provides quality information on generalized patterns of growth release regardless of individual-tree model reliability. Moreover, even if growth-time models with extreme estimates (predicted dbh change $>\pm$ 20 cm of the observed value) were excluded, statistical tests yielded the same general results (data not shown). However, due to poor predictive ability, we do not attempt to estimate percent change in growth as a result of neighbor death, focusing instead on the direction of the response (above or below predicted growth) and mean stand-level differences between observed and expected diameters.

Comparison of Observed and Expected Growth - Our second step was to use measured focal-tree diameter in the final neighbor measurement year (2017 or death-year) as the observed value for comparison to the model-estimated expected value of diameter in that year. Focal trees with dead neighbors were separated from those with healthy neighboring trees, and tree growth within these two datasets was considered separately. Within each of these two datasets, we compared predicted and observed diameter growth-estimates of individual trees using paired two-tailed Wilcoxon Signed-Rank Test. Use of a rank-based test allowed us to assess growth responses without having to make assumptions about how growth values are distributed or to predict the magnitude of the difference between pairs of observed and expected values. Specifically, for the year neighbor-death was noted, observed tree diameters were compared to model-predicted expected diameter across the full dataset to assess generalized patterns of growth-response to neighbor death in all 1256 focal-trees with dead neighbors (Fig. 1). To be certain that our sometimes improbable individual models were not, in aggregate, biased toward predicting a growth increase or decrease, we also compared observed and expected diameter pairs in the 5644 growth-modeled trees with living neighbors (Fig. 1). Following this broad examination, we repeated the Wilcoxon Signed-Rank Test procedure on subsets of the data, splitting the full data set by focal tree size, neighbor size, and neighbor species (same or different). We used Bonferroni corrections to adjust the alpha level for significance based on the number of Wilcox tests performed within each hypothesis family. For hypotheses relating to species identity, we used 16 tests, resulting in an alpha of 0.003. For hypotheses related to tree size we used four tests, leading to a corrected alpha level of 0.013.

In the case of neighbor and focal tree size, we categorized all trees with a diameter below 15 cm as "small", and all larger trees $>$ 15 cm in diameter as "regular", and explored growth-response within these size classes. The largest trees in this study were $\sim$ 2.5-m thick, making "regular" an intentionally broad category that we see as representing established, mature trees. We chose these two categories and their cut-off points to be consistent with previous work in the stands (eg. Graham et al. 2021), and because we were interested in whether the "small" trees were partially dependent on their larger neighbors. Lumping all trees $>$ 15 cm in diameter into a single group helps remove bias from differences in the size of mature trees of different species, the "small" class can be best considered as a generic post-sapling establishment phase. Our sub-setting procedure allowed us to compare the impacts of neighbor death on focal-tree growth within the context of tree size or species.

To confirm that the results of our tree-sized based hypothesis test were not a reflection of the characteristics of plots with more small trees, we used a linear mixed-effects model to predict growth response, with stand as a random effect, and neighbor status (live or dead), focal tree dbh, and neighbor dbh as fixed effects. We tested whether trees with heterospecific nearest-neighbors were more likely to die than those with conspecific nearest-neighbors with a Chi-squared contingency test. Lastly, we examined the potential growth impact of neighbor distance in all 1256 focal-trees with dead neighbors using linear regression.

Stand-Level Trends - In a final step aimed at exploring how stand-level differences like elevation and climate influence growth release at the aggregate, stand scale. Specifically, we first calculated the mean stand-level difference between expected and observed diameter, separately for focal trees with dead neighbors and living neighbors. Then, we used separate linear regressions to assess how these stand-level mean differences varied depending on stand characteristics (Table 1). With the existing plant-association based rankings for each stand from Acker et al. (2006), we applied stand-rank from most to least "warm and dry", as one of the potential predictors of mean growth release to bring ecological-community context into the analysis. We discovered during our analyses that 3 of the 15 stands exhibited a general trend of growth suppression following neighbor death (stand mean growth response was negative), inclusion of these stands, which had many newly recruited trees, showed the same general correlations with stand-level differences, but these associations were weak. Because we were primarily interested in factors influencing growth release, we proceeded in our stand-level analysis with the 12 stands where growth release was the general trend, but report the results for both sets of stands. Starting with a saturated model, containing all stand features and their two-way interactions as predictors, we preformed multiple linear regression with stand-mean growth release as the predictand. We selected the models where all error terms were less than half of the parameter estimate, then chose the most likely model in this model-set based on AICc. Finally, to more comprehensively account for multicollinearity, we preformed LASSO regression on the most likely model to be certain that no predictor estimates were shrunken to zero, that is, that all predictors added additional information.

3. Results

Observed vs Expected Growth from All Tree Growth Models - Of the 9156 trees monitored in the permanent plots, we were able to make growth models for the 6900 individuals categorized as healthy with sufficient pre-mortality data to calculate diameter expectations. Of the 6900 growth-modeled trees, 1256 had dead nearest-neighbors and 5644 had live neighbors. When all trees were pooled, observed diameter growth was typically greater than expected growth for focal trees with dead neighbors (V = 429261, p-value = 0.007), while focal trees with live neighbors grew no more, or less, than expected (V = 7952289, p-value = 0.935, Fig. 1). However, this general trend of growth release was not seen in all situations, as described in more detail below. We observed additional differences in mortality rates, across all plots the mean annual mortality rate for "small" trees was 0.57 %, while for "regular" trees it was 0.43 %. Mortality clustering was minimal, 73.9 % of dead individual trees had a nearest-neighbor that was classed as "healthy". After 40 years of monitoring 18.2 % of health trees lost their neighbor, while dead trees were 7.9 % more likely to have a dead neighbor than health trees.

Comparison of Observed vs Expected Growth by Tree Size - Focal-tree growth response to neighbor death depended on the size of the tree (Fig. 2). Growth of small trees ($<$15 cm diameter) was suppressed following neighbor death (N = 269, V = 4052, p-value $< 2.2*10^{-16}$). This is in contrast to the response of larger-diameter focal trees, in which growth was faster than expected after their nearest neighbor died (N = 987, V = 314018, p-value = $4.5*10^{-15}$). When considering the size of the dead neighboring tree, small neighbors did not noticeably impact trunk diameter growth (N = 424, V = 44290, p-value = 0.763), while the death of trees over 15-cm in diameter led to a general growth increase in their healthy nearest-neighbor (N = 832, V = 197622, p-value = 0.0004). Our confirmatory mixed effects model (with stand as a random

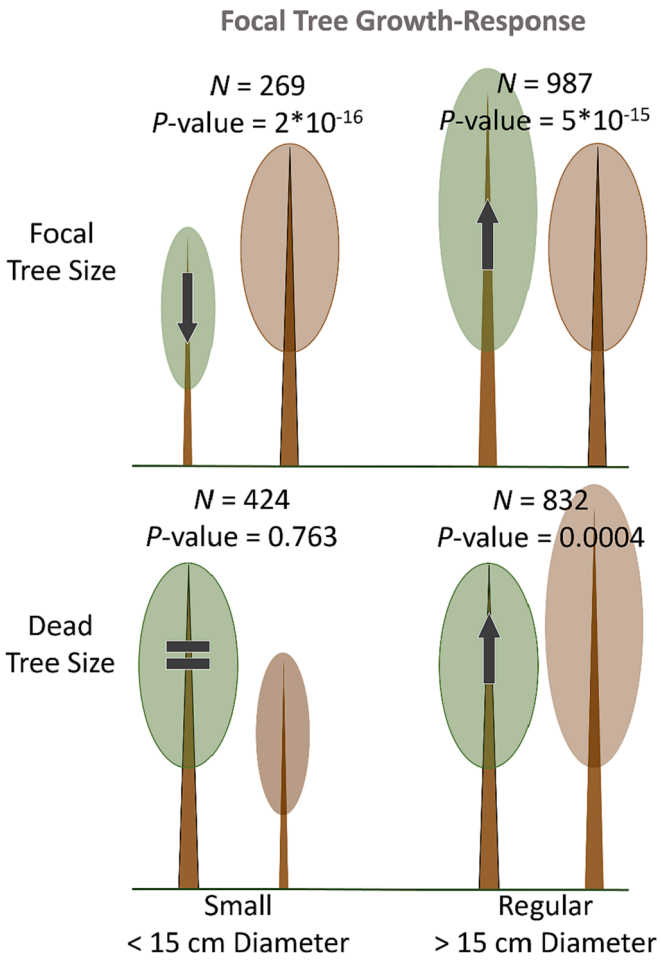

Fig. 2. Growth-response to mortality depends on both the size of the focal tree and the dead neighbor. While mature focal trees generally experienced growth release following the natural mortality of their nearest neighbor, there was no impact on their growth if the lost neighbor was smaller than 15 cm in "diameter. In contrast, small focal trees experienced growth suppression following neighbor death, suggesting a loss of facilitative interactions that formally supported their growth. In this figure, small trees are shown as small, regular trees are shown as large, and 'all-trees-pooled' is indicated by medium-sized trees with distinct borders. To account for family-wise error, *p*-values should be considered significant below the Bonferroni corrected α of 0.013.

effect) revealed that the magnitude of growth release increased with focal-tree size, implying that the growth suppression of small trees we observed was not entirely reliant on the characteristics of stands with many small trees, but did not show a significant effect of neighbor tree size on growth response. This model had a negative intercept (-38.541671 ± 2.180670), supporting the idea that small trees have suppressed growth following neighbor death.

Comparison of Observed vs Expected Growth by Tree Species - Of the 9156 monitored trees, 3330 had a nearest-neighbor of the same species. The probability of tree death was not contingent on neighbors being the same or different species (χ^2 = 1.3578, *p*-value = 0.244). When a neighbor of the same species died, the growth of the focal-tree was not noticeably different from the expected value across all species were pooled (N = 429, V = 47867, *p*-value = 0.496). In contrast, growth increases following neighbor death were generally observed when the neighbor was a different species (N = 827, V = 190092, *p*-value = 0.006). Although we did not have sufficient data to explore the response to dead-neighbor shared species-identity for all individual species, these general trends were not entirely consistent at the species-level for those species for which we had enough data. For example, growth suppression following neighbor death occurred in *Abies lasiocarpa*, *Picea engelmannii*, and *Pinus contorta*, while *Pseudotsuga menziesii* growth was released, even when their dead neighbor was of the same species (full results in Table 2).

Stand-Level Trends in Observed - Expected Growth - The mean difference between observed and expected growth was positive, indicating an average growth release following the death of a neighbor, in 12 of 15 forest stands (Table 1). Two of the three stands where growth was less than what was expected following neighbor death had the greatest changes in basal area (PP17 & AV06, Acker et al. 2006), and all three are high-density stands with rapid recruitment (AV06, PP17, & TO04) prior to 2006 and high mortality of small trees (Acker et al. 2006, Table 1). When considering only the 12 stands exhibiting growth release, increased growth was negatively correlated with elevation (relationship follows a power function R^2 = 0.83, Fig. 3), density of trees within the stand (R^2 = 0.81), and positively related to mean dbh (R^2 = 0.82). Although mean dbh and elevation are closely correlated, the different forms the responses took (power *vs* linear, see Fig. 3), indicated to us that their impact on tree growth response is largely independent. Interestingly, after mean growth release was corrected for by mean dbh (to better focus on climatic factors), the most likely linear model for relative growth release (multiple-adjusted R^2 = 0.86) contained the predictors elevation, density, and the vegetation-based "warm and dry" ranking from Acker et al. (2006). We do not recommend the use of this model to predict actual growth following neighbor death, but it is useful for understanding the factors influencing growth release (Final form: growth release ~ Intercept [0.589 ± 0.0629] + Elevation [-4.243e-04 ± 9.223e-05] + "warm and dry" [2.382e-02 ± 5.918e-03] + stand density [-3.480e-04 ± 5.261e-05]; F-statistic: 23.77 on 3 and 8 df, *p*-value: 0.0002). Because elevation and "warm and dry" are correlated (R^2 = 0.67), we conducted an additional LASSO regression using these three predictors, finding that none of the parameter estimates were shrunken toward zero (*i.e.*, below 0.00001), suggesting that these predictors are reliable regardless of multicollinearity.

4. Discussion

Following natural neighbor tree mortality, the growth of most individual trees is released (increases) in the primary coniferous forests of Mt. Rainier (Fig. 1). A general trend of growth release suggests that competitive interactions are common between individual trees and their nearest neighbors and that growth-limiting resource availability increases for the nearest healthy tree after neighbor-loss. Considering that many trees in these plots remain standing after death (Larson & Franklin 2010), it therefore appears that formation of a substantial gap is not a requirement for the release of individual neighboring trees. However, the growth release we found very much depends on the ecological context in which tree-death occurs, in some cases even suggesting facilitation. Specifically, we found that the size of both focal and dying tree, the species identity of both individual trees, and stand-level conditions all have an influence on individual-tree growth responses. Our results are limited in that we have a 5-year range in which neighbor death occurred, making it impossible to assess the stability of growth response (Harrington and Reukema 1983) or lags in response. However, we have no biological reason to expect that the subsets of trees we explore would have differences in how close neighbor death was to our stand measurement years. Below, we discuss these points and their implications, as well as caveats, in more detail.

Competitive interactions lead to growth release — Like many other studies, our results reveal that competition with neighbors limits growth for many individual trees. On the whole, growth release occurred following neighbor death suggesting that limited availability of resources, such as light and moisture, had previously been a source of competitive interaction. Tree size is a particularly important feature in determining individual-level growth response to neighbor death. In the interaction of two trees, both > 15-cm in diameter, growth release was

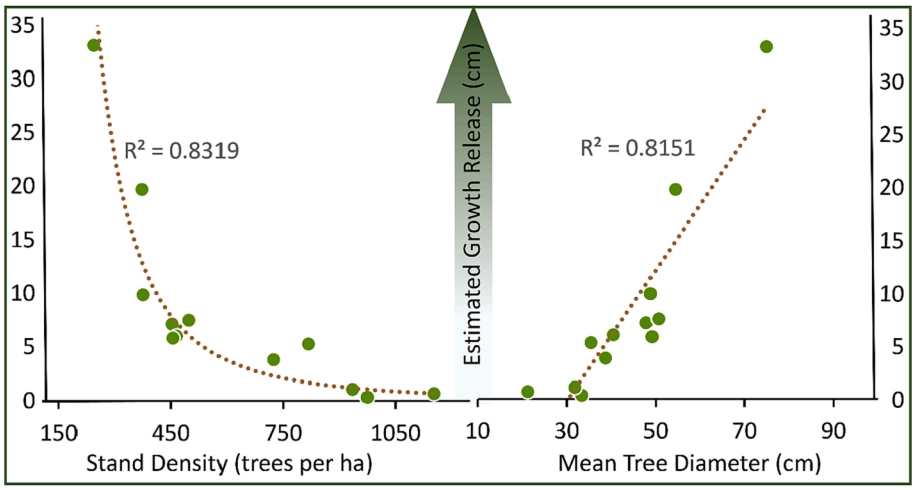

Fig. 3. Estimated growth release is strongly correlated with both stand density and tree size. Although stand density and mean tree diameter are closely correlated (R^2 = 0.8), their relationship to estimated growth release does not take the same form, strongly suggesting that they have independent effects on tree growth response. Scale is excluded from the y-axis because we wish to avoid prediction of growth response from this data, while still exploring its magnitude.

typical (Fig. 2). Reflecting this, stand-level mean dbh was positively associated with growth release, suggesting that this effect might increase with tree size (Fig. 3). Consistent with this finding, when openings were experimentally created in similar forests, diameter growth increased 30 % in individual trees > 90-yr-old (York et al. 2004), although these suppressed trees were not necessarily very large, we presume that they were mostly > 15-cm in diameter.

Our results also suggest that in addition to competition among large trees, competition among species and within stands also plays a role in growth release – with species identity and stand density both influencing competition. Growth release generally occurred if the dead neighboring tree was a different species than the focal tree. However, among individual tree species with sufficient data for analysis, only *Pseudotsuga menziesii* exhibited growth release when conspecific neighbors died (Table 2). It may seem counter-intuitive that in most cases conspecific competition, and thus presumably, conspecific negative density dependence, was not readily apparent in our study system because, as species coexistence in forests is theoretically stabilized by conspecific competition outweighing heterospecific competition (Chesson 2000). In diverse temperate forests, such as Mt. Rainier, we might expect conspecific negative density dependence to be relatively high (Johnson et al. 2012). Yet, there have been very few studies of individual-level interactions between tree pairs where little-known factors such as kin selection (Ehlers & Bilde 2019) or grafting may contribute to growth response. Although, in similar temperate forests relationships with ectomycorrhizal fungi, which we would expect for most of our study trees, may lead to facilitative interactions with conspecifics when close neighbors share common fungal associates (Bennett et al. 2017). It appears that *P. menziesii* is a tough competitor across many forests. Following experimental tree removal elsewhere in the state of Washington, *P. menziesii* saw the greatest jump in growth when a single individual neighbor was removed, with the largest growth release seen in already-dominate individuals (Staebler, 1956). In the Mt. Rainier forests, living *P. menziesii* have a strong negative effect on the growth of neighboring conspecific trees, as well as *Abies amabils*, *Thuja plicata*, and *Tsuga heterphylla*, with no positive growth effects reported (Graham et al. 2021, supplemental information). As may be expected from our results on the importance of tree size, stands with larger diameter trees see a greater degree of mean growth release, and so do the lowest density stands (Fig. 3), many of which are dominated by *P. menziesii*. Curiously, density-dependent mortality is not characteristic of more open forests with large old trees unless driven by the work of biotic agents (Acker *et al.* 1996, Das et al. 2011, Larson et al. 2015), being more commonly seen in dense stands or those with young trees (Das et al. 2011, Lutz et al. 2014). It is possible that competitive stress is more likely to reach mortality-inducing levels in small-size trees, whereas larger tree-pairs might survive competitive interactions in a mutually-suppressed state until the eventual death of one individual releases the other. In dense stands competitive interactions may be visible more on the neighborhood-level than between the nearest individuals. Indeed, group-selection cuts can increase their effect on edge-tree growth release with increasing stand density (York et al. 2004).

Evidence for facilitation — Our results revealed that facilitative interactions among neighbor-pairs may be equally ubiquitous, although confined to certain life stages. Rather than the growth release that occurs in larger individuals, small trees (5–15 cm diameter), exhibit suppressed growth if their nearest-neighbor dies (Fig. 2). Growth suppression following neighbor death likely indicates a net reduction in the availability of resources for small surviving-trees. Limitations on surviving small-tree growth, when light availability is presumably greater, could indicate a loss of sugar, nutrient, or water subsidies previously received from the dead neighbor. Young trees can be partially heterotrophic in their early years (Francis & Read 1984), receiving growth-supplementing sugars from their neighbors through grafted roots (Fraser et al. 2006) and shared mycorrhizal networks along a source-sink gradient (Simard et al. 1997, Simard & Durall 2004). Shared mycorrhizal networks promote survival of fungal pathogens in large-diameter trees, but do not appear to decrease mortality in small trees (Germain & Lutz 2021), which had a higher mortality rate in our plots. Regardless, a lack of protection from pathogen-induced mortality does not imply a lack of resource sharing, where trees are connected by networked roots or fungi, we can expect that sugars would always flow down concentration gradients, drawn by the free energy in the system. Although "small" trees in this study may not all be young, they are<15-cm in diameter and thus can still be considered establishing and possibly reliant on subsidies from larger trees (Sillett et al. 2020). We do not believe crown loss is responsible for these patterns, although crushing damage is common in these stands if a neighbor falls or drops branches and is experienced by trees of all sizes (Larson & Franklin 2010). We likely avoided the majority of crushing damage by looking only at the growth of healthy focal trees in this analysis, so crown loss is probably not the cause of the observed small-tree growth decline, especially because the damage to the crowns of small trees is more likely to have been visible and noted during measurement.

Certainly, factors other than, or in addition to, facilitation could explain reduced growth in small trees, for example changes in growth

allocation, such as a rush to grow taller (Briggs & Kantavichai 2018) or spread roots into vacated space, might explain slowed radial growth rates following neighbor death. Future research would benefit from the inclusion of fungal networks as well as the addition of non-radial growth metrics to better verify facilitation. Additionally, this study does not investigate the relationship of tree size to mortality clustering, which may play a role in growth suppression if morality clusters are due to disease (Meng & Cieszewski 2006) or in some way cause shock to the neighborhood (Harrington & Reukema 1983). If none of our small trees with healthy neighbors were found in areas with pockets of root rot, but small trees with dead neighbors were, then our control would be inadequate to detect the reason for their growth decline, however we do not expect that is would explain our observation of post-mortality growth suppression. Likewise, other mortality factors such as drought may have uneven impacts on small trees. Thinning shock, while usually associated with the removal of multiple neighboring trees, is another potential cause of post-mortality growth suppression due to sugars drawn into stumps through grafted roots (Tarroux et al. 2010), while we do not expect that this would only be apparent in small trees, it may be stronger or small-tree acclimation to radiation stress may take longer. Regardless of possible alternative explanations, rather than small trees being "dominated" by larger neighbors, our results suggest that they are instead nurtured. The relative cost of this facilitative interaction for the resource-donor appears to be negligible, larger trees did not grow any differently than expected in the event that their small nearest-neighbor died. Although growth release by mature trees following experimental gap creation has been observed in similar forests, seedling height growth slowed in large openings (York et al. 2004). Likewise, individual tree removal only has a substantial positive effect on the growth of canopy-dominate neighbors (Staebler, 1956). However, in addition to tree size, individual-level growth response to neighbor mortality, depends on the species involved.

In contrast to *P. menziesii*, in living *Abies amablis*, we saw little evidence for growth release from neighbor death, likewise, *Pinus contorta*, seems to decrease growth when neighbors of a different species die (Table 2), both species have positive effects on growth of some heterospecific neighbors (Graham et al. 2021, supplement). While *P. menziesii* growth in the forests is more dry-sensitive in uncrowded stands, the growth of *A. amabilis* is much less effected by competition, possibly because the effects of high climatic sensitivity dominates its growth variation regardless of stand crowding (Ford et al. 2017). However, *A. amabilis* readily forms root-grafts with other species and such grafts can allow trees to persist under conditions where they might otherwise be competitively excluded (Graham & Bormann 1966, Fraser et al. 2006). We cannot be sure why we found more apparently limiting competition among trees of different species but not within species (except *P. menziesii*), part of the difference may be that we explored nearest-neighbor interactions rather than neighborhood competitive processes. It could be that rather than facilitation in cases where a conspecific neighbor died, a competitive battle had already been fought and won, with the surviving tree growing as normal in the absence of the dead individual because they were thriving as the other tree declined. Heterospecific neighbors decrease tree mortality rates in sub-tropical forests (He et al. 2022), perhaps due to a lower prevalence of the shared biotic mortality agents that are associated with mortality clusters in old forests (Franklin & Van Pelt 2004, Das et al. 2011, Clyatt et al. 2016).

In Mt. Rainier forests, it appears that positive individual-level conspecific interactions are more frequent, perhaps due to shared ectomycorrhizal fungi (Bennett et al. 2017), while heterospecific interactions between individual neighboring trees are more likely to be net-competitive. However, this may further depend on stand-level characteristics that influence the nature of individual tree interactions. The interactions of individual tree-pairs are poorly represented the literature on density dependence which is mostly focused on stand and neighborhood effects, our results suggest that individual interactions may be an area worthy of more detailed exploration, especially among pairs of trees that have both survived to maturity side-by-side. Crucially, the species-level interactions observed here many shift as the climate continues to warm, models predict that heterospecific-linked density dependent mortality will increase more as a result of climate change than will mortality due to competitive interactions with conspecific neighbors (Germain & Lutz 2022). The climate-related increase in heterospecific competition could be particularly important for *P. menziesii* in dry forests, potentially destabilizing forest community structure (Germain & Lutz 2022). As an already strong competitor, *P. menziesii* might be especially likely to experience altered adult mortality rates as the climate warms. The connection between climate and the influence of species identity on density dependence, especially how it might change the relative importance of conspecific and heterospecifc competition, is something we hope can be resolved by additional monitoring of these plots which were established prior to severe climate change.

The mean strength of the mortality-induced growth response in individual neighboring trees, is closely linked to the location and type of stand in which the trees occur. Trees in the two stands with the highest recruitment (from Acker et al. 2006) typically had suppressed growth following neighbor death. These high-recruitment stands do not stand out from the others in terms of climate or stand age. Interestingly, when including the stands with general growth-suppression following neighbor death in our models, relationships between growth-response and stand age, PET, AET, and climatic water deficit all had $R^2 \leq 0.05$, and stand density had an $R^2 = 0.29$, compared to the $R^2 = 0.63$ when these three stands without post-mortality growth release were excluded. Stands with many small trees, densely packed together, may not see the benefits of growth release for several reasons. Small trees may receive subsidies from larger neighbors (Fig. 2), single-tree mortality may have a limited effect on light availability in dense stands, and high recruitment increases both the abundance of small trees and tree density. It is possible that in dense stands group-level influences may be more important than that of a single neighbor, especially in terms of resource availability. However, the weakened relationship between growth response and tree density when the three high-recruitment, negative growth-response stands are included in the analysis, suggests that this is not the case for "small" trees.

Implications for climate change — Climate change is expected to increase individual growth in less crowded stands (Ford et al. 2017), and that may have contributed to our observations of more frequent growth release at low tree density. Further influencing the net-effect of neighbor mortality, is forest elevation, which we found to be negatively correlated with the estimated degree of stand-level growth release after controlling for tree size. Tree mortality in Mt. Rainier stands decreases with elevation, with the lowest rates in 5–30 cm-diameter trees (Larson & Franklin 2010). Recent rates of tree mortality in these forests have been low, even at the lower elevational range limits of species where stress may be increasing, however, low recruitment may slowly shift the composition of species in a hotter future (HilleRisLambers et al. 2015). Such changes in the abundance of small-size trees and altered species composition, could influence growth-response to neighbor mortality. Likewise, added system-energy from climate change may increase future competition in higher elevation stands on Mt. Rainier (Ford et al. 2017), further altering patterns of growth release. In addition, our finding that small trees may be negatively affected by neighboring tree mortality implies that rates of community turnover due to climate-change induced mortality may be slowed, or at least complicated by, lost facilitative interactions between these small trees and their larger neighbors.

5. Management and future directions

The mortality of individual trees drives neighbor growth-responses that are highly context dependent. While growth release is frequently observed, growth suppression is a possible outcome of nearest-neighbor death, particularly for small surviving trees which may be the

beneficiaries of growth subsidization (Fig. 2). Large trees in low-density, low-elevation stands exhibit the greatest growth release, but predominantly when the dead neighbor belongs to a different species (Figs. 2, 3; Table 2). Species that may have facilitative interactions with some other species, such as *A. amablis* (Graham et al. 2021), may not respond to neighbor mortality, even in low-density forests which saw the most growth release in our study (Table 2). It seems logical that small group, rather than individual-tree, selection may be required to free sufficient resources to induce observable growth release in the densest stands. Most dead trees in our study had a living nearest neighbor, suggesting that mortality was mostly not clustered. Based on the results from *P. menziesii*, pioneer species may receive a greater benefit from highly-localized selective removal of single neighbors, perhaps because they are the least shade-tolerant, and any level of light increase is likely to be impactful (Table 2). Thinning has induced nearly 4-fold growth increases in *P. menziesii* (Renninger et al. 2006), and this species is also less susceptible to weakening bark beetle attacks in low-density forests (Clyatt et al. 2016). In contrast to *P. menziesii*, shade-tolerant species are more suited to establishment in small gaps and thus are often found in understory positions, potentially remaining in a suppressed state for centuries until an opportunity for growth arises (Frothingham 1915, Lutz 1928, Franklin & DeBell 1988). However the release of these suppressed, shade-tolerant trees, may require more than the death of a single dominate neighbor (Staebler, 1956).

A mix of tree ages within a stand could allow for a diversity of interactions, including facilitation, and should be considered whether thinning to enhance old-growth characteristics or for fire suppression. In contrast to larger trees, the removal of small individual trees may not lead to an increase in neighbor growth rates (Fig. 2), this may be especially true in cold-wet forest communities at high elevations. Our results suggest that small tree growth benefits from the support of larger neighbors, with negligible cost to large-tree radial growth. The observation of growth suppression in small trees following neighbor loss suggests that retention of large neighbors is beneficial for the productivity of the next tree generation.

Long-term site monitoring, long recognized as a valuable tool for the study of forest ecology (Franklin 1989, Acker et al. 1998), is becoming increasingly important as the length of monitoring time increases in sites established decades ago, particularly those that pre-existed the most pronounced effects of climate change. Further data collection will help clarify species-level differences in competitive and facilitative interactions, as well as the importance of aspect to growth response, allowing for finely tuned management decisions. Future analyses, after 3–4 more measurement increments, could and should attempt to work with multi-predictor growth models to account for inter-annual climatic variation and the effects of tree size on growth, this has the potential to *greatly* reduce the error we see in our simple growth predictions. Likewise, is important to note that our approach may have failed to detect growth responses in cases where they legitimately occurred, this potential for omission errors should be considered, especially in the species level comparisons where sample size was small and a response often not statistically significant. Continued monitoring of permanent forest plots over the coming decades is important to detect among-species differences in the potential for growth release, as well joint impacts of increased thermal energy and potentially lower recruitment rates on the dynamics of tree interactions.

CRediT authorship contribution statement

Alana R.O. Chin: Conceptualization, Formal analysis, Visualization, Methodology, Writing – original draft. **Janneke Hille Ris Lambers:** Conceptualization, Data curation, Funding acquisition, Supervision, Methodology, Writing – review & editing. **Jerry F. Franklin:** Data curation, Funding acquisition, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Mt. Rainier (taqwuma) is part of the homelands of the Cowlitz, Muckleshoot, Nisqually, Puyallup, and Yakama peoples, and the forests in which we work may have been used by other tribes of this region such as the Squaxin Island and Coast Salish, we respectfully acknowledge that our research takes place in their unceded territory. The permanent forest plots used in this study were established over 40 years ago, and thus the present study stands on the shoulders of the many people and organizations who have measured the trees, curated the data, published their insights, and funded this work, including the USDA Forest Service Pacific Northwest Research Station, DOE: DE-FC02-06ER64159, and U.S. National Science Foundation: Career DEB-1054012. Data were provided by the HJ Andrews Experimental Forest and Long Term Ecological Research (LTER) program, administered cooperatively by Oregon State University, the USDA Forest Service Pacific Northwest Research Station, and the Willamette National Forest and based upon work supported by the U.S. National Science Foundation under the grant LTER8 DEB-2025755. A.R.O.C. was supported by an ETH Postdoctoral Fellowship. We are also grateful for very helpful advice from two anonymous reviewers. We especially wish to acknowledge and thank the US National Park Service for their stewardship of these lands and ongoing cooperation (NPS permit MORA-00099).

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