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Complex Interactions Among Agents Affect Shore Pine Health in Southeast Alaska

Abstract

Permanent plots are essential for tracking long-term forest change and have become more important given the projected increase in widespread tree mortality and forest health issues associated with climate change, invasive pests, altered disturbance regimes, and other novel stressors. Inventory and monitoring plots can reveal otherwise undetected loss of tree biomass, initiating targeted biological investigations. Shore pine is an understudied subspecies of lodgepole pine that reaches its northern extent in southeast Alaska. U.S. Forest Service Forest Inventory Analysis data detected a significant loss of live shore pine biomass in Alaska, with greater losses among larger trees and no known cause. We installed 46 permanent plots to monitor shore pine health and survival. Mortality was higher in shore pine (13%) than most associated conifers, and 43% of pines > 40 cm diameter at breast height were dead. Western gall rust, bole wounds, and Dothistroma needle blight were the most common forms of damage to live shore pine. Western gall rust bole gall presence best predicted crown dieback. Shore pine had more bole wounds than associated trees, with wound incidence and severity of live trees increasing with tree diameter. Secondary bark beetles and stain fungi were detected on dying and dead shore pine. Prevalent biotic injury and stressful site conditions accumulate, making large, old shore pine vulnerable to secondary bark beetle attack and vectored stain fungi. This study outlines how inventory networks can detect changes in tree biomass, highlighting knowledge gaps and prompting intensive, long-term monitoring.

Keywords: shore pine, *Pinus contorta*, western gall rust, forest health monitoring, crown dieback

Introduction

Unexplained, elevated tree mortality is pervasive, frequently linked to climate change, and expected to increase under future climate scenarios (Cook and Johnson 1989, Jones et al. 1993, Lindner et al. 2010, Allen et al. 2010). In each instance, detailed biological investigations are necessary to distinguish abiotic climate stressors, predisposing site factors, individual biotic agents or complexes of agents, and their interactions, and to develop specific mechanistic explanations for tree death (e.g., Worrall et al. 2010, Hennon et al. 2012). This can facilitate modeling efforts or yield management guidance to prioritize active management and restoration where it is most likely to be successful (Rehfeldt et al. 2009). Broad scale forms of monitoring (e.g., inventory plots and aerial surveys) may reveal otherwise undetected mortality, particularly for noncommercial tree species that have not traditionally been the focus of biological assessments. Subsequent intensive sampling of biotic agents and long-term tree condition and survival provides the foundation for understanding key causes of tree damage and mortality and forecasting future change.

Changes in live tree biomass for specific tree species or forest types between inventory measurements can serve as an early indicator of forest health problems (biomass loss) or post-disturbance recovery (biomass gain). A 4.6% (SE 2.1%) decline in live shore pine (*Pinus contorta* ssp. *contorta*) biomass was detected in southeast Alaska using data from the Forest Inventory and Analysis (FIA) program of the U.S. Forest Service between the measurement periods 1995–2000 (plot installation) and 2004–2008 (plot re-measurement) (Table 1) (Barrett and Christensen 2011). Greater biomass

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TABLE 1. Net changes of live tree biomass by species in Forest Inventory and Analysis plots of coastal Alaska between 1995–2003 and 2004–2008. Adapted from Table 10 in Barrett and Christensen 2011 and used with permission. Bold signifies a significant net change in biomass.

Species	Remeasured Plots	Biomass (1995–2003)		Survivor Growth		Ingrowth		Mortality		Harvest		Net Change		
		Total	SE	Total	SE	Total	SE	Total	SE	Total	SE	Total	SE	Change (%)
		Thousand tons												
Callitropsis nootkatensis	266	82 836	6319	3651	353	359	47	2485	855	1064	811	525	1332	0.6
Picea glauca	121	7706	1009	1030	406	410	65	1394	436	9	7	48	434	0.6
Picea sitchensis	545	242 935	16 653	17 017	2612	2622	454	12 320	3152	6374	2695	1155	5516	0.5
Pinus contorta[1]	**130**	**12 123**	**1351**	**344**	**90**	**90**	**18**	**1001**	**240**	**8**	**10**	**-561**	**258**	**-4.6**
Thuja plicata	**141**	**47 820**	**5992**	**2812**	**210**	**214**	**48**	**951**	**480**	**73**	**55**	**2025**	**598**	**4.2**
Tsuga heterophylla	556	376 590	20 677	22 903	2688	2724	349	20 067	3298	9025	4897	-3166	6243	-0.8
Tsuga mertensiana	432	105 414	7795	4341	458	464	47	3589	636	421	381	859	970	0.8
Alnus rubra	**36**	**2162**	**575**	**617**	**517**	**533**	**163**	**273**	**133**	**11**	**13**	**872**	**299**	**40.3**
Betula papyrifera	104	11 651	1754	1 046	205	206	90	742	193	144	144	377	343	3.2
Populus balsamifera	**49**	**8379**	**1859**	**1 017**	**89**	**90**	**28**	**121**	**66**	**50**	**50**	**952**	**265**	**11.4**
Other species[2]	-	4888	-	465	-	293	-	459	-	3	-	300	-	6.1
All species	895	902 505	28 930	55 244	7919	8007	741	43 402	4731	17 183	6944	3384	9598	0

[1] *Pinus contorta* ssp. *contorta* was the subspecies present in 128 of 130 plots with *P. contorta*.

[2] Other species include *Abies amabilis*, *Abies lasiocarpa*, *Picea mariana*, *Taxus brevifolia*, *Malus fusca*, and *Populus tremuloides*.

loss was detected for trees > 20 cm diameter at breast height (dbh) compared to trees 13–20 cm dbh (Tara Barrett, USDA Forest Service, Personal communication, September 14, 2011). The FIA program monitors the status and trends of forests across the United States through a permanent ground-based plot network on a grid pattern that is re-measured at regular intervals (~10% of plots are measured annually) (USDA-Forest Service 2007). Shore pine, a non-commercial tree with negligible harvest, was the only tree species in Alaska with a statistically significant decline in live biomass. Shore pine mortality had not been detected through other forms of monitoring, and no cause of mortality was determined. Generally, inventory plots are not designed to elucidate complex causes of tree mortality, such as those incited by multiple biotic agents in combination with environmental stressors. This lack of information about the specific cause(s) of mortality is common among long-term monitoring plots, and inventories are of greatest value when paired with intensive studies that address specific forest health or resource issues.

This study was initiated to investigate the recent decline in shore pine biomass in southeast Alaska and to systematically gather baseline information about the pathogens, insects, and other damage agents of shore pine. Knowledge of shore pine's disease and insect pests is extremely limited (Reeb and Shaw 2010). Warmer temperatures and increased precipitation as rain projected for the region will likely affect the incidence and severity of biotic damage agents (e.g., increased foliage disease severity) and environmental stressors (e.g., changes in water table depth) (Wolken et al. 2011). There is low tree diversity in Alaska's coastal rainforest, and shore pine serves a unique role by growing under the harsh conditions of peatland bogs and fens where few other tree species thrive. The loss of shore pine and the ecosystem services that it provides in these habitats may create a void that other trees are unable to fill. It is crucial that we understand the basic biology, mortality agents, and ecological drivers of each of our trees and forest types in order to forecast ecosystem change and guide forest management. Understanding the processes that have contributed to the loss of shore pine biomass will help us to gauge the vulnerability of shore pine populations and predict their response to specific damage agents in the context of a changing climate.

Our primary objectives were to: 1) gather baseline forest health information on southeast Alaska's shore pine populations, 2) evaluate the proportion of trees dead by tree diameter class and the distribution of shore pine snag decay classes, 3) identify the primary causes of live shore pine crown dieback, and 4) evaluate potential spatial patterns of dieback or mortality. Our approach was to install a permanent plot network in shore pine-dominated forests to facilitate long-term monitoring and detailed forest health assessments. With continued monitoring of this network, we will gain information about the types of damage most often associated with shore pine mortality and the expected population trajectory. Our shore pine plot network can be used with the FIA plot network to determine if and why there is reason for heightened concern regarding the health and survival of shore pine populations in southeast Alaska, with applications throughout the species' range. This study provides a template for the type of focused biological investigations required to determine complex causes of tree mortality detected through various forms of broad scale forest monitoring, especially for understudied trees and forest types near their range limits.

Methods

Study Species

Shore pine is one of four morphologically and geographically distinct subspecies of *Pinus contorta* (ssp. *bolanderi*, *contorta*, *latifolia*, *and murrayana*) (Critchfield 1957). It occurs in sand dunes, rocky cliff faces, and wetlands along the coastline from northern California to Yakutat Bay in southeast Alaska. All four subspecies have two-needle fascicles and scaly bark, but vary in crown shape, tree form, and reproductive strategy. Each grows in a discrete portion of the species' range and is hypothesized to be adapted to local climate and environmental conditions (Ying and Liang 1994; Rehfeldt et al. 1999, 2001). In Alaska, shore pine is most common in peatland bogs and fens (known as muskegs) that have saturated, acidic soils. It is outcompeted by western hemlock (*Tsuga heterohpylla*) and Sitka spruce (*Picea sitchensis*) in the coastal buffer zone and on other more productive sites with better drainage and nutrient availability (Martin et al. 1995, Bisbing et al. 2015).

Shore pine trees and forests have been understudied, despite their ecological value, because shore pine is not commercially managed for timber. Despite their low productivity, shore pine plant associations host the greatest plant species richness of any forest type in Alaska's coastal rainforest (Neiland 1971, Martin et al. 1995). Percent canopy cover transitions along drainage gradients in forested bogs and fens, creating a mosaic of scattered individual seedlings and stunted trees, clumps of trees, and shore pine-dominated mixed-conifer forest. As the dominant tree in peatland bogs and fens, shore pine serves a significant ecological role by providing vertical structure, shade, habitat, and a seed and inner bark food source for birds, small mammals, and porcupines (Lotan and Perry 1983, Cope 1993, Martin et al. 1995). Robins and thrushes nest in branches of live shore pine, greater yellow-legs nest beneath shrubby shore pine (Piston and Heinl 2006), and the authors observed sapsuckers and abundant nesting cavity holes in large shore pine snags with heart rot.

Study Area and Site Selection

The study was located in the southeastern Panhandle of Alaska on islands of the Alexander Archipelago and the adjacent coastal mainland (N54.5–58.5°, W130.0–136.5°). Regional climate is hypermaritime, consisting of mild, wet winters and cool, wet summers (Carrara et al. 2007). Mean annual precipitation exceeds 300 cm in many areas and is estimated to reach 1000 cm in some places, such as the higher elevations on southern Baranof Island (O'Clair et al. 1997, Carrara et al. 2007). Mean monthly temperatures near sea level range from 13.3 °C in July to approximately 0 °C in January (Western Regional Climate Center 2014), although temperature, precipitation, and precipitation as snow vary with latitude, elevation, and topography. The landscape of the study area transitions abruptly from the Pacific Ocean to steep, glaciated mountains. Key features of this ocean to mountain system include glacier-fed rivers, conifer forests, and *Sphagnum* species-dominated peatlands (Alaback 1982, DellaSala et al. 2011).

A permanent plot network was established in summers 2012 and 2013, covering the range of shore pine in Alaska (Figure 1). Five locations were selected as study areas, including: mainland Juneau and Douglas Island, NE Chichagof Island, Mitkof Island, Wrangell Island, and Price of Wales Island. Plot locations were randomly selected in each study area from National Wetland Inventory (NWI) polygons (Cowardin et al. 1979) that met the following criteria: known to reliably contain shore pine (palustrine emergent wetland, PEM, and palustrine scrub-shrub wetland, PSS), classified as containing needle-leaved evergreens, located within 0.8 km of a road or trail, and at least 1.6 ha in size. The Generalized Random-Tessellation Stratified (GRTS) process was used to identify forty potential plot locations (20 PEM and 20 PSS) within each of the five study areas ($n = 200$). This spatially-balanced, probability-based survey was performed in R 2.9.2 (R Core Team 2008) using the spsurvey package, the GRTS function, and equal probability selection (Stevens and Olsen 2004, Detenbeck et al. 2005). Due to the remoteness of our field sites, Geographic Information System tools (ArcMap 10.0, ESRI, Redlands, CA) were used to preliminarily assess and accept or reject the selected wetland polygons in order of GRTS selection based on accessibility and shore pine forest type. Potential plots were further sequentially assessed on the ground until at least eight of the 40 potential sites at each study location were selected for plot installation. Bisbing et al. (2015) followed the same selection procedures at three of our five locations; our project used their selected polygons where possible. On Wrangell, Mitkof, and Prince of Wales Islands, only two of the 8–10 plots per location were installed in PSS wetlands, representative of the broader landscapes of these islands on which PSS polygons were uncommon, small in size, and/or lacking sufficient shore pine composition.

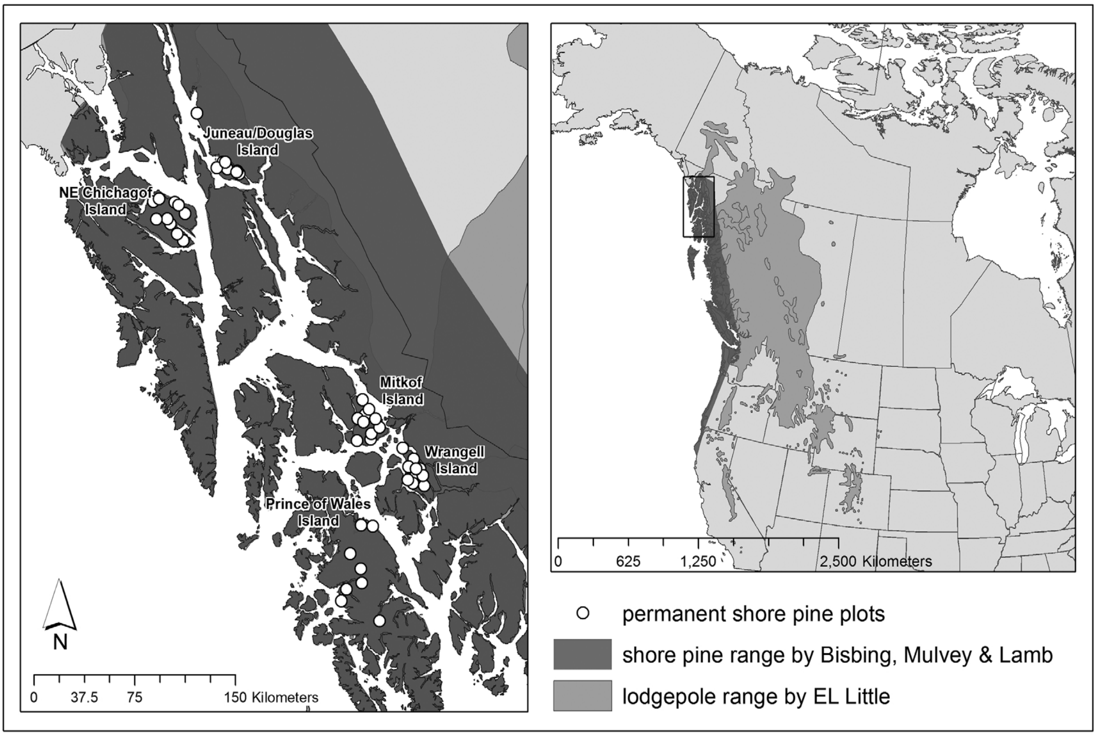

Figure 1. Permanent shore pine plots (46) established at five locations in southeast Alaska in 2012 and 2013 (left) with a location map (right) showing the range of shore pine (*Pinus contorta* ssp. *contorta*) against the broader range of *Pinus contorta* (Little 1971). The shore pine range layer was developed from inventory plot data and maps were produced by M. Lamb, USDA Forest Service.

Plot Layout and Data collection

Forty-six 0.05 ha permanent monitoring plots were established across our five study areas in southeast Alaska: Juneau/Douglas Island (8 plots), NE Chichagof Island (10 plots), Mitkof Island (10 plots), Wrangell Island (10 plots), and Prince of Wales Island (8 plots). A modified FIA plot layout was used. Plots consisted of three 7.3 m-radius subplots (located at 360° and 120°, 36.6 m from a central subplot), each with a 2.1 m-radius microplot to measure regeneration (nested plot, subplot, microplot design; USDA-Forest Service 2010). To facilitate establishment of one plot per field day, we excluded the subplot at 240° used by FIA. FIA defines a tree as ≥ 12.7 cm diameter at breast height (dbh), but we monitored all plot trees ≥ 1.37 m tall (breast height) since many shore pine stands consist of old, small-stature trees. Counts of seedlings and saplings (< 1.37 m tall) by species were conducted in microplots, including information about live/dead status and the presence of western gall rust (WGR) infection on shore pine. Yellow-cedar commonly exhibited dense branch-layering vegetative reproduction, with each stem counted as an individual. Lower branches of shore pine were sometimes buried by sphagnum, emerging away from the parent stem; shore pine were counted as individual seedlings unless their belowground branch connection to a parent tree was evident without destructive digging. Following data collection, trees < 12.7 cm dbh within microplots were added to the regeneration counts to make them comparable to the FIA methods and dataset.

Plots were placed within selected polygons to maximize shore pine composition in subplots and to capture a range of shore pine size classes. Flexibility in plot placement within randomly selected polygons allowed us to capture shore-pine dominated forested wetland and to avoid commonly-occurring treeless areas and adjacent upland forest with a limited shore pine component (Cowardin et al. 1979). For more information on shore pine community composition, see Neiland 1971. Subplot centers were marked with 2.54 cm-diameter polyvinyl chloride poles. A prism count (Basal Area Factor 5), slope, aspect, percent cover of vegetation types and plant species, and a breast-height tree core from the largest non-defective shore pine were collected in each subplot. Tree cores were mounted at the orientation at which they occurred in the tree, sanded with increasingly fine grit sandpaper, and aged and measured using a dissecting microscope. Further analysis of tree cores from this plot network are presented in a separate manuscript (Sullivan et al. 2015).

Live and dead trees ≥ 1.37 m tall were labeled with numbered metal tags near breast height. Data collected from live trees included height, dbh, lower crown height, crown dieback (%, visually estimated), wound type and severity, and presence of conks, decay, or topkill. Crown dieback was estimated as the percentage of the tree crown with stem and branch mortality other than that caused by normal self-pruning of lower branches (Reed and Mroz 1997). For live shore pine, we recorded WGR severity, crown dieback associated with galled boles or branches (%), the location of WGR bole galls, and whether topkill was associated with bole galls. We visually estimated years of foliage retention (current year foliage = year 0) and foliated branch length (cm, current year foliage excluded) from the ground, and documented the severity and type of foliar damage. Foliage disease severity was rated low if less than 50% of the foliage was affected, moderate if 50–75% was affected, and high if > 75% of the foliage was affected. Symptomatic foliage (attached to twigs) was collected from shore pine to facilitate identification of foliar pathogens and insects. Foliage samples collected in 2012 were overwintered outdoors in mesh bags until May 2013 to promote the development of fungal fruiting bodies for foliar pathogen identification. Height, dbh, decay class (1–5, as defined by FIA), and damage information was collected from snags.

The fungus that causes WGR, *Peridermium harknessii* (J. P. Moore), only infects hard pines and is an obligate parasite. To quantify WGR severity, a 0–6 scale was adapted from the Hawksworth (1977) dwarf mistletoe rating system. The live tree crown was vertically divided into thirds, each 1/3 of crown had a maximum rating of 2 (assigned if > 50% of branches were infected and/or bole galls were present), and ratings from each 1/3 of crown were summed. WGR severity ratings were assigned to dead shore pine when galls were observed, but evidence of infection is lost as trees decay causing WGR incidence and severity to be underestimated in snags. Nearly 300 WGR galls were haphazardly collected from newly-killed infected branches with red foliage at all study locations, usually en route to study plots and along roadways, to determine whether insects or fungi were responsible for girdling the infected tissue.

Wound types recorded included: mechanical injury, root exposure, porcupine feeding, antler rub, bole canker, burl, old dead bole gall, frost crack, bear scratch, bark rubbing from neighboring trees, sapsucker feeding, and limb or leader harvest for Christmas trees. Wound severity rating was based on the relative circumference of the bole or root collar affected (< 1/3: low severity; 1/3–2/3 moderate severity; or > 2/3 high severity). Some wound types (e.g., frost cracks) were labeled moderate or severe when they extended vertically along or deep into the tree bole. Damage from logging equipment did not occur in our plots; bole wounds were recorded as mechanical damage whenever the specific cause could not be determined. Diamond-shaped wounds that were recorded as mechanical damage in 2012 were further distinguished as cankers in 2013. Since the specific cause of bole wounding was often unknown, all types of bole wounds were lumped for analysis. Root exposure wounds were noted when there was a gap between the root system and ground substrate near the root collar. In some cases the root system was all or partly submerged in water. In other cases, trees were rooted in sphagnum moss mounds with apparently poor anchorage.

Statistical Analyses

Statistical summaries allowed us to compare the proportion of dead or wounded trees across species and shore pine diameter classes and to quantify the overall incidence and severity of WGR. Exploratory analyses also included one-way ANOVAs to test for differences in the proportion of shore pine with bole wounds as compared to associated conifers, and for differences in WGR severity rating, percent dead, and crown dieback by location and tree diameter.

Prior to fitting statistical models, we examined the dataset for spatial autocorrelation and correlations among predictor variables. We tested for spatial autocorrelation of WGR-associated crown dieback using the *spdep* package in R (R Core Team 2015) to compute *Moran's I* and *Geary's C.* Spatial dependence was also evaluated through incorporation of plot coordinates as fixed effects terms in full models. We ran principal components analysis (PCA) on all potential predictors to reduce model parameters to a set of minimally correlated variables (< 0.65, Bothwell et al. 2013), which eliminated numerous variables related to tree health. Although moderately correlated (0.68), WGR severity rating and bole gall occurrence were retained after considering that these variables may influence crown dieback differently (i.e., we noticed that individual bole galls had the potential to cause a greater portion of the crown to die compared to individual branch galls when gall tissue was girdled). Variables retained as fixed effects in the model included: bole gall occurrence, WGR severity rating, gall rust-related topkill, bole wound severity, and root exposure severity. Analyses initially considered wetland type (PEM or PSS), but we found no significant relationship and therefore excluded this factor from model fitting.

Logistic regression models and arcsine square-root transformations were considered but not used for model fitting due to our lack of strict binomial data and the lack of interpretability of arcsine-transformed data (Warton and Hui 2011). We instead fit generalized additive mixed models (GAMMs), incorporating geographic coordinates as fixed effects to account for spatial dependence and random effects to account for unmeasured drivers of variation (Wood 2006). Models were fit with the *mcgv* package in R (R Core Team 2015) using maximum likelihood tests to avoid under-smoothing random effects and to allow for comparison of models with different fixed effects (Wood and Augustin 2002).

We ran two GAMMs on the following response variables: 1) crown dieback presence or absence (binary, 0/1; binomial distribution and logit link function) and 2) proportion of crown dieback (proportional, 0.01–1.00; beta distribution and logit link function). The binary model was used to identify damage type(s) that best explained the presence or absence of shore pine crown dieback. The proportional model was used to further evaluate the relationship between damage types and the proportion of crown dieback, only considering trees for which dieback occurred. The fixed effects in each full model included: geographic coordinates (NW, continuous), bole gall occurrence (BoleGall, binary), WGR severity rating (WGRrating, factor), WGR-related topkill (GallTopkill, binary), bole wound severity (BoleWound_Sev, factor), and root exposure severity (ExposedRoot_Sev, factor). Plot and subplot were both included as random effects to account for unmeasured variation at both spatial scales (Bolker et al. 2009). We used quadratically penalized regression splines selected by Restricted Maximum Likelihood (REML) to smooth geographic coordinates and a ridge penalty for random effects (Wood 2011). After fitting the full model, a simplified model was created by removing all insignificant fixed and random effects ($p > 0.05$). Reduced models were compared to full models using likelihood ratio tests and AIC criterion (Burnham and Anderson 2002). We calculated odds-ratios of non-smoothed parameters with 95% confidence intervals using the estimated coefficients for predictor variables. Odds-ratios were converted to predicted probabilities for interpretability. All analyses were implemented in R 3.2.1 (R Core Team 2015).

Results

Data Summary

Across 46 plots, data were collected from 5,452 trees ≥ 1.37 m tall (Table 2), including 1,031 trees ≥ 12.7 cm dbh. Tree species included shore pine, yellow-cedar (*Callitropsis nootkatentis*), mountain hemlock (*Tsuga mertensiana*), western hemlock,

TABLE 2. Number of live and dead trees ≥ 1.37 m tall and percentage of trees dead by species in 46 plots in Southeast Alaska. Shore pine is subdivided by tree diameter class (cm).

Species	Live	Dead	Total trees	Percentage dead
shore pine				
0.1-10.0 cm	1562	219	1781	12%
10.1-20.0 cm	591	88	679	13%
20.1-30.0 cm	268	36	304	12%
30.1-40.0 cm	71	9	80	11%
40.1-60.0 cm	12	9	21	43%
shore pine (total)	2504	361	2865	13%
yellow-cedar	1113	177	1290	14%
mountain hemlock	577	32	609	5%
western hemlock	467	20	487	4%
Sitka spruce	60	3	63	5%
western redcedar	60	–	60	0%
red alder	5	–	5	0%
unknown snags	–	73	73	100%
Total	4786	666	5452	12%

Sitka spruce, western redcedar (*Thuja plicata*), and red alder (*Alnus rubra*). Of 666 total snags, 73 (11%) could not be definitively identified due to advanced decay class. These 73 snags were thought to include 18 hemlock (mountain or western), 7 shore pine, 5 yellow-cedar, and 43 unknown (likely pine or hemlock based on wood strength). Plots (0.05 ha) averaged a basal area of 21.7 m^2/ha (SE 7.8 m^2/ha), 119 total trees (62 shore pine) ≥ 1.37 m tall, and 22 total trees (19 shore pine) ≥ 12.7 cm dbh. Tree cores collected from the largest diameter shore pine per subplot (average age 230 yrs, range 80–472 yrs) revealed a mean radial growth rate of 0.6 mm/yr, seldom exceeding 1 mm/yr (Sullivan et al. 2015).

The percentage of dead trees was higher for shore pine (13%) and yellow-cedar (14%) compared to other species (< 5%) (Table 2). Even with unknown snags tallied as hemlock (western and mountain combined), the percentage of dead hemlock did not exceed 10%. Among shore pine, the highest percentage of snags (43%) occurred in the largest diameter class (40.1–60.0 cm; Table 2). Fifteen percent of shore pine snags > 20 cm dbh retained fine branches (decay class 1) while 46% retained coarse branches (decay class 2).

Of 1698 live seedlings and saplings (< 12.7 cm dbh) recorded in 2.1 m-radius regeneration microplots, there were 541 shore pine, 801 yellow-cedar, 198 mountain hemlock, 134 western hemlock, 15 spruce, 9 western redcedar, and 4 hardwoods. Shore pine regeneration was present in 102 of our 138 microplots, and in at least one of the three microplots in 44 of our 46 plots. On average, there were 11.8 live and 0.7 dead shore pine seedlings/saplings per plot (2800 live and 200 dead shore pine/ha). The highest count of shore pine seedlings/saplings was 31 per microplot (22 000/ha) and 41 per plot (10 000/ha). Shore pine and yellow-cedar regeneration counts were generally higher in PEM wetlands compared to PSS. Shore pine regenerated most prolifically in plots on Wrangell, Mitkof, and Prince of Wales Islands, consistent with the larger proportion of PEM plots installed at those locations. Sitka spruce and western and mountain hemlock regeneration counts were usually higher in PSS wetlands. Shore pine seedlings comprised 25–43% of the regeneration by location. Shore pine regeneration was least abundant where large patches of layering yellow-cedar regeneration occurred, most notably on Wrangell Island.

Wounds—The percentage of live shore pine wounded and general wound severity increased with diameter (Figure 2). Bole wounds were significantly more common on live shore pine (32%) compared to associated species (2–8%) (ANOVA $p < 0.001$) (Table 3). Snow loading and animal feeding or marking are likely major sources of bole wounds, but specific causes were usually unknown. Poor root anchorage (exposed root wounds) in saturated soils, mossy mounds, or standing water affected 5–32% of trees (by species) and was the most common wound for non-pines (Table 3). Exposed root wounds were rated high severity for just 1% of live shore pine, compared to 7–8% of live spruce and hemlocks (data not shown); this type of wound is likely to only harm trees when severe.

Western gall rust (WGR)—WGR was detected in all subplots and on 85% of all live shore pine, with 52–100% of pines infected per plot. Incidence of WGR did not differ between PEM and PSS sites ($p > 0.10$). For snags, WGR incidence was only

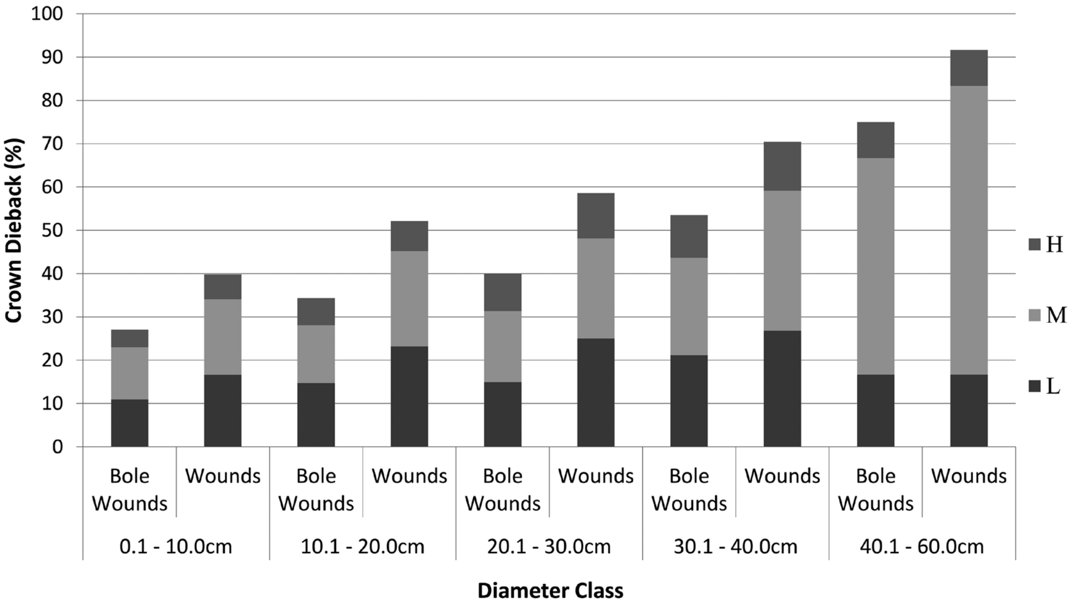

Figure 2. Percentage of live shore pine across 46 plots in southeast Alaska with low (L), moderate (M), and high (H) severity bole wounds (left columns) and overall wounds (right columns) by diameter size class. Bole wounds include damage to the tree bole from animal feeding, deer antler rub, frost cracks, neighboring tree fall, and unknown causes.

TABLE 3. Percentage of live and dead trees with bole wounds, exposed root wounds, and all wounds by species in 46 plots in southeast Alaska.

Live	Exposed Root Wounds (%)[a]	Bole Wounds (%)[b]	All Wounds (%)[c]
shore pine	17%	32%	47%
yellow-cedar	5%	2%	7%
mountain hemlock	23%	3%	26%
western hemlock	32%	3%	36%
Sitka spruce	30%	8%	38%
w redcedar	12%	7%	18%
Dead			
shore pine	14%	20%	31%
yellow-cedar	9%	0%	9%
mountain hemlock	25%	9%	31%
western hemlock	40%	0%	40%
Sitka spruce	0%	0%	0%
Unknown	7%	0%	8%

[a] Indicates that a gap was present between the root system and ground substrate near the root collar. Groups situations in which the root system was all or partly submerged in water or rooted in sphagnum mounds with poor anchorage.

[b] Damage to the tree bole from animal feeding, deer antler rub, frost cracks, old dead bole galls, neighboring tree fall, and unknown causes.

[c] Some trees had both wound types, and some uncommon wound types did not fall under these wound categories.

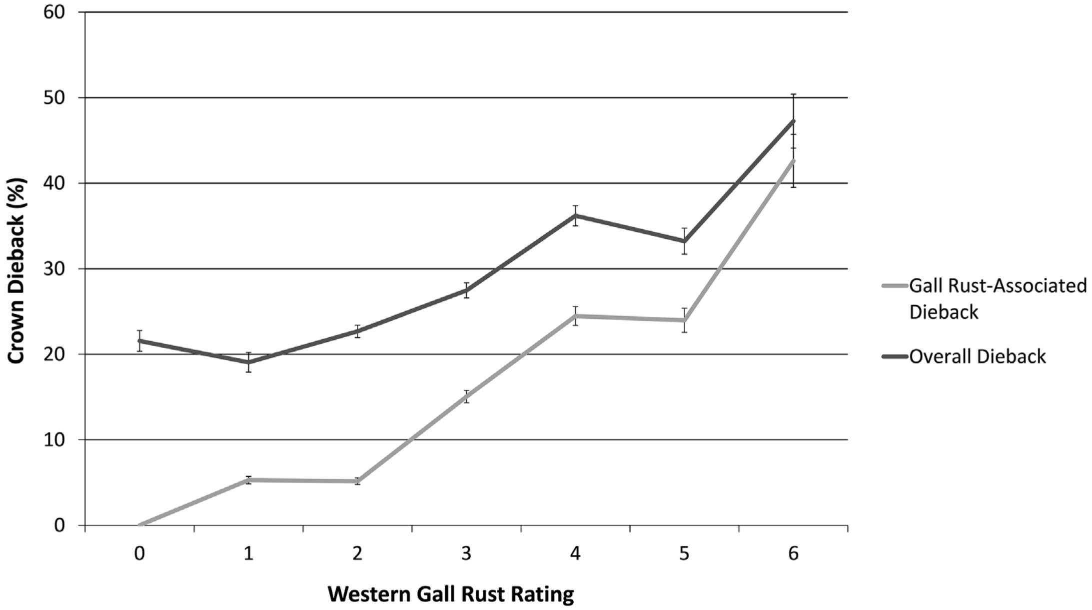

Figure 3. Mean crown dieback (%) and mean crown dieback associated with western gall rust (%) by western gall rust severity rating (0–6). Standard error bars are shown.

32%. WGR severity ratings for live shore pine were distributed as follows: 39% low severity (1–2), 36% moderate severity (3–4), and 10% high severity (5–6). Slight but statistically significant differences in WGR infection incidence and WGR rating were detected between our five locations (ANOVA $p < 0.001$). From highest to lowest WGR rating, sites were ranked Juneau, Prince of Wales, Wrangell, Hoonah, and Mitkof, with the mean estimated WGR rating for Juneau 0.7 (SE 0.1) higher than that of Mitkof. WGR rating and bole gall incidence both increased with tree diameter (ANOVA $p < 0.001$). The smallest diameter class had the lowest infection incidence (0.1–10.0 cm dbh, 79%), while all pines in the largest diameter class (40.1–60.0 cm) were infected. Seedlings and saplings in the regeneration microplots had the lowest rate of infection at 27%.

Bole galls were observed on 35% of live shore pine (9 to 78% per plot), and 7% had bole infections in more than one portion of the live crown. Among snags, bole gall incidence was 21%, which may be underestimated due to snag deterioration. WGR-associated topkill was observed on 25% of live shore pine (> 70% of trees with bole galls). When topkill occurred, 40% of trees developed new leaders; some trees showed one or more iterations of topkill, new leader development (40% of top-killed trees), subsequent bole infection (37% of trees with new leaders), and repeated topkill (7% of trees with new leaders). WGR-associated dieback averaged just 3.5% for trees without bole galls, compared to 25, 35, and 48% for pines with bole galls in one, two, and three crown-thirds, respectively. Overall crown dieback and WGR-associated crown dieback were significantly correlated with WGR rating (ANOVA $p < 0.001$) (Figure 3). Insects and fungi were frequently detected girdling branch and bole tissue in the nearly 300 galls collected from recently-killed gall-infected branches with red foliage (see Table 4 for agents observed in galls).

Other Biotic Damage Agents—Foliage disease or leaf mining insects caused low to moderate severity damage to 38% of live shore pine; severe foliar damage was uncommon in plots. Although prevalent, foliage disease did not actively contribute to branch dieback or tree mortality at the time of survey. Collected symptomatic foliage overwintered in mesh bags most often yielded

TABLE 4. Biotic damage agents of shore pine other than western gall rust detected in the study area in southeast Alaska and a description of the damage.

Foliar Pathogens & Insects	
Dothistroma needle blight (*Dothistroma septosporum*)	Widespread with variable severity; probably limits foliage retention of shore pine; not causing mortality in plots at time of survey, but a localized epidemic near Gustavus, AK (2010-2015) is causing significant shore pine mortality (R. Mulvey, unpublished data)
Lophodermella needle cast (*Lophodermella concolor*)	Scattered discolored shoots, causes limited damage
Lophodermium needle cast (*Lophodermium seditiosum*)	Scattered discolored needles, causes limited damage
Defoliating weevils (*Magdalis* or *Scythropus* sp.)	Tentatively identified based solely on photographs of feeding damage, not insects (Elizabeth Willhite, U.S. Forest Service, Personal communication, March 07 2014)
Lodgepole pine sawfly (*Neodiprion nanulus contortae*)	Detected at all study locations; previously undocumented in Alaska; defoliation usually limited to scattered or clustered branches; discussed in Ciesla 1976 and Ciesla and Smith 2011
Lodgepole needle miner (*Coleotechnites milleri*)	Identified based on circular exit holes on needles; apparently low populations at the time of survey
Bark Beetles (Coleoptera: Curculionidae) & Stain Fungi	
Pseudips mexicanus	Secondary bark beetle (Smith et al. 2009) collected from large dying pines; oviposition and overwintering galleries evident on larger shore pine snags associated with fungal stain; the most common bark beetle collected and identified
Hylurgops porosus	Secondary bark beetle collected from one large dying pine; originally misidentified as *Dendroctonus murrayanae*
Dryocoetes sp.	Most are secondary bark beetles; *D. autographus* and *D. affaber* are known to attack *Pinus* spp. and have been collected in Alaska, including Juneau, AK (Bright 1963)
Trypodendron lineatum	Ambrosia beetle associated with already dead trees
Leptographium sp.	Blue stain fungus associated with beetle galleries; sample collected from dying shore pine with nearest ITS sequence match (92%) to *L. wingfieldii*, considered a virulent pathogen (Solheim et al. 1993); stain present on large dying shore pine and snags up to decay class 3
Heart Rot Fungi	
Porodaedalia pini	The only heart rot fungus detected on live shore pine, often on branch stubs; noted on 14 live and 6 dead shore pine; increment coring live shore pine without conks often revealed hidden white rot
Onnia spp.	Collected from two large shore pine snags in Hoonah (NE Chichagof Is.); *O. tomentosa* or *O. circinata*
Laetiporus sulphureus	Detected on one shore pine snag outside of study plot on Douglas Is., Juneau
Fungi & Insects in Western Gall Rust Galls	
Nectria cinnabarina	Red-orange spherical fruiting bodies observed on 1/5 collected galls; the authors' observations suggest that this pathogen significantly contributes to mortality of galled-branches
Dioryctria spp. (Lepidoptera: Pyralidae)	Most common insect detected in recently-killed galled-branches; larvae create extensive, wide galleries and coarse frass; 1/4 collected galls showed evidence of insect girdling; reared adults could facilitate identification; cryptic species complex (Roe et al. 2011)
Pityophthorus twig beetles (Coleoptera: Curculionidae)	Beetles or larvae occasionally found in gall tissue of recently-killed branches
Pseudips mexicanus bark beetles (Coleoptera: Curculionidae)	Beetles or larvae occasionally found in gall tissue of recently-killed branches

fruiting bodies of *Dothistroma septosporum*. Visually estimated foliage retention averaged 3.3 yrs (SD 1.2 yrs, range 0.3–7.0 yrs), and foliated branch length averaged 8.1 cm (SD 4.0 cm, range 0.8–35.6 cm). Stem decay fungi infrequently fruited on live shore pine, but increment coring often revealed hidden heart rot and excavated cavities were regularly observed on large snags. Secondary and tertiary bark beetles were collected from dying and recently-killed snags; pathogenic blue stain fungi were consistently associated with some bark beetle galleries. Foliar pathogens and insects, bark beetles, heart rot and stain fungi, and secondary WGR gall invaders are summarized in Table 4. None are suspected to be non-native or invasive to southeast Alaska.

Generalized Additive Mixed Models (GAMMs)

Spatial autocorrelation of WGR-associated crown dieback was minimal across the five study area locations, with *Moran's I* falling close to 0 and *Geary's C* close to 1 ($I = 0.058$, $p = 0.10$; $C = 0.92$, $p = 0.06$). Inclusion of spatial dependence in model fitting, however, produced different results for the binary versus proportional dataset. Plot coordinates were not a significant factor in proportion of crown dieback ($p = 0.115$) but were a driving factor in crown dieback occurrence ($p < 0.05$). The lack of significance in the proportional model supports the *Moran's I* and *Geary's C* tests of spatial autocorrelation in dieback.

The likelihood of crown dieback occurring (0/1) was best explained by WGR rating ($p < 0.01$). Of the seven assigned WGR ratings (0–6), moderate severity categories (3–4) and the highest severity category (6) led to the greatest predicted probability of dieback occurring (Table 5). Overall, as WGR rating increased, the odds of crown dieback also increased. The odds of dieback occurring was highest (100%) when the WGR rating was 6, and lowest (62–66%) when the WGR rating was 1 or 2. The high predicted probability associated with no WGR is consistent with dieback observed on uninfected shore pine, which generally affected a small portion of the tree crown (Figure 3). Model retention of random effects indicated unexplained variation in crown dieback presence/absence at the plot and subplot levels, with the majority of this variation occurring at the subplot level (Table 5). This reduced GAMM model better explained dieback occurrence than the full model when compared using AIC ($AIC_{final} = 747.58$, $AIC_{full} = 757.07$) and REML criterion ($Deviance_{final} = 663.41$, $Deviance_{full} = 670.29$).

When crown dieback occurred, the proportion of crown dieback (0.01–1.00) was best explained by the presence of WGR bole galls (BoleGall; $p < 0.01$) and WGR-associated topkill (GallTopkill; $p < 0.01$). The predicted probability of percent dieback was 61% when WGR-associated topkill occurred and 54% when bole galls were present (Table 5). Geographic coordinates and subplot were removed from the final model, and retention of plot as a random effect revealed that unexplained variation was significant at this sampling scale (Table 5). This reduced GAMM model better explained the proportion of crown dieback than the full model when compared using AIC ($AIC_{final} = -1366.35$, $AIC_{full} = -1353.27$) and REML criterion ($Deviance_{final} = 1708.10$, $Deviance_{full} = 1702.20$).

Discussion

The loss of shore pine biomass from the national forest inventory plots in southeast Alaska highlighted significant gaps in our knowledge about this ecologically-valuable, non-commercial tree at the northern extent of its range. Consistent with the recent mortality that FIA detected from 2004–2008, our targeted plot network observed higher mortality among shore pine compared to most other tree species, especially larger shore pine (> 40 cm). Most shore pine snags were in early decay classes (especially decay class 2), suggesting a similar timeframe of tree death compared to the shore pine mortality detected in the FIA plots. Shore pine had a very high incidence of damage. This short-term assessment of our monitoring plots provided insight into the main damage and mortality agents of shore pine across southeast Alaska. All agents found in our plot network are presumed to be native, but some new state records were detected. Cataloging the key pathogens and insects of shore pine provides a reference condition against which to measure

TABLE 5. Generalized Additive Mixed Model (GAMM) selection results showing damage types and random effects that contributed to live shore pine crown dieback for two models: 1) dieback occurrence (0/1, Binomial distribution with logit link function), and 2) proportion of dieback (0.01–1.00, Beta distribution with logit link function). Table shows log odds parameter coefficient estimates for non-smoothed fixed effects, degrees of freedom for smoothed parameters, and criterion for model comparison.

Dieback (0/1)				
Fixed effects	Estimate coefficient	SE	Predicted Probability	
WGRRating				
none (0)*	15.82	1.30		
low (1)	1.91	1.54	66%	
low (2)	1.61	1.34	62%	
moderate (3)	**2.81**	**1.43**	**74%**	
moderate (4)	**7.59**	**1.75**	**88%**	
high (5)	1.98	1.55	66%	
high (6)	211.17	101.00	100%	
Smooth Terms	edf	Residual Df		
NW	3.54	4.06		
Subplot	**19.13**	**136.00**		
Plot	**12.42**	**43.00**		
	AIC	AIC Df	Residual Df	Residual Deviance
$\text{Model}_{\text{full}}$	757.05	43.48	2389.60	670.29
$\text{Model}_{\text{final}}$	747.58	42.09	2390.90	663.41
Proportion of Dieback (0.01 - 1.00)				
Fixed effects	Estimate coefficient	SE	Predicted Probability	
(Intercept)	**0.39**	**1.04**		
BoleGall	**1.17**	**1.06**	**54%**	
GallTopkill	**1.58**	**1.06**	**61%**	
Smooth Terms	edf	Residual Df		
Plot	**31.24**	**45.00**		
	AIC	AIC Df	Residual Df	Residual Deviance
$\text{Model}_{\text{full}}$	-1353.27	49.36	1885.60	1702.20
$\text{Model}_{\text{final}}$	-1366.35	35.80	1896.80	1708.10

* Intercept for binary model

AIC_{full} = s(NW) + BoleGall + WGRRating + GallTopkill + BoleWound_Sev + ExposedRoot_Sev + s(Plot) + s(Subplot), with s() denoting smoothed terms

BOLD = significant to $p < 0.01$

edf = estimated degrees of freedom

change and detect invasive pest introductions (Fierke et al. 2011), and this working list will grow with continued monitoring.

Shore pine occurs in stressful environments that hinder tree growth. It was evident from site observations and tree core analyses that many shore pine trees endure suboptimal growing conditions for centuries. We hypothesize that shore pine succumbs to injury and environmental stress directly over time (e.g., girdling bole wounds, root hypoxia from flooding, complete crown death associated with WGR bole galls) or that stress and injuries compound until weakened large trees become susceptible to secondary bark beetles, some carrying pathogenic stain fungi. Small diameter trees typically lack sufficient phloem thickness to attract adult bark beetles or support their broods (Wood 1982). The steady increase in bole wound incidence and severity with shore pine tree diameter exemplified the accumulation of injury with age.

Trees may be gradually exposed to greater stress on small, finite, marginally-favorable microsites. Alternatively, dynamic hydrologic conditions in forested bogs and fens may cause microsites on which trees have established to become more or less conducive to growth and survival (Zach 1950, Ugolini and Mann 1979). Together, our shore pine network and national inventory plots (FIA) will allow us to track whether in-growth is keeping pace with observed mortality of large trees, which may be hindered by slow tree growth on harsh sites.

Key Drivers of Mortality and Crown Dieback

A long-term goal is to identify drivers of shore pine mortality. A similar incidence of damage from key agents was detected among snags compared to live trees (excluding foliage disease), so no single agent emerged as the consistent and pervasive cause of mortality. Instead, the cause is complex, with interactions between the most common damage agents (WGR, bole wounds, foliage disease), site stressors, and bark beetles. Over time we will learn more about the conditions and agents associated with mortality of permanently-marked live trees. Secondary bark beetles and stain fungi associated with dead and dying trees are clearly important to the mortality process, but multiple agents and conditions weaken large trees before they are susceptible to bark beetle attack.

Although crown dieback is not necessarily linked to long-term tree survival, it provides a measure of live tree stress. Our two dieback models showed that WGR bole galls are key drivers of crown dieback. Other studies have found that the risk of mortality from bole galls increased with the proportion of the stem encircled by galls (Wolken et al. 2006) and that bole galls reduce the ability of stems to conduct water (Wolken et al. 2009). We observed that WGR bole galls frequently caused topkill, thereby reducing photosynthetic capacity and compromising tree form. New leader development sometimes facilitated full recovery of the tree crown, which is why some trees with gall-related topkill did not display crown dieback. However, new leaders were often subsequently galled and girdled under high disease pressure. Bole wounds may contribute to dieback but were not the primary cause. Similarity in crown dieback among trees at the same site indicated that dieback was partially driven by unmeasured variables.

The percentage of live shore pine with WGR bole galls varied widely between plots (9–78%). The patchy distribution of WGR in interior British Columbia and other parts of the west has been linked to wave years, when weather conditions in certain locations are conducive to spread and infection (Peterson 1971, van der Kamp 1988). Mild, wet conditions of Alaska's coastal rainforest are thought to provide consistently conducive infection conditions; we saw no evidence of the wave year phenomenon but did not investigate it directly. The variation in WGR that we observed is likely controlled by unmeasured abiotic factors or tree genetics (Old et al. 1986, Yang et al. 1997) but was partly explained by tree diameter. WGR rating, WGR incidence, and bole gall incidence all increased with tree diameter. Assuming that smaller trees are generally younger, lower disease incidence in smaller trees may be an artifact of the stochasticity of infection and the time lag in symptom expression. Small trees also provide a smaller target for inoculum and have less foliar tissue, through which infection occurs. Like other studies of WGR-associated branch and bole mortality (Byler et al. 1972, Rocchini et al. 1999), we found that secondary agents often girdle galled boles and branches. Unexplained spatial variation in WGR-driven crown dieback may be attributed to different levels of activity of these secondary agents.

Foliage Disease and Climate

Although *Dothistroma septosporum*, cause of Dothistroma needle blight, was not observed causing mortality or branch dieback of trees in our study plots at the time of survey, low to moderate severity disease was common and widespread. The prevalence of low severity disease and the difficulty of distinguishing Dothistroma needle blight from other types of foliar damage when fruiting bodies were absent made the inclusion of foliage disease severity in our crown dieback models untenable. However, Sullivan et al. (2015)

analyzed tree cores collected from this plot network and found a steep and continuing decline in shore pine growth from the 1960s to the present. This growth decline signature was correlated with an increase in diurnal minimum air temperature. One proposed explanation is that warmer temperatures are more favorable for *Dothistroma septosporum*, with negative impacts on tree growth (Sullivan et al. 2015), which is consistent with climate-correlation analyses of historic outbreaks in British Columbia (Welch et al. 2014). There, increases in summer precipitation and temperature have led to unprecedented damage and mortality of lodgepole pine (*Pinus contorta* ssp. *latifolia*) from this disease in managed stands, demonstrating how moderate changes in local climate can significantly affect the severity of native diseases (Woods et al. 2005). Near Glacier Bay National Park, 15 miles north of our northernmost plots, a localized Dothistroma epidemic (2010-2015) has resulted in significant shore pine mortality (FS–R10–FHP 2015, Sullivan et al. 2015). This disease may already be an important factor limiting shore pine needle retention and growth, and its impacts could become more severe under future climate scenarios.

Community Response and Population Dynamics

In most forest types with elevated mortality of one or more dominant tree species, measuring the growth response of associated tree species can help to assess how community composition is expected to change or recover (Oakes et al. 2014). Our research and regional observations indicate that associated trees are not adapted to fill the niche that shore pine occupies in forested bogs and fens (Bisbing et al. 2015). Yellow-cedar often displayed crown dieback and discoloration symptoms of root-freezing injury associated with yellow-cedar decline (Hennon et al. 2012), and a similar percentage of yellow-cedar and shore pine were dead. Sitka spruce, western hemlock, and mountain hemlock were often stunted, chlorotic, and occurred on elevated microsites. Hemlocks attained larger size and regenerated more abundantly in the shaded understory of mixed-conifer forest on the periphery of shore pine-dominated muskegs. In contrast, shore pine was the most prolific conifer in peatland bogs and fens, regenerating and persisting on moderately wet microsites with abundant light and negligible competition.

We detected greater regeneration of shore pine seedlings and saplings in PEM wetlands compared to PSS wetlands, likely due to higher light availability associated with lower tree and shrub cover (Cowardin et al. 1979, Bisbing et al. 2015). Although yellow-cedar regeneration was more abundant overall, this was primarily driven by localized clumps of layering yellow-cedar regeneration compared to the more diffuse regeneration of shore pine. Shore pine regeneration may be more successful outside of treed plots, in adjacent open areas away from the shade of tree crowns. Annual field observations suggest that establishment is probably episodic and linked to water table depth, with establishment occurring during dry springs (S. Bisbing, unpublished data). Continuing to address ecological niche and regeneration questions will facilitate a better understanding of this species' potential response to climate variation and local environment. Evaluating the health of any tree or forest type, or assessing a population's future trajectory, requires knowledge of population age structure and regeneration patterns.

Research Needs and Future Protocol

Several information needs could be addressed through continued and supplemental monitoring of this plot network. There is a need to gain a better understanding of abiotic factors that influence crown dieback, mortality, and population dynamics of biotic damage agents. The climate data available for the study area is too coarse for these purposes and does not incorporate hydrological variables, which we consider influential to tree health and survival in this wet region and ecosystem type. Changes in seasonal and annual temperature and precipitation patterns forecasted in the region are likely to impact populations of forest pathogens and insects (Wolken et al. 2011). Building our knowledge of the relationship between biotic agents, abiotic variables, and tree stress will help us to understand and anticipate potential future change. Our understanding would also benefit from an expansion of this permanent plot system throughout the subspecies full range.

A protocol that distinguishes between root exposure associated with saturated versus dry microsites could be used to qualify or quantify physiological stress to affected trees. Additionally, the key causes of shore pine bole wounding remain to be determined, since many wounds lacked defining characteristics, and wounding was uncommon among associated conifers. Abundant diamond-shaped canker-like wounds at some locations may be caused by the fungus *Atropellis piniphila*, but this fungus has not been reported in Alaska. This canker is usually associated with dense stands of *Pinus contorta* ssp. *latifolia* on dry sites in western North America (Hopkins 1963). Collecting and culturing canker fungi from affected shore pine will help to facilitate identification.

Diverse and Complementary Monitoring

We installed a plot-network to gather forest health information on shore pine trees rather than revisiting inventory plots in order to focus sampling efforts on shore pine-dominated forests that could be reliably accessed for regular monitoring. Inventory monitoring systems can detect many forest resource changes, but detailed studies are necessary to investigate and interpret the extent and causes of tree damage, dieback, mortality, and suspected forest declines. Forest insect and disease data collection is not the primary focus of broad scale inventory networks, and many forms of tree damage are difficult for non-specialists to identify, quantify, or record. Forest inventories are unlikely to detect or assign causes to ephemeral or localized forest health issues (e.g., defoliator outbreaks) that result in limited tree mortality, and are not a means to comprehensively catalogue forest pests. Non-permanent plots or surveys can provide baseline information about common biotic damage agents, but are insufficient for elucidating complex causes of tree mortality or calculating mortality rates. It may take multiple decades of plot measurements and analysis to identify episodic or gradual forest declines for long-lived tree species. In short, diverse and complementary forms of monitoring are needed to evaluate complex forest health issues.

This study exemplifies how permanent inventory plot system can reveal otherwise undetected changes in tree biomass, initiating intensive biological surveys and long-term monitoring. We have gathered valuable information about the current status and key damage agents of shore pine and intend to monitor these plots every five years to continue to address our original research questions and to collect supplemental information on abiotic factors, key damage agents, and shore pine physiology, population structure, and regeneration.

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