

Historic declines in growth portend trembling aspen death during a contemporary leaf miner outbreak in Alaska

MELISSA A. BOYD^{ID},^{1,†} LOGAN T. BERNER^{ID},² ADRIANNA C. FOSTER^{ID},² SCOTT J. GOETZ,²
BRENDAN M. ROGERS,³ XANTHE J. WALKER,¹ AND MICHELLE C. MACK¹

¹Center for Ecosystem Science and Society and Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011 USA

²School of Informatics, Computing, and Cyber Systems, Northern Arizona University, Flagstaff, Arizona 86011 USA

³Woodwell Climate Research Center, Falmouth, Massachusetts 02540-1644 USA

Citation: Boyd, M. A., L. T. Berner, A. C. Foster, S. J. Goetz, B. M. Rogers, X. J. Walker, and M. C. Mack. 2021. Historic declines in growth portend trembling aspen death during a contemporary leaf miner outbreak in Alaska. *Ecosphere* 12(6):e03569. 10.1002/ecs2.3569

Abstract. Climate change-driven droughts and insect outbreaks are becoming more frequent and widespread, increasing forest vulnerability to mortality. By addressing the impacts of climate and insects on tree growth preceding death, we can better understand tree mortality risk under a changing climate. Here, we used tree stature and interannual growth (basal area increment; BAI) to assess processes leading to trembling aspen (*Populus tremuloides*) survival or mortality during an unprecedented leaf miner (*Phyllocnistis populiella*) outbreak in boreal North America. We identified eight sites (22 plots) in the longest running forest monitoring network in Alaska, spanning ~350 km of latitude, that experienced ≥ 0.25 Mg·ha⁻¹·yr⁻¹ aspen mortality during the outbreak. We compared the size and canopy position, growth patterns, and sensitivity to climate and leaf mining of aspen that survived (living; $n = 84$) vs. died (dying; $n = 76$) and linked the normalized difference vegetation index (NDVI) to plot-level aspen growth and stand biomass recruitment, growth, and mortality. Dying aspen were in the subcanopy, smaller in diameter, and after a drought in 1957 had lower growth than living aspen until death. Before the outbreak, growth of all trees was positively influenced by moisture and negatively by temperature, but only living trees maintained this climate response during the outbreak. Leaf mining reduced growth of both groups, exerting at least a two-fold greater impact than climate. The NDVI captured plot-level tree growth and stand biomass growth and mortality, yet it was nearly two times more strongly associated with living than dying tree growth and 12 times more strongly associated with biomass growth than mortality. These differences suggest that NDVI may inadequately detect insect-driven dieback and dispersed mortality of aspen across the boreal biome. Our findings reveal that a historic drought triggered a multi-decadal growth decline that predisposed aspen to mortality during the leaf miner outbreak and that while aspen growth is influenced by moisture and temperature, it is more strongly affected by *P. populiella*. We conclude that as the climate warms and insect outbreaks increase in frequency and magnitude at high latitudes, we should expect to see persistent and greater declines in aspen growth and increases in mortality.

Key words: aspen epidermal leaf miner; boreal forest; climate change; dendroecology; insect outbreaks; normalized difference vegetation index; tree mortality; tree rings; trembling aspen.

Received 2 July 2020; revised 3 December 2020; accepted 17 February 2021; final version received 8 April 2021. Corresponding Editor: Songlin Fei.

Copyright: © 2021 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** melissa.boyd@nau.edu

INTRODUCTION

Extensive and unprecedented tree mortality has been documented worldwide as a result of drought, insect outbreaks, and their interactions with climate change (Mantgem et al. 2009, Allen et al. 2010, 2015, Zhang et al. 2014, Berner et al. 2017). Forest mortality can have widespread and long-lasting impacts on the global carbon cycle (Breshears and Allen 2002, Kurz et al. 2008*a, b*), community dynamics (Anderegg et al. 2013), and ecosystem services (Fischlin et al. 2007). Despite the widespread consequences of forest mortality, our understanding of what drives tree death is lacking, including why some individuals die while others persist. By assessing the influence of abiotic and biotic disturbance on tree growth and death, we can develop a more comprehensive understanding of tree mortality risk and better model forest structure and dynamics under a changing climate.

Differences in growth sensitivity to climate and insects, radial growth patterns, and stature between trees that die vs. survive can provide insight into processes driving tree mortality. Tree-ring measurements are particularly valuable for examining causal agents and processes that lead to tree death on both short (seasonal to annual) and long (decadal to centennial) time-scales (Cailleret et al. 2017, 2019). Climate-driven tree mortality has been linked to a strong and negative radial growth response to drought prior to death (Suarez et al. 2004, Hereş et al. 2012). Conversely, competition (Macalady and Bugmann 2014) or pest attacks (Mamet et al. 2015, Sangüesa-Barreda et al. 2015) can diminish climate sensitivity in dying trees. Gradual growth declines that persist for many years to decades may precede death, highlighting the importance of low-level, accumulated stress (Cailleret et al. 2017) and carbon starvation (McDowell et al. 2008, McDowell and Sevanto 2010, Galiano et al. 2011, McDowell 2011). Abrupt growth reductions before death can occur during more extreme disturbance events (Cailleret et al. 2017), such as a severe drought that results in rapid hydraulic failure (McDowell et al. 2008, Anderegg et al. 2012, Sevanto et al. 2014). Tree size and canopy position are other potential indicators of mortality risk, as tall trees are more susceptible to hydraulic failure (Bennett et al. 2015) whereas

shading and competition increase the vulnerability of small and subcanopy trees to death (Hurst et al. 2011).

Linking satellite-based measurements, such as the normalized difference vegetation index (NDVI), to tree-ring time series and mortality can increase our spatial inference. The NDVI is a proxy for gross primary productivity (Tucker 1979, Goetz and Prince 1999) that has been associated with tree radial growth (Berner et al. 2011, Vicente-Serrano et al. 2016, Boyd et al. 2019) and mortality (Breshears et al. 2005, Ogaya et al. 2015). However, NDVI does not always capture interannual tree growth (Brehaut and Danby 2018), and complexities in stand structure make it difficult to interpret the NDVI signal (Berner et al. 2011, Brehaut and Danby 2018, Loranty et al. 2018). Assessing the relative influence of living and dying tree growth and stand processes, such as growth and death, on NDVI will improve our ability to interpret the NDVI signal and utilize it to detect climate change impacts on forests over large spatial scales.

High-latitude boreal forests are ideal for addressing tree vulnerability to insect- and climate-driven mortality because both temperatures (AMAP 2017, IPCC 2018) and the occurrence, severity, and extent of insect outbreaks (Bale et al. 2002, Bentz et al. 2010, Seidl et al. 2017) are increasing in this region. In boreal North America, trembling aspen (*Populus tremuloides* Michx.; henceforth “aspen”) has experienced widespread and persistent growth declines in association with moisture stress and insect outbreaks (Hogg et al. 2002, Cahoon et al. 2018, Chen et al. 2018). This includes Interior Alaska, where a damaging outbreak of the aspen epidermal leaf miner (*Phyllocnistis populiella* Cham.) has affected aspen since the late 1990s (USDA FS 2020, Yukon Department of Energy, Mines, and Resources 2020). *P. populiella* is an insect herbivore that disrupts leaf photosynthesis, stomatal conductance, and water relations (Wagner et al. 2008, 2020), decreases tree radial growth (Cahoon et al. 2018, Boyd et al. 2019), and contributed to recent aspen mortality (Trugman et al. 2018). As the climate warms, models predict a shift toward deciduous dominance in boreal Alaska (Mann et al. 2012, Foster et al. 2019, Mekonnen et al. 2019), yet have not accounted for insect pests. To improve these

predictions and determine the fate of aspen under a changing climate, it is foundational to understand aspen mortality risk during pest outbreaks and the compounding effects of climate and insects on aspen growth and death.

The overarching goal of our study was to determine what processes led to aspen mortality during the *P. populiella* outbreak (1997–2013). Our retrospective approach combined tree radial growth and forest inventory measurements to compare attributes of aspen that survived (living) and aspen that died (dying). We considered how (1) size and canopy position, (2) pre-outbreak growth patterns and growth response to climate, and (3) outbreak growth patterns and growth response to *P. populiella*, climate, and their interaction differed between living and dying aspen. Because NDVI is widely used as an index of gross primary productivity, we assessed whether ecologically important growth patterns of living and dying trees, as well as stand processes of recruitment, growth, and mortality, were detected by Landsat NDVI.

METHODS

Site description

In the summer of 2016, we sampled eight long-term inventory sites in Interior Alaska that are a part of the Cooperative Alaska Forest Inventory (CAFI; Malone et al. 2009). The complete CAFI archive currently contains 204 sites that were established in Interior and Southcentral Alaska and the Kenai Peninsula as early as 1994. In general, each CAFI site contains three plots arranged in a triangle, one at each corner, spaced 30–63 m apart, with each plot covering 405 m². Plots are re-sampled every five years following standard forest inventory procedures (Curtis 1983). We chose to sample all CAFI sites that were both aspen dominated (>50% aspen stems) and had aspen mortality recorded between one or more sampling periods (1.24–39.3 Mg/ha site biomass mortality every five years). The eight sites that met this criterion were established between 1994 and 2000, and the final census year ranged from 2012 to 2015. Sites were in central Alaska extending from the Copper River Valley north to the Tanana Valley (Appendix S1: Table S1). All the plots sampled also experienced aspen mortality between one or more sampling periods (see

Appendix S1: Fig. S1 for site and plot biomass mortality). Tree data from the CAFI database were used to quantify aboveground aspen biomass at each plot and measurement period for trees with a minimum diameter at breast height (DBH; at 1.3 m) of 3.8 cm using allometric relationships from Alexander et al. (2012) if $DBH \geq 4.1$ cm and Ung et al. (2008). Aspen biomass mortality was determined by subtracting live tree biomass in the current year of measurement from the previous year for all years that a plot was measured. Snags that had been previously tagged and died from natural causes were recorded as dead trees. Site-level aspen biomass mortality was determined by summing biomass mortality across the plots associated with each site.

Field and laboratory methods

At each site, we obtained two increment cores from 12 mature live aspen and stem disks from 12 mature, standing dead aspen at the standard height of 1.3 m. We sampled one live and one dead tree closest to each plot corner, outside the CAFI sampling area. One site was composed of a single plot, so four live and four dead trees were sampled at each corner of this plot (Appendix S1: Table S1). We recorded the DBH of each tree and their relative position in the canopy (upper = dominant/codominant or lower = intermediate/suppressed). In total, we sampled 192 aspen for tree-ring analysis (96 live and 96 dead). In the laboratory, tree cores and disks were air-dried and sanded with increasingly finer sandpaper up to 1500 grit to make ring boundaries visible. Annual ring widths were measured on live trees (two cores per tree) and dead trees (two radii per stem disk) at a resolution of 0.001 mm in WinDendro software version 2012b (Regent Instruments 2012). We crossdated live trees visually and statistically at each site using COFECHA version 6.06 (Grissino-Mayer 2001). Dead tree-ring width measurements were crossdated against live tree chronologies at the same site in COFECHA to determine the last year dead trees put on a full growth ring and the year of death. Trees that we were unable to cross-date were excluded from all analyses (12 live and 7 dead; Appendix S1: Table S2). If a dead tree's last year of full growth preceded the *P. populiella* outbreak (before 1997; see *Aerial surveys of insect*

activity), it was also excluded because we were interested in aspen vulnerability to mortality during the *P. populiella* outbreak (13 dead trees excluded; Appendix S1: Fig. S2).

We averaged raw ring widths from the two cores or radii measured for every tree and used these measurements to calculate annual basal area increment (BAI; mm² wood/yr) in the package dplR (Bunn 2008) at the tree level. This and all other statistical analyses were performed in R version 3.5.2 (R Development Core Team 2018). We chose to use BAI for our analyses because it is a more relevant biological measure of growth than tree-ring width and reduces tree size- and age-related effects while maintaining the high- and low-frequency signals in tree-ring chronologies (Biondi and Qeadan 2008). Since we were interested in comparing growth patterns of living and dying trees, we used BAI because it preserves long-term trends in tree growth (Duchesne et al. 2002, 2003), such as decreases in growth that are indicative of declining tree condition (Leblanc 1990). Across all sites, we had a total of 84 aspen that survived and 76 that died during the *P. populiella* outbreak. The year that live and dead trees established was not statistically different (Appendix S1: Table S3). The last year of full growth for dead trees was 2013 (Appendix S1: Figs. S2, S3), so analyses that include tree BAI measurements were performed up until this year. We truncated time series to 1946 to have the greatest overlap of complete tree-ring chronologies (Bunn 2008). Trees sampled for radial growth analyses that were alive and dead will hereafter be referred to as living and dying, respectively.

Climate data

Downscaled climate data were obtained from ClimateNA version 5.20 (Wang et al. 2016) of monthly maximum temperature, minimum temperature, average temperature, and total precipitation corresponding to each of our study sites from 1945 to 2013. For each month from 1945 to 2013, we computed a climate moisture index (CMI; cm/month), calculated as precipitation minus potential evapotranspiration, using the simplified Penman-Monteith method by Hogg (1997). Negative values of CMI indicate dry conditions where evaporative demand exceeds precipitation and positive values indicate wetter conditions (Hogg

1994, 1997). We summed monthly CMI over different seasonal periods: the growing season (GS; May–September), spring (February–April), fall and winter (previous October–January), and the previous growing season (PGS; previous May–previous September). The same seasonal metrics were estimated for precipitation and average temperature by calculating a sum for precipitation and an average for temperature.

Aerial survey estimates of insect activity

We used annual estimates of the area of Alaska infested by *P. populiella* (ha/yr) from the USDA Forest Service aerial surveys as the measure of *P. populiella* mining from 1997 to 2013 (USDA FS 2020). High densities of *P. populiella* were first observed near Fairbanks, Alaska, in 1996 (R. Werner, unpublished data, <http://www.lter.uaf.edu>), but *P. populiella* activity has been estimated by the aerial surveys since 1997. We chose to use the aerial measurements (ha/yr infested by *P. populiella*) as the metric of infestation because (1) the surveys provide the longest statewide time series of annual *P. populiella* activity, (2) our sites are a part of the survey's routine flight path, (3) the survey measurements (ha/yr infested by *P. populiella*) have been related to aspen radial growth (Cahoon et al. 2018), and (4) CAFI database measurements of *P. populiella* presence are only available for a few years. Additionally, site-level *P. populiella* leaf mining (average % site mining) from aspen stands near Fairbanks, Alaska (Boyd et al. 2019), was highly correlated with the aerial estimates of *P. populiella* activity from 2004 to 2015 ($r_s = 0.81$, $P < 0.001$; data not shown). This suggests that the aerial surveys, although spatially coarse, are correctly detecting *P. populiella* leaf mining. Henceforth, “leaf mining” or “mining” refers only to *P. populiella* and no other insect pests. We also used USDA Forest Service reports to determine when outbreaks of other aspen pests occurred in Alaska, particularly the large aspen tortrix (*Choristoneura conflictana* Wlkr.), an aspen defoliator that has had a significant presence in Interior Alaska. These reports are available from 1950 to present, although a few measurement years are absent (USDA FS 2020).

Landsat NDVI data

We estimated annual maximum summer NDVI (NDVI_{max}) during the *P. populiella*

outbreak (1997–2013) for each plot using surface reflectance measured by 30-m resolution Landsat satellites. We focused only on the outbreak period because Landsat observations are not widely available in Interior Alaska before the late 1990s. For this analysis, we used the United States Geological Survey's Landsat Collection 1 dataset that includes atmospheric and terrain corrections based on the LEDAPS (Landsats 5 and 7; Masek et al. 2006) and LaSRC (Landsat 8; Vermote et al. 2016) processing algorithms. For each plot, we used Google Earth Engine (Gorelick et al. 2017) to extract all surface reflectance data that were acquired from early May through September (Julian days 121–273) by Landsats 5, 7, and 8. Given the need for high-quality, clear-sky observations, we filtered out observations affected by clouds, cloud shadows, snow, and water using flags from the CFmask (Zhu et al. 2015) and also removed observations from scenes acquired during high cloud cover (>80%) or solar zenith angle (>60°) conditions.

We computed NDVI using each clear-sky observation, cross-calibrated NDVI among sensors and then estimated annual NDVI_{max} using a new phenology-based modeling approach (Berner et al. 2020). To account for systematic differences in NDVI among Landsat sensors, we linearly adjusted Landsats 5 and 8 to better match Landsat 7 using published cross-calibration coefficients (Ju and Masek 2016, Roy et al. 2016). We then estimated annual NDVI_{max} using a new approach that helps alleviate issues due to the irregular timing and often limited availability of Landsat observations during each growing season at high latitudes (Berner et al. 2020). This approach involves first determining land surface phenology during the growing season at each plot using flexible cubic splines iteratively fit through NDVI data pooled across multiple years. Land surface phenology is repeatedly evaluated at each site using a moving window centered on each growing season (here ± 3 yr), thereby capturing potential phenological changes due to disturbance or succession. Information on land surface phenology is then used to determine the likely deviation of each observation from peak summer conditions, thereby making it possible to estimate annual NDVI_{max} (Berner et al. 2020). Aspects of this approach are similar to a previous approach that was

developed to assess interannual variability in growing season timing across forests in the eastern United States using Landsat (Melaas et al. 2013, 2016).

Statistical methods

Our analyses were performed using individual tree measurements and individual tree BAI chronologies unless otherwise specified. In traditional dendrochronology, site-level time series are built by averaging tree-ring width measurements from multiple individuals (Fritts 1976, Cook and Kairiukstis 1990). While this methodology is extremely useful for determining the mean climate signal, it results in the loss of individual tree response to other environmental stressors. Performing analyses using individual tree chronologies has become a more prevalent approach in tree-ring studies (e.g., Galván et al. 2014, Walker and Johnstone 2014, Buras et al. 2016, Jochner et al. 2017, Rohner et al. 2018) and conserves tree-specific variability in radial growth and sensitivity to biotic and abiotic stress.

For the majority of our analyses, we fit hierarchical linear mixed effects models (LMMs) using the package nlme (Pinheiro et al. 2018). For all LMMs, we (1) visually inspected residual vs. fitted values for all explanatory variables and each grouping level of the random effects to verify that the assumptions of homogeneity of variance and normality were met (Zuur et al. 2009), (2) tested for collinearity of covariates when there was more than one predictor using variance inflation factors ($\text{VIF} < 5$; Sheather 2009) in the car package (Fox and Weisberg 2019), (3) determined the significance of fixed effects using maximum likelihood ratio tests comparing the full model to a reduced model and confirmed their importance with small sample corrected Akaike information criterion (AIC_c ; Zuur et al. 2009), (4) performed model reduction only of interaction terms (Bolker et al. 2009) so that we could address the relative influence of non-interactive fixed effects, (5) and calculated optimal model coefficients using restricted maximum likelihood estimation (Zuur et al. 2009).

Tree size and canopy position.—To determine whether living and dying trees that were sampled for tree-ring analysis differed in size, we fit a LMM with the response variable of tree DBH at the onset of the *P. populiella* outbreak (1997) and

the fixed effect of tree status (living/dying). The random intercepts of site and plot nested in site were included to account for spatial non-independence of plots within a site and trees within a plot, and DBH was natural-log-transformed to ensure normality. We chose to use DBH in 1997 instead of the year of sampling (2016) so that we were comparing living and dying trees of approximately the same age. To determine tree DBH in 1997, we summed raw ring widths for each tree from 1998 to 2015 and subtracted this from their DBH in 2016. To differentiate between living and dying tree canopy position, we fit a hierarchical mixed effects logistic regression using the lme4 package (Bates et al. 2015) with canopy position (upper/lower) as the response variable, tree status as a fixed effect (living/dying), and the same random effects as above. This model met the assumptions of logistic regression (Stoltzfus 2011). The significance of the fixed effect was determined as described for LMMs.

Pre-outbreak growth patterns and growth response to climate.—To assess whether living and dying tree growth differed prior to the *P. populiella* outbreak, we fit 51 LMMs, one for each year from 1946 to 1996, with BAI of all trees as the response variable, the fixed effect of tree status (living/dying), and random intercepts of site and plot nested in site. BAI was natural-log-transformed to ensure normality for these and all analyses in which it was included. Prior to this transformation, we added one to each annual BAI measurement because some trees had missing rings and therefore radial growth values of zero, which cannot be natural-log-transformed. *P*-values were corrected using the false discovery rate because we had multiple response variables with the same experimental units (Benjamini and Hochberg 1995). Since our objective was to evaluate differences in living and dying tree growth patterns before the *P. populiella* outbreak, we also assessed trends in BAI from 1946 to 1957 and 1958 to 1996 by fitting a LMM for each time period that included living or dying tree BAI as the response variable, the fixed effect of year, and random intercepts of site, plot nested in site, and tree nested in plot. Tree was included as a random intercept to account for the repeated measures of BAI over the same individual. We chose to assess BAI trends during these time periods

because the preceding analysis revealed a large difference in living and dying tree BAI after 1957 that persisted until the *P. populiella* outbreak (see *Pre-outbreak growth patterns and growth response to climate* in Results).

To evaluate whether living and dying tree growth response to climate differed before the *P. populiella* outbreak, we fit LMMs for three 12-year time periods (1946–1957, 1971–1982, and 1983–1994) with living or dying tree BAI as the response variable, the fixed effects of CMI and temperature in the GS, spring, fall and winter, and PGS, and random intercepts of site, plot nested in site, and tree nested in plot. Models were fit in these time periods to compare the impacts of climate on living and dying trees when their BAI overlapped (1946–1957) and when their BAI differed (1971–1982 and 1983–1994) as revealed by our prior analysis (see *Pre-outbreak growth patterns and growth response to climate* in Results). Climate variables were scaled and centered to compare the effect size of CMI and temperature. We chose not to assess the climate–growth response from 1958 to 1970 because of the severity of the large aspen tortrix outbreak in the 1960s (Torgersen and Beckwith 1974, USDA FS 2020) that could confound the climate signal (Trotter et al. 2002, Rolland and Lempérière 2004, Sangüesa-Barreda et al. 2015). The impact of previous year climate on BAI was tested because tree growth in the current year can be significantly influenced by climate in the preceding year (Lebourgeois et al. 2004, Hart et al. 2010, Huang et al. 2010). Precipitation was not included in these models because seasonal CMI and precipitation were highly collinear (Appendix S1: Table S4). We chose to use CMI instead of precipitation because of the strong relationships it has shown with aspen radial growth (Hogg et al. 2002, 2008).

Outbreak growth patterns and growth response to P. populiella, climate, and their interaction.—To assess whether living and dying tree growth differed during the *P. populiella* outbreak (1997–2013), we fit a LMM with BAI of all trees throughout the outbreak period as the response variable, the fixed effect of tree status (living/dying), and random intercepts of site, plot nested in site, and tree nested in plot. To further compare patterns in living and dying tree growth during *P. populiella* infestation, we evaluated BAI trends

by fitting LMMs with living or dying tree BAI from 1997 to 2013 as the response variable, the fixed effect of year, and the same random effects as above.

To evaluate whether living and dying tree growth response to climate, leaf mining, and their interaction differed, we fit LMMs with living or dying tree BAI as the response variable, the fixed effects of PGS CMI, GS temperature, previous year leaf mining, the interaction between PGS CMI and previous year leaf mining, and the interaction between GS temperature and previous year leaf mining, and random intercepts of site, plot nested in site, and tree nested in plot. Covariates were scaled and centered to improve interpretability of interaction terms or to compare the effect size of climate and leaf mining. For testing the influence of the interaction between climate and *P. populiella* on tree BAI, we used previous year leaf mining because it had a greater impact than current year leaf mining on both living and dying tree BAI from 1997 to 2013 (Appendix S1: Table S5). We included PGS CMI and GS temperature as the climate parameters in these models because they strongly influenced living and dying tree BAI before the *P. populiella* outbreak (see *Pre-outbreak growth patterns and growth response to climate* in Results).

Normalized difference vegetation index.—To determine whether NDVI_{max} captured growth patterns of living and dying trees during the *P. populiella* outbreak (1997–2013), we fit a LMM with NDVI_{max} as the response variable, the fixed effects of mean plot-level living tree BAI and mean plot-level dying tree BAI, and random intercepts of site and plot nested in site. For this analysis, we used plot-averaged living and dying tree BAI and not individual tree BAI measurements because NDVI_{max} was calculated at the plot level given the 30-m pixel size of Landsat. The sample size of dying trees decreased over time, and we were not using tree as a random effect. Thus, we also performed this analysis by truncating individual tree BAI chronologies to maximize complete tree BAI time series that were used to calculate plot-averaged dying tree BAI (Appendix S1: Fig. S3). Truncating the time series resulted in a weaker relationship between mean plot-level dying tree BAI and NDVI_{max} (Appendix S1: Table S6) but did not change the

interpretation of our results, so we present findings across the complete outbreak period. As NDVI can vary more rapidly than tree growth (Bhuyan et al. 2017, Vicente-Serrano et al. 2020), we tested for the effect of positive one-year lags of mean plot-level living tree BAI and mean plot-level dying tree BAI on NDVI_{max} by including them as covariates in the above model. The one-year lags did not substantially improve our model (analysis not shown).

To determine what stand processes were captured by NDVI_{max}, we fit a LMM with NDVI_{max} as the response variable, the fixed effects of plot-level aspen biomass recruitment, aspen biomass growth, and aspen biomass mortality, and random intercepts of site and plot nested in site. Aboveground plot-level aspen biomass recruitment and growth were calculated using tree data from the CAFI database at each plot and measurement period using the allometric relationships previously described. Recruitment represents the biomass of trees that passed the DBH threshold (3.8 cm) between measurement periods. Aboveground plot-level aspen biomass mortality was calculated using tree data from the CAFI database as described in *Site description in Methods*.

RESULTS

Tree mortality, climate, leaf mining, and NDVI

The majority of dead aspen sampled for radial growth analyses died during the height of the recent *P. populiella* outbreak (2001–2010; Fig. 1a; Appendix S1: Fig. S2), but there was not a particular year associated with high aspen mortality (Appendix S1: Fig. S2). The mean age of tree death was 83 yr (± 14 SD), and in 2016, the mean age of living trees was 94 yr (± 15 SD). Prior to *P. populiella* infestation (1946–1996), GS CMI across sites was lowest in 1957 (-23.0 ± 2.88 cm/season; mean GS CMI $\pm$ SD; Fig. 1b) and followed by a large reduction in BAI of living and dying trees in 1958 (173 ± 130 and 121 ± 93.1 mm², respectively; mean BAI $\pm$ SD; Fig. 1a). There was a noticeable decline in living and dying tree BAI in 1968 and 1969 (Fig. 1a), which coincided with a negative spike in GS CMI (Fig. 1b) and an outbreak of the large aspen tortrix (Torgersen and Beckwith 1974, USDA FS 2020). During *P. populiella* infestation (1997–

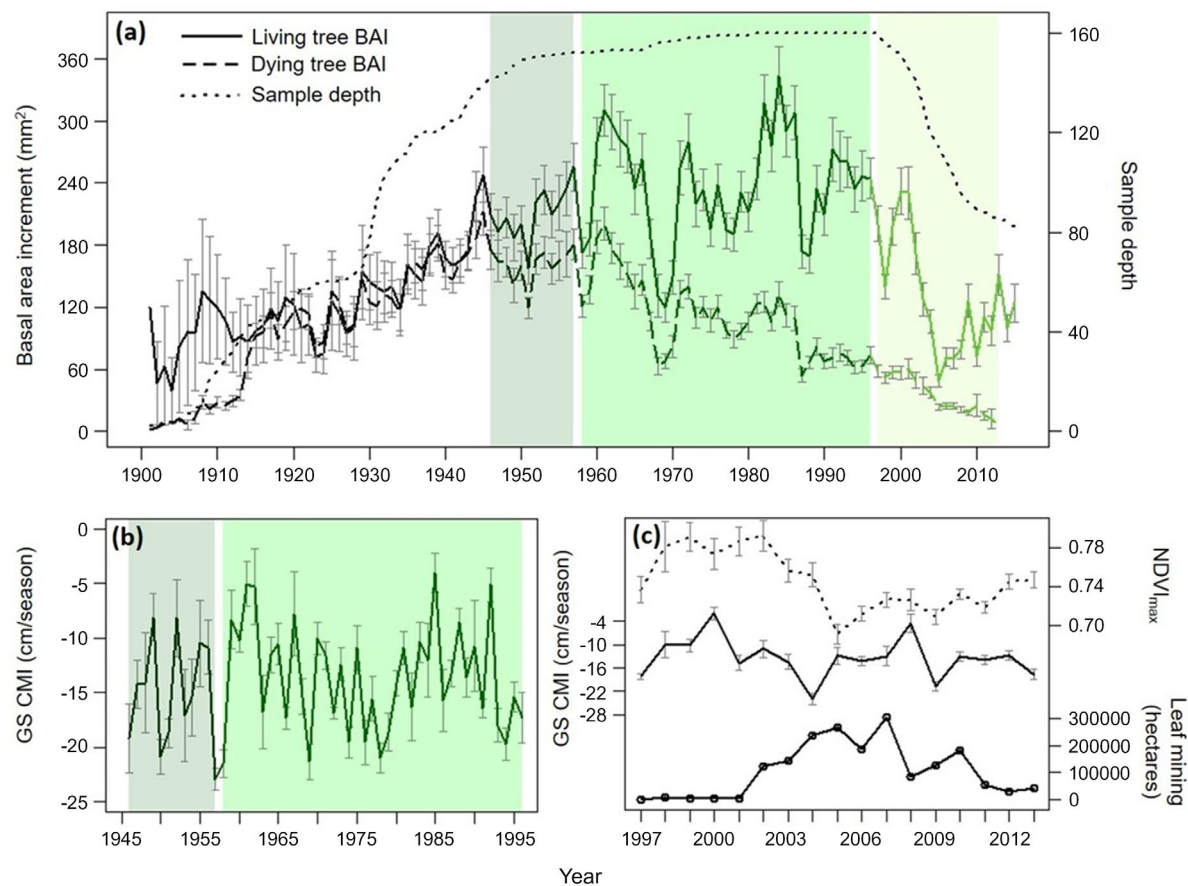


Fig. 1. (a) Basal area increment (BAI; mean $\pm$ SE) of living trees (solid line) from establishment to 2015 and dying trees (dashed line) from establishment to 2013 and the number of sampled trees (sample depth; dotted line); (b) growing season climate moisture index (GS CMI; mean $\pm$ SE) prior to the *Phyllocnistis populiella* outbreak (1945–1996); and (c) GS CMI (mean $\pm$ SE), the maximum summer normalized difference vegetation index (NDVI_{max}; mean $\pm$ SE), and leaf mining (hectares of Alaska infested) during the *P. populiella* outbreak (1997–2013). Tree BAI measurements prior to 1946 were not used for analyses (unshaded area in (a); see Methods). In (a) and (b), dark green shading denotes when living and dying tree BAI overlapped (Appendix S1: Table S10), intermediate green shading denotes when living tree BAI was greater than dying tree BAI (Appendix S1: Table S10), and in (a), light green shading denotes the *P. populiella* outbreak. See Appendix S1: Fig. S4 for growing season (GS) temperature time series.

2013), living tree BAI was the lowest in 2005 (48.9 ± 54.1 mm²; mean BAI $\pm$ SD; Fig. 1a) and preceded by the driest year across the time period examined (1946–2013; -24.1 ± 3.94 cm/season; mean GS CMI $\pm$ SD in 2004; Fig. 1c). In 2005, the highest GS temperature during the *P. populiella* outbreak was recorded (12.4 ± 0.43 °C/season; mean GS temperature $\pm$ SD; Appendix S1: Fig. S4), over 260,000 hectares of Alaska were infested by *P. populiella*

(Fig. 1c), and NDVI_{max} was at its lowest point (0.69 ± 0.06 ; mean NDVI_{max} $\pm$ SD; Fig. 1c).

Tree size and canopy position

Dying trees were smaller in diameter than living trees (Fig. 2a; Appendix S1: Table S7) and were more likely to be lower in the canopy strata than living trees (Fig. 2b; Appendix S1: Tables S8, S9). Similarly, dead trees from the CAFI network were smaller in diameter and more likely

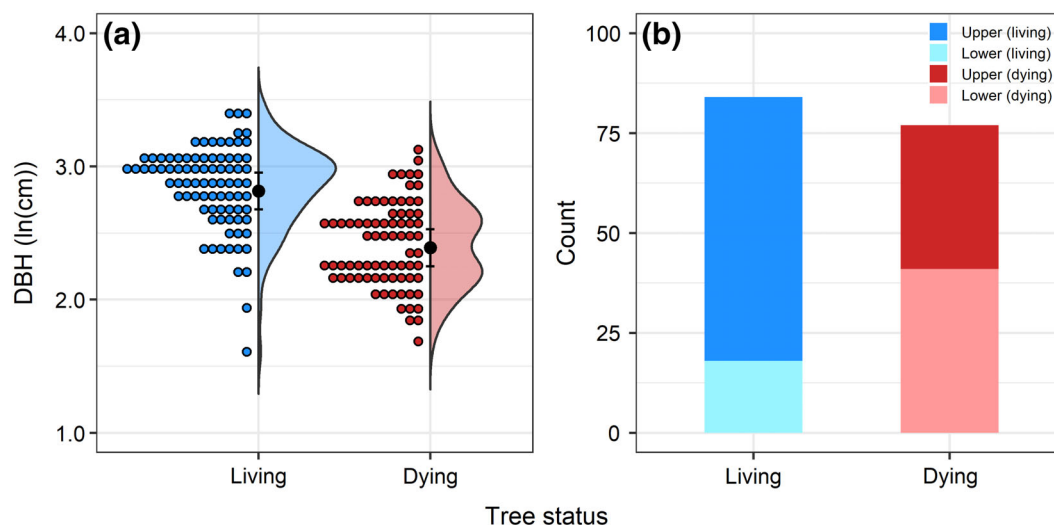


Fig. 2. (a) Diameter at breast height (DBH) and (b) canopy position (upper: dominant/codominant, lower: intermediate/suppressed) of living and dying aspen. In (a), black points and error bars represent mean ($\pm$ SE) based on a hierarchical linear mixed effects model fit (Appendix S1: Table S7), red/blue points represent the DBH of each sampled tree, and (b) shows the total count of living and dying aspen in each canopy position (Appendix S1: Tables S8, S9).

to be in a lower canopy position than live trees from the CAFI network (Appendix S2).

Pre-outbreak growth patterns and growth response to climate

From 1946 to 1957, living and dying tree BAI was similar (Fig. 1a; Appendix S1: Table S10) and BAI of both groups increased (Fig. 1a; Appendix S1: Table S11). After 1957 up to the leaf miner outbreak (1958–1996), living tree BAI was consistently greater than dying BAI (Fig. 1a; Appendix S1: Table S10) and dying tree BAI decreased whereas living tree BAI continued to increase (Fig. 1a; Appendix S1: Table S11). The greatest difference in living and dying tree BAI prior to *P. populiella* infestation was in 1996 (Fig. 1a; Appendix S1: Table S10).

During the time periods examined preceding leaf miner infestation (1946–1957, 1971–1982, 1983–1994), living and dying tree growth response to climate was similar. Notably, for both groups, PGS CMI consistently had a strong and positive effect on BAI, and sensitivity to PGS CMI was strongest after 1957. After 1957, the magnitude and direction of living and dying tree response to GS temperature shifted (Fig. 3; Appendix S1: Tables S12, S13). Both groups

responded positively to GS temperature from 1946 to 1957 but negatively and more strongly to GS temperature initially preceding the *P. populiella* outbreak (1983–1994; Fig. 3; Appendix S1: Tables S12, S13), which coincided with a rise in GS temperature (Appendix S1: Table S14). Despite these similarities, living and dying tree response to climate slightly differed immediately preceding the *P. populiella* outbreak (1983–1994). Specifically, during this time period dying tree BAI was most strongly and negatively influenced by GS temperature whereas living tree BAI was most strongly and positively influenced by PGS CMI (Fig. 3; Appendix S1: Tables S12, S13).

Outbreak growth patterns and growth response to P. populiella, climate, and their interaction

During the *P. populiella* outbreak, living tree BAI was significantly greater than dying tree BAI (Fig. 1a; Appendix S1: Table S15), but BAI of both groups declined (Fig. 1a; Appendix S1: Table S11). The interactions between previous year leaf mining and PGS CMI and previous year leaf mining and GS temperature were not statistically significant predictors of living or dying tree BAI (Appendix S1: Table S17). In the presence of leaf miner, living tree BAI continued to be

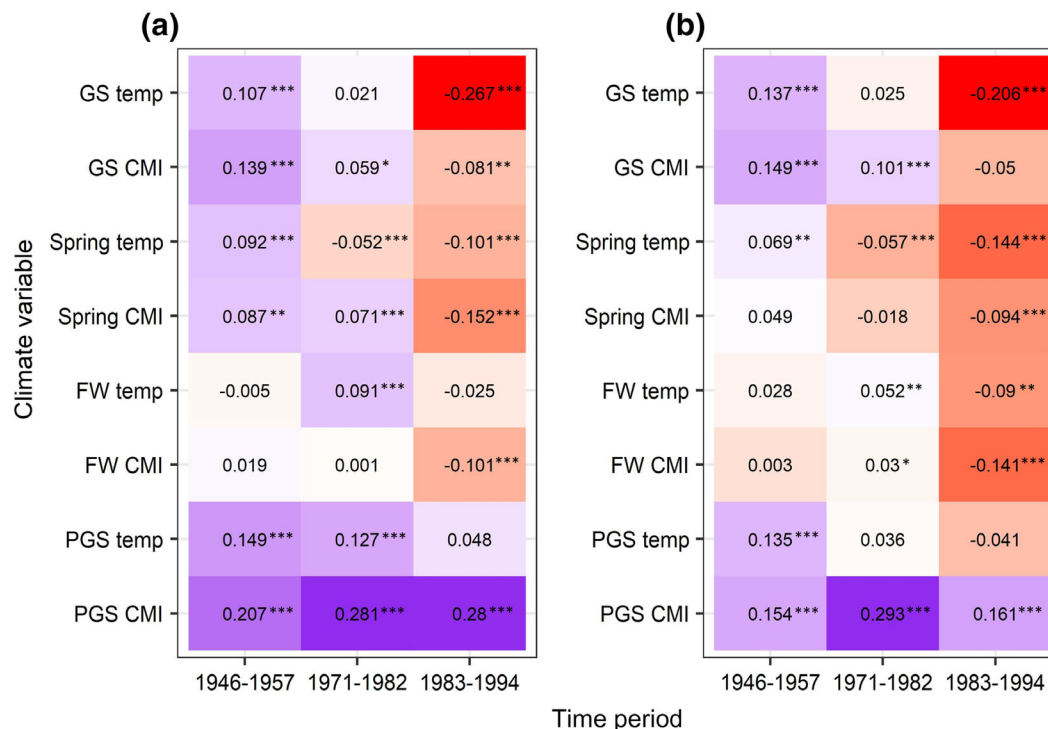


Fig. 3. Effects of growing season (GS), spring, fall and winter (FW), and previous growing season (PGS) temperature and climate moisture index (CMI) on (a) living tree basal area increment (BAI) and (b) dying tree BAI when growth of both groups was similar (1946–1957) and different (1971–1982 and 1983–1994). Values in boxes are regression coefficients from hierarchical linear mixed effects models. Climate variables were scaled and centered for analyses to compare the effect size among covariates. Purple text indicates a positive effect and red text a negative effect, gradient of shading indicates the strength of the relationship, and asterisks denote level of significance (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). For model outputs, see Appendix S1: Tables S12, S13 for living and dying trees, respectively.

positively influenced by PGS CMI (Fig. 4a; Appendix S1: Table S17) and negatively by GS temperature (Fig. 4b; Appendix S1: Table S17), whereas dying tree BAI was not influenced climate (Appendix S1: Table S17). Living tree BAI was negatively influenced by previous year leaf mining, and this negative effect was two times greater than the effect of moisture availability or temperature (Fig. 4c; Appendix S1: Table S17). Previous year leaf mining had a significant and negative impact on dying tree BAI (Fig. 4d; Appendix S1: Table S17).

Normalized difference vegetation index

NDVI_{max} was positively related to annual variation in plot-averaged living and dying tree BAI. This association was primarily driven by living trees because the relationship between NDVI_{max}

and mean plot-level living tree BAI was almost twofold greater than between NDVI_{max} and mean plot-level dying tree BAI (Fig. 5; Appendix S1: Table S18). NDVI_{max} captured inventory measurements of plot-level aspen biomass growth and mortality but not recruitment, exhibiting a positive association with growth and a negative association with mortality. The positive association between NDVI_{max} and biomass growth was 12 times stronger than the negative association between NDVI_{max} and biomass mortality (Fig. 6; Appendix S1: Table S19).

DISCUSSION

As the frequency and severity of drought and insect outbreaks increase at high latitudes (Bale et al. 2002, Bentz et al. 2010, AMAP 2017, Seidl

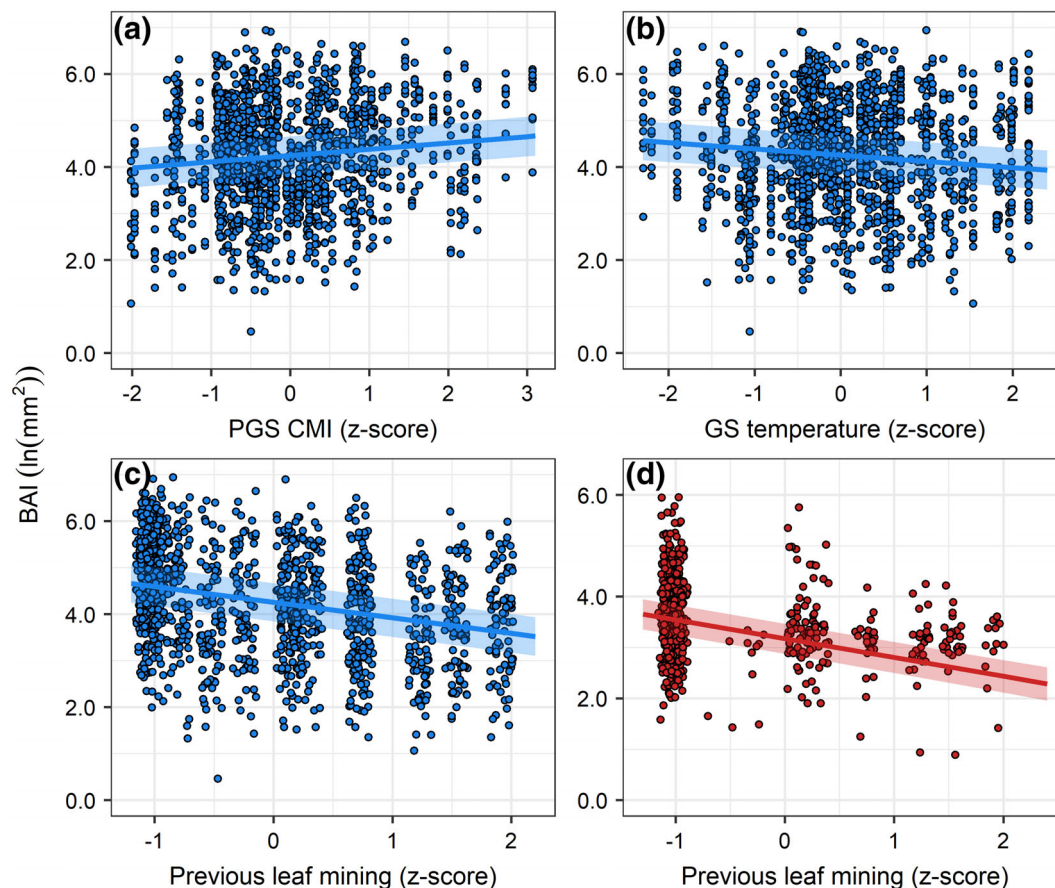


Fig. 4. Relationships from 1997 to 2013 between basal area increment (BAI) of living trees (blue points and lines) and (a) previous growing season climate moisture index (PGS CMI), (b) growing season (GS) temperature and (c) previous year *Phyllocnistis populiella* leaf mining, and (d) BAI of dying trees (red points and line) and previous year leaf mining. Lines represent effects based on hierarchical linear mixed effects models, and shading around lines indicates the 95% confidence interval. Points are the raw data, and each point is a year within a tree. Points are jittered in (c) and (d) to better see the data at a width of 0.1. Covariates were scaled and centered to compare the effect size of climate and leaf mining and improve model interpretability. All plotted effects are significant (Appendix S1: Table S17). Interactions between climate and leaf mining were not important predictors of living or dying tree BAI (Appendix S1: Table S16).

et al. 2017, IPCC 2018), identifying processes and disturbance events that lead to tree death is important for determining the mortality risk of boreal tree species. Our findings reveal that dying aspen were in the subcanopy and their growth was lower than that of living aspen after a drought in 1957. Subsequent insect outbreaks and adverse climate conditions further decreased dying aspen growth, culminating in tree death during the *P. populiella* outbreak. During the outbreak, only living aspen growth was positively

influenced by moisture and negatively by temperature, yet the negative effect of leaf mining was much greater than the effect climate on both living and dying aspen growth. Although NDVI captured plot-level tree growth and stand biomass growth and mortality, it was more strongly linked to plot-level living than dying aspen growth, and to stand biomass growth than mortality. These results, in combination with the subcanopy position of dying trees, suggest that NDVI may be limited in its ability to detect

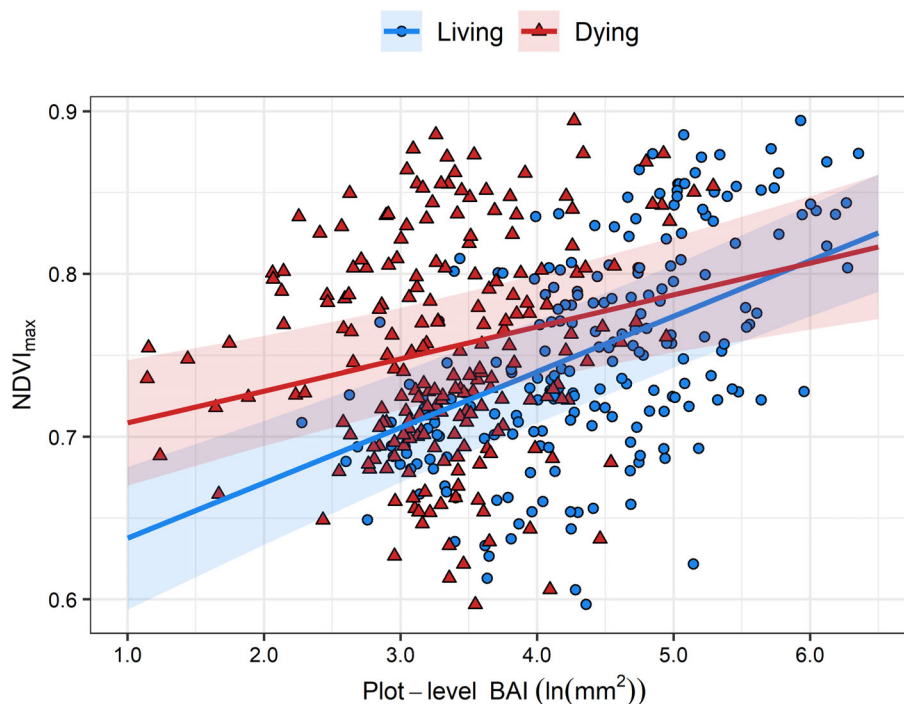


Fig. 5. Relationships from 1997 to 2013 between maximum summer normalized difference vegetation index ($NDVI_{max}$) and mean plot-level living tree basal area increment (BAI; blue circles and line) and mean plot-level dying tree BAI (red triangles and line). Lines represent effects based on a hierarchical linear mixed effects model, and shading around lines indicates the 95% confidence interval. Points are the raw data, and each point is a year within a plot. All plotted effects are significant (Appendix S1: Table S18).

insect-driven diffuse mortality and dieback of aspen in boreal ecosystems, especially when mortality is linked to canopy position. Overall, our findings show that a historic drought prompted a growth decline in aspen that increased their mortality risk and that *P. populiella* was the dominant driver of aspen growth and ultimately death. Thus, with continued climate warming and associated increases in insect outbreaks, aspen mortality may become increasingly prevalent in the boreal biome.

Tree size, canopy position, and pre-outbreak growth patterns

We found that dying aspen were lower in the canopy strata, suggesting that low light levels may have contributed to aspen mortality risk. Aspen is a light-demanding species (Perala 1990) that experiences substantial declines in photosynthesis, growth, and production of defensive compounds under low light (Calder et al. 2011).

This includes the production of defensive compounds, such as phenolic glycosides (Calder et al. 2011), that decrease *P. populiella* mining damage (Young et al. 2010). Shading also leads to a reduction in stored carbohydrates (Wiley et al. 2017), which are important for tree survival during environmental stress (Wiley and Helliker 2012). Additionally, dying aspen were smaller in diameter than living aspen, and if surrounded by large neighbors, the negative effects of reduced light availability are exacerbated for small trees (Hurst et al. 2011).

We compared living and dying aspen canopy position in the year of sampling (2016), when trees had been dead for a few years, which may have contributed to our observation that dying trees were lower in the canopy strata than living trees. However, living aspen DBH was greater than dying aspen DBH when we compared them in both 1997 (Fig. 2; Appendix S1: Table S7) and 2016 (analysis not shown). Furthermore, dead

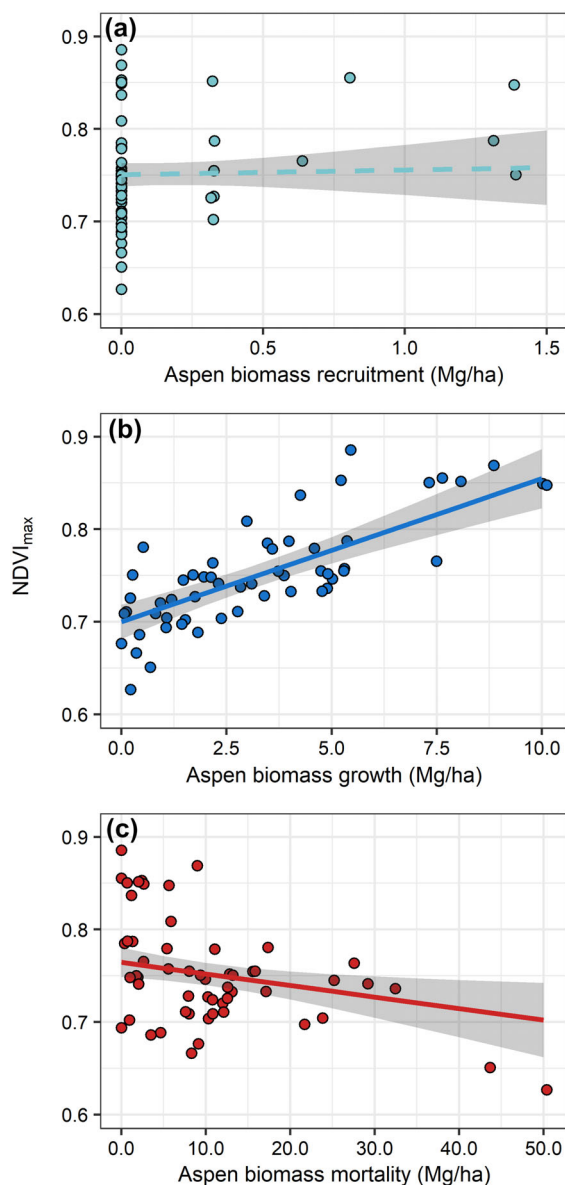


Fig. 6. Relationships from 1997 to 2013 between maximum summer normalized difference vegetation index ($NDVI_{max}$) and aboveground aspen plot-level biomass (a) recruitment, (b) growth, and (c) mortality based on measurements from the CAFE database. Measurements of biomass are at five-year intervals. Lines represent effects based on a hierarchical linear mixed effects model, and shading around lines indicates the 95% confidence interval. Points are the raw data, and each point is a year within a plot. Significant relationships are represented by a solid line (Appendix S1: Table S19).

aspen from CAFE database were in the subcanopy at the onset of the leaf miner outbreak (Appendix S2). As such, we are confident that dying trees sampled for tree-ring analysis were in the subcanopy prior to and at death.

We observed declining and significantly lower growth in dying than living aspen three decades before the *P. populiella* outbreak. These differences were noticeable starting in 1944 but were statistically significant following a drought in 1957. The decline of dying trees was enhanced by the large aspen tortrix outbreak in the late 1960s (Torgersen and Beckwith 1974, USDA FS 2020). This indicates that aspen mortality was incited by the drought in 1957, and subsequent stressors continued to reduce dying tree growth. Growth of both living and dying trees was extremely low during these disturbances (Fig. 1a), particularly in years when large aspen tortrix defoliation co-occurred with low moisture availability (1968 and 1969; Fig. 1b). However, living tree growth did not decline after these events, suggesting a level of resilience to drought and insect defoliation. Similar to our findings, Mamet et al. (2015) observed a large growth reduction in dying jack pine (*Pinus banksiana*) that was prompted by a drought and budworm outbreak in the 1960s, and growth continued to decline in dying trees for 16–24 yr until mortality. Low growth as a metric of tree mortality risk has been documented in aspen (Ireland et al. 2014) and numerous other tree species (Bigler et al. 2006, Cailleret et al. 2017, 2019). These results highlight the importance of accounting for historic disturbance events and long-term trends in tree growth when assessing tree mortality risk.

The subcanopy position, small stature, and low growth of dying trees that we observed support the idea that an accumulation of physical and biotic stress influenced aspen death (Manion 1981, Franklin et al. 1987). Our findings also suggest that long-term exhaustion of carbon reserves likely contributed to tree death, as shading substantially reduces reserve concentration in aspen (Wiley et al. 2017), and multi-decadal growth declines are indicative of gradual carbon depletion (Cailleret et al. 2017, Buras et al. 2018). Carbon reserves are important for sustaining metabolic processes (McDowell et al. 2011, Hartmann and Trumbore 2016), enhancing survival

during drought (O'Brien et al. 2014) and other environmental pressures (Kobe 1997, Landhäusser and Lieffers 2002), and building defensive compounds (Guérard et al. 2007, Najar et al. 2014). These reserves are also particularly important for deciduous species because they use stored carbon for re-foliation (Barbaroux et al. 2003, Silpi et al. 2007). We conclude that compounding stress, which likely resulted in a slow depletion of carbon reserves, contributed to aspen mortality risk.

Pre-outbreak growth response to climate

Living tree growth and dying tree growth were strongly and positively influenced by previous growing season moisture availability (PGS CMI) prior to the *P. populiella* outbreak, indicating that current year growth was influenced by storage of photosynthates produced in the previous year. Growth sensitivity to previous year climate is common in deciduous species because they rely on photosynthates from preceding years for canopy production (Kramer and Kozlowski 1979). Drought conditions reduce photosynthesis, stomatal conductance, and carbon reserves in aspen (Galvez et al. 2013), in turn limiting resource availability for spring re-foliation. Similar to our findings, aspen in Interior Alaska (Cahoon et al. 2018) and eastern boreal Canada (Huang et al. 2010) exhibited a negative growth response to monthly moisture deficits in the preceding year. The importance of previous year moisture on current year aspen growth has been demonstrated in western Canada, where aspen radial growth was positively influenced by previous summer precipitation (Leonelli et al. 2008) and a metric of annual CMI that takes into account preceding summer climate (Hogg et al. 2005).

Initially before the *P. populiella* outbreak (1983–1994), GS temperature increased, had a negative impact on both living tree growth and dying tree growth, and was the primary climatic driver of dying tree growth. A negative association between tree radial growth and temperature has been documented in other boreal tree species (Barber et al. 2000, Walker et al. 2015). High temperatures can decrease photosynthesis (Gustafson et al. 2017), drive earlier stomatal closure (Zhao et al. 2013), and increase plant maintenance respiration (Atkin and Tjoelker 2003),

thereby decreasing net photosynthetic carbon uptake and in turn radial growth. Additionally, extreme heat stress can permanently damage leaf tissue and consequently reduce whole tree photosynthesis (O'Sullivan et al. 2017).

While living and dying trees exhibited a negative growth response to GS temperature from 1983 to 1994, the effect of GS temperature on growth was positive from 1946 to 1957. A change in the tree growth response to temperature after the mid-20th century has been observed in other boreal tree species, either diminishing or changing from a positive to negative relationship (Jacoby et al. 2000, Lloyd and Fastie 2002, D'Arrigo et al. 2004, 2008, Wilmking et al. 2004, Wilson et al. 2007), and has been attributed to temperatures exceeding thresholds for optimal growth (D'Arrigo et al. 2004, Beck et al. 2011). Overall, we show that moisture deficits and temperature negatively affected growth of both living and dying aspen prior to *P. populiella* infestation and that temperature stress was greatest right before the outbreak.

*Outbreak growth patterns and growth response to *P. populiella* and climate*

During the *P. populiella* outbreak, dying aspen exhibited a strong, negative growth response to previous year leaf mining but no growth response to climate, suggesting that *P. populiella* was the final factor driving aspen mortality. Dying aspen growth declined rapidly and remained lower than that of living aspen during the outbreak, further emphasizing the damaging effect of leaf mining on dying aspen growth. Leaves mined by *P. populiella* have lower photosynthesis (Wagner et al. 2008, 2020) and abscise earlier in the growing season than unmined or less mined leaves, resulting in reduced carbon uptake (Wagner et al. 2008). Insect defoliation decreases carbon reserves in aspen, consequently increasing tree mortality risk (Anderegg and Callaway 2012, Landhäusser and Lieffers 2012). Furthermore, because growth of dying trees was low prior to the outbreak and these trees were suffering from shade stress, they likely lacked resources to defend against or recover from leaf mining.

Recent aspen mortality at the southern limit of the boreal forest and in the western United States was primarily driven by moisture deficits, yet

conditions were considerably drier preceding and during mortality events in these regions than in our study sites (Hogg et al. 2008, Michaelian et al. 2011, Worrall et al. 2013). This further supports our conclusion that *P. populiella* was the final driver of aspen death in Interior Alaska and that drought was not severe enough to kill declining trees. Moreover, severe insect infestation can distort tree growth response to climate (Trotter et al. 2002, Sangüesa-Barreda et al. 2015) and reduce photosynthesis and increase carbon depletion to the extent that trees die (Eisenbies et al. 2007, Zhang et al. 2014, Hyde et al. 2016).

Unlike dying aspen, living aspen continued to respond positively to PGS CMI and negatively to GS temperature during the *P. populiella* outbreak. A stronger growth response to climate in surviving vs. dead trees has previously been observed (Ogle et al. 2000, Millar et al. 2012, Macalady and Bugmann 2014). For example, Macalady and Bugmann (2014) showed that dying trees were less responsive to drought than surviving trees, and suggested that enhanced photosynthesis of surviving trees during wet or cool years increased tree carbon reserves and, consequently, the ability of these trees to withstand stress. Our findings indicate that when climate conditions were favorable, surviving aspen were able to increase photosynthesis and thus had a greater amount of resources available for growth, defense, and storage. This was likely important for their survival during the *P. populiella* outbreak. The contrast in climate–growth response between living and dying trees that we observed could be because leaf mining distorted the climate signal in dying but not living trees (Trotter et al. 2002, Sangüesa-Barreda et al. 2015). However, it could also be explained by differences in genetics (Millar et al. 2012, Heer et al. 2018), nutrient availability (Lévesque et al. 2016), or microsite conditions (Wolken et al. 2016).

Although living trees maintained their growth response to moisture availability and temperature during *P. populiella* infestation, the negative impact of previous year leaf mining alone on living tree growth was much greater than climate. The strong impact of *P. populiella* on growth of living and dying aspen suggests that as insect outbreaks become more severe and common at high latitudes, we should expect to see greater declines in aspen growth and more mortality.

Consequently, increases in aspen dominance at high latitudes in response to climate change may not be as great as projected by current models that do not incorporate the influence of insect pests.

In addition to the biotic and abiotic factors identified in our objectives, competition can influence tree growth and mortality (Lussier et al. 2002, Cortini and Comeau 2019). When we included metrics of competition (density [stems/ha] and biomass [Mg/ha]) in our models of tree growth during the *P. populiella* outbreak, we found that dying tree growth was not influenced by intra- or interspecific competition whereas living tree growth was influenced by interspecific competition (Appendix S3). These results provide additional support for our conclusion that *P. populiella* was the dominant driver of dying tree growth and death, but also highlight the importance of interspecific competition on growth of surviving aspen.

Normalized difference vegetation index

The NDVI was positively associated with mean plot-level living and dying tree growth, but the relationship between NDVI and living tree growth was nearly two times greater than between NDVI and dying tree growth. At high latitudes, NDVI has been positively linked to tree radial growth increment (Lopatin et al. 2006, Beck et al. 2011, Bunn et al. 2013, Boyd et al. 2019). However, landscape heterogeneity and differences in growth-limiting factors of dominant species can weaken this relationship (Berner et al. 2011, Brehaut and Danby 2018). Although the sites we sampled were all aspen dominated, the structure within stands was not homogenous. Living and dying aspen were intermixed, and dying trees were in the subcanopy and smaller in diameter and lower in growth than living trees. Furthermore, dying trees were not sensitive to climate during *P. populiella* infestation. These differences could explain why the association was weaker between NDVI and dying than living tree growth. Additionally, leaf productivity, which has been linked to NDVI (Turner et al. 1999, Xie et al. 2014), was likely higher for living compared with dying trees during the leaf miner outbreak due to their size and greater resource availability for spring re-foliation.

Stand biomass growth and mortality were captured by NDVI, such that NDVI was significantly and positively associated with biomass growth and negatively with biomass mortality. However, biomass growth had a 12 times greater influence than biomass mortality on the NDVI signal, and the association between NDVI and biomass mortality was only significant when mortality values >40 Mg/ha were included in the model (analysis not shown). While the latter suggests that NDVI has relevance for detecting larger aspen mortality events, more measurements are necessary to support this conclusion as only two mortality observations were >40 Mg/ha. Also, analogous to trees sampled for tree-ring analysis, aspen from the CAFI database that survived the leaf miner outbreak were higher in the canopy strata and larger in diameter than aspen that died. Taken together, these findings suggest that NDVI is a better metric of overstory aspen growth than understory aspen death and thus may not detect insect-driven mortality of aspen at high latitudes, particularly when tree die-off is gradual and related to canopy position.

Due to the lack of Landsat data prior to 1999, we were unable to address the link between NDVI and aspen growth and mortality before the *P. populiella* outbreak. Such analyses would be useful for assessing relationships between long-term NDVI trends (i.e., greening and browning) and aspen stand demographics as well as determining the utility of multi-decadal NDVI time series for predicting mortality and growth (e.g., Rogers et al. 2018). Nevertheless, our work provides a greater understanding of the utility as well as potential limitations of NDVI for detecting climate change impacts on boreal ecosystems.

CONCLUSIONS

Climate change-driven droughts and insect outbreaks have resulted in unprecedented forest mortality worldwide (Mantgem et al. 2009, Allen et al. 2010, 2015, Zhang et al. 2014, Berner et al. 2017) and are projected to increase in frequency and severity with continued climate change (Bale et al. 2002, Bentz et al. 2010, Seidl et al. 2017, IPCC 2018). Assessing short- and long-term processes that lead to tree death is required to understand tree mortality mechanisms and the risk of forests to dieback and mortality. We show that

small, subcanopy aspen are vulnerable to mortality during *P. populiella* infestation, and drought events can incite growth declines that increase aspen mortality risk. Our findings also reveal that moisture deficits and temperature decrease aspen growth but that the negative impact of *P. populiella* on growth supersedes the impact of climate. Lastly, we found that NDVI more strongly captured the growth of living compared with dying trees and stand biomass growth compared with death. This suggests that NDVI may not reliably detect insect-associated aspen dieback and diffuse mortality in boreal ecosystems. We conclude that accounting for tree stature, climate, biotic disturbance agents, and historic growth patterns is important for addressing aspen mortality risk at high latitudes, and consequently, determining the structure and composition of the boreal biome under a changing climate.

ACKNOWLEDGMENTS

This project was supported by funding from the NASA Terrestrial Ecology Program, Arctic Boreal and Vulnerability Experiment (ABOVE; grant NNX17AE44G), Strategic Environmental Research and Development Program (SERDP; Project Number RC18-C2-1183), the Bonanza Creek LTER supported by the NSF (DEB-1636476), and the USDA Forest Service, Pacific Northwest Research Station (RJVA-PNW-01-JV-11261952-231). We thank Norma Rivera, Samantha Miller, and Julia Stuart for assistance in the field, and Jesse McLaughlin for his help navigating the CAFI network.

LITERATURE CITED

- Alexander, H. D., M. C. Mack, S. J. Goetz, P. S. A. Beck, and E. F. Belshe. 2012. Implications of increased deciduous cover on stand structure and above-ground carbon pools of Alaskan boreal forests. *Ecosphere* 3:1–21.
- Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259:660–684.
- Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6:1–55.
- AMAP [Arctic Monitoring and Assessment Programme]. 2017. Snow, Water, Ice and Permafrost in

- the Arctic (SWIPA) 2017. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway.
- Anderegg, W. R. L., J. A. Berry, D. D. Smith, J. S. Sperry, L. D. L. Anderegg, and C. B. Field. 2012. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proceedings of the National Academy of Sciences of the United States of America* 109:233–237.
- Anderegg, W. R. L., and E. S. Callaway. 2012. Infestation and hydraulic consequences of induced carbon starvation. *Plant Physiology* 159:1866–1874.
- Anderegg, W. R. L., J. M. Kane, and L. D. L. Anderegg. 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change* 3:30–36.
- Atkin, O. K., and M. G. Tjoelker. 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science* 8:343–351.
- Bale, J. S., et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8:1–16.
- Barbaroux, C., N. Bréda, and E. Dufrene. 2003. Distribution of above-ground and below-ground carbohydrate reserves in adult trees of two contrasting broad-leaved species (*Quercus petraea* and *Fagus sylvatica*). *New Phytologist* 157:605–615.
- Barber, V. A., G. P. Juday, and B. P. Finney. 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature* 405:668–673.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Beck, P. S. A., G. P. Juday, C. Alix, V. A. Barber, S. E. Winslow, E. E. Sousa, P. Heiser, J. D. Herriges, and S. J. Goetz. 2011. Changes in forest productivity across Alaska consistent with biome shift. *Ecology Letters* 14:373–379.
- Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Methodological)* 57:289–300.
- Bennett, A. C., N. G. McDowell, C. D. Allen, and K. J. Anderson-Teixeira. 2015. Larger trees suffer most during drought in forests worldwide. *Nature Plants* 1:15139.
- Bentz, B. J., J. Régnière, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *BioScience* 60:602–613.
- Berner, L. T., et al. 2020. Summer warming explains widespread but not uniform greening in the Arctic tundra biome. *Nature Communications* 11:4621.
- Berner, L. T., P. S. A. Beck, A. G. Bunn, A. H. Lloyd, and S. J. Goetz. 2011. High-latitude tree growth and satellite vegetation indices: correlations and trends in Russia and Canada (1982–2008). *Journal of Geophysical Research* 116:G01015.
- Berner, L. T., B. E. Law, A. J. H. Meddens, and J. A. Hicke. 2017. Tree mortality from fires, bark beetles, and timber harvest during a hot and dry decade in the western United States (2003–2012). *Environmental Research Letters* 12:065005.
- Bhuyan, U., C. Zang, S. M. Vicente-Serrano, and A. Menzel. 2017. Exploring relationships among tree-ring growth, climate variability, and seasonal leaf activity on varying timescales and spatial resolutions. *Remote Sensing* 9:526.
- Bigler, C., O. U. Bräker, H. Bugmann, M. Dobbertin, and A. Rigling. 2006. Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. *Ecosystems* 9:330–343.
- Biondi, F., and F. Qeadan. 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Research* 64:81–96.
- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S.-S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–135.
- Boyd, M. A., L. T. Berner, P. Doak, S. J. Goetz, B. M. Rogers, D. Wagner, X. J. Walker, and M. C. Mack. 2019. Impacts of climate and insect herbivory on productivity and physiology of trembling aspen (*Populus tremuloides*) in Alaskan boreal forests. *Environmental Research Letters* 14:085010.
- Brehaut, L., and R. K. Danby. 2018. Inconsistent relationships between annual tree ring-widths and satellite-measured NDVI in a mountainous subarctic environment. *Ecological Indicators* 91:698–711.
- Breshears, D. D., et al. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America* 102:15144–15148.
- Breshears, D. D., and C. D. Allen. 2002. The importance of rapid, disturbance-induced losses in carbon management and sequestration. *Global Ecology and Biogeography* 11:1–5.
- Bunn, A. G. 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26:115–124.
- Bunn, A. G., M. Hughes, A. V. Kirdyanov, M. Losleben, V. V. Shishov, L. T. Berner, A. Oltchev, and E. A. Vaganov. 2013. Comparing forest measurements from tree rings and a space-based index of

- vegetation activity in Siberia. *Environmental Research Letters* 8:035034.
- Buras, A., et al. 2016. Tuning the voices of a choir: detecting ecological gradients in time-series populations. *PLOS ONE* 11:e0158346.
- Buras, A., et al. 2018. Are Scots pine forest edges particularly prone to drought-induced mortality? *Environmental Research Letters* 13:025001.
- Cahoon, S. M. P., P. F. Sullivan, A. H. Brownlee, R. R. Pattison, H.-E. Andersen, K. Legner, and T. N. Hollingsworth. 2018. Contrasting drivers and trends of coniferous and deciduous tree growth in interior Alaska. *Ecology* 99:1284–1295.
- Cailleret, M., et al. 2017. A synthesis of radial growth patterns preceding tree mortality. *Global Change Biology* 23:1675–1690.
- Cailleret, M., et al. 2019. Early-warning signals of individual tree mortality based on annual radial growth. *Frontiers in Plant Science* 9:1964.
- Calder, W. J., K. J. Horn, and S. B. St. Clair. 2011. Conifer expansion reduces the competitive ability and herbivore defense of aspen by modifying light environment and soil chemistry. *Tree Physiology* 31:582–591.
- Chen, L., J.-G. Huang, A. Dawson, L. Zhai, K. J. Stadt, P. G. Comeau, and C. Whitehouse. 2018. Contributions of insects and droughts to growth decline of trembling aspen mixed boreal forest of western Canada. *Global Change Biology* 24:655–667.
- Cook, E. R., and L. Kairiukstis. 1990. *Methods of Dendrochronology: applications in the environmental sciences*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Cortini, F., and P. G. Comeau. 2019. Pests, climate and competition effects on survival and growth of trembling aspen in western Canada. *New Forests* 51:175–190.
- Curtis, R. O. 1983. Procedures for establishing and maintaining permanent plots for silvicultural and yield research. PNW-GTR-155. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- D'Arrigo, R. D., R. K. Kaufmann, N. Davi, G. C. Jacoby, C. Laskowski, R. B. Myneni, and P. Cherubini. 2004. Thresholds for warming-induced growth decline at elevational tree line in the Yukon Territory, Canada. *Global Biogeochemical Cycles* 18:GB3021.
- D'Arrigo, R. D., R. Wilson, B. Liepert, and P. Cherubini. 2008. On the “divergence problem” in northern forests: a review of the tree-ring evidence and possible causes. *Global and Planetary Change* 60:289–305.
- Duchesne, L., R. Ouimet, and D. Houle. 2002. Basal area growth of sugar maple in relation to acid deposition, stand health, and soil nutrients. *Journal of Environmental Quality* 31:1676–1683.
- Duchesne, L., R. Ouimet, and C. Morneau. 2003. Assessment of sugar maple health based on basal area growth pattern. *Canadian Journal of Forest Research* 33:2074–2080.
- Eisenbies, M. H., C. Davidson, J. Johnson, R. Amateis, and K. Gottschalk. 2007. Tree mortality in mixed pine-hardwood stands defoliated by the European gypsy moth (*Lymantria dispar* L.). *Forest Science* 53:683–691.
- Fischlin, A., G. F. Midgley, J. T. Price, R. Leemans, B. Gopal, C. Turley, M. D. A. Rounsevell, O. P. Dube, J. Tarazona, and A. A. Velichko. 2007. Ecosystems, their properties, goods, and services. Pages 211–272 in M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden, and C. E. Hanson, editors. *Climate Change 2007: impacts, Adaptation and Vulnerability*. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Foster, A. C., A. H. Armstrong, J. K. Shuman, H. H. Shugart, B. M. Rogers, M. C. Mack, S. J. Goetz, and K. J. Ranson. 2019. Importance of tree-and species-level interactions with wildfire, climate, and soils in interior Alaska: implications for forest change under a warming climate. *Ecological Modelling* 409:108765.
- Fox, J., and S. Weisberg. 2019. *An R companion to applied regression*. Third edition. SAGE Publications, Thousand Oaks, California, USA.
- Franklin, J. F., H. H. Shugart, and M. E. Harmon. 1987. Tree death as an ecological process. *BioScience* 37:550–556.
- Fritts, H. C. 1976. *Tree rings and climate*. Academic Press, London, UK.
- Galiano, L., J. Martínez-Vilalta, and F. Lloret. 2011. Carbon reserves and canopy defoliation determine the recovery of Scots pine 4 yr after a drought episode. *New Phytologist* 190:750–759.
- Galván, J. D., J. J. Camarero, and E. Gutiérrez. 2014. Seeing the trees for the forest: drivers of individual growth responses to climate in *Pinus uncinata* mountain forests. *Journal of Ecology* 102:1244–1257.
- Galvez, D. A., S. M. Landhäusser, and M. T. Tyree. 2013. Low root reserve accumulation during drought may lead to winter mortality in poplar seedlings. *New Phytologist* 198:139–148.
- Goetz, S. J., and S. D. Prince. 1999. Modelling terrestrial carbon exchange and storage: evidence and implications of functional convergence in light-use efficiency. *Advances in Ecological Research* 28:57–92.

- Gorelick, N., M. Hancher, M. Dixon, S. Ilyushchenko, D. Thau, and R. Moore. 2017. Google Earth Engine: planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment* 202:18–27.
- Grissino-Mayer, H. D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research* 57:205–221.
- Guérard, N., P. Maillard, C. Bréchet, F. Lieutier, and E. Dreyer. 2007. Do trees use reserve or newly assimilated carbon for their defense reactions? A ^{13}C labeling approach with young Scots pines inoculated with a bark-beetle-associated fungus (*Ophiostoma brunneo ciliatum*). *Annals of Forest Science* 64:601–608.
- Gustafson, E. J., B. R. Miranda, A. M. G. De Bruijn, B. R. Sturtevant, and M. E. Kubiske. 2017. Do rising temperatures always increase forest productivity? Interacting effects of temperature, precipitation, cloudiness and soil texture on tree species growth and competition. *Environmental Modelling & Software* 97:171–183.
- Hart, S. J., D. J. Smith, and J. J. Clague. 2010. A multi-species dendroclimatic reconstruction of Chilko River streamflow, British Columbia, Canada. *Hydrological Processes* 24:2752–2761.
- Hartmann, H., and S. Trumbore. 2016. Understanding the roles of nonstructural carbohydrates in forest trees – from what we can measure to what we want to know. *New Phytologist* 211:386–403.
- Heer, K., et al. 2018. Linking dendroecology and association genetics in natural populations: Stress responses archived in tree rings associate with SNP genotypes in silver fir (*Abies alba* Mill.). *Molecular Ecology* 27:1428–1438.
- Hereş, A.-M., J. Martínez-Vilalta, and B. Claramunt López. 2012. Growth patterns in relation to drought-induced mortality at two Scots pine (*Pinus sylvestris* L.) sites in NE Iberian Peninsula. *Trees* 26:621–630.
- Hogg, E. H. 1994. Climate and the southern limit of the western Canadian boreal forest. *Canadian Journal of Forest Research* 24:1835–1845.
- Hogg, E. H. 1997. Temporal scaling of moisture and the forest-grassland boundary in western Canada. *Agricultural and Forest Meteorology* 84:115–122.
- Hogg, E. H., J. P. Brandt, and B. Kochtubajda. 2002. Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. *Canadian Journal of Forest Research* 32:823–832.
- Hogg, E. H., J. P. Brandt, and B. Kochtubajda. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951–2000. *Canadian Journal of Forest Research* 35:610–622.
- Hogg, E. H., J. P. Brandt, and M. Michaellian. 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. *Canadian Journal of Forest Research* 38:1373–1384.
- Huang, J., J. C. Tardif, Y. Bergeron, B. Denneker, F. Berninger, and M. P. Girardin. 2010. Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest. *Global Change Biology* 16:711–731.
- Hurst, J. M., R. B. Allen, D. A. Coomes, and R. P. Duncan. 2011. Size-specific tree mortality varies with neighbourhood crowding and disturbance in a montane *Nothofagus* forest. *PLOS ONE* 6:e26670.
- Hyde, K., S. Peckham, T. Holmes, and B. Ewers. 2016. Bark beetle-induced forest mortality in the North American Rocky Mountains. Pages 119–135 in R. Sivanpillai, editor. *Biological and environmental hazards, risks, and disasters*. Elsevier, New York, New York, USA.
- IPCC. 2018. Summary for Policymakers. I. V. Masson-Delmotte, P. Zhai, H.-O. Pörtner, H.-O. Pörtner, J. Skea, P. R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidock, S. Connors, J. B. R. Matthews, Y. Chen, X. Zhou, M. I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield, editors. *Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty*. World Meteorological Organization, Geneva, Switzerland.
- Ireland, K. B., M. M. Moore, P. Z. Fulé, T. J. Ziegler, and R. E. Keane. 2014. Slow lifelong growth predisposes *Populus tremuloides* trees to mortality. *Oecologia* 175:847–859.
- Jacoby, G. C., N. V. Lovelius, O. I. Shumilov, O. M. Raspopov, J. M. Karbainov, and D. C. Frank. 2000. Long-term temperature trends and tree growth in the Taymir region of northern Siberia. *Quaternary Research* 53:312–318.
- Jochner, M., H. Bugmann, M. Nötzli, and C. Bigler. 2017. Among-tree variability and feedback effects result in different growth responses to climate change at the upper treeline in the Swiss Alps. *Ecology and Evolution* 7:7937–7953.
- Ju, J., and J. G. Masek. 2016. The vegetation greenness trend in Canada and US Alaska from 1984–2012 Landsat data. *Remote Sensing of Environment* 176:1–16.

- Kobe, R. K. 1997. Carbohydrate allocation to storage as basis of interspecific variation in sapling survivorship and growth. *Oikos* 80:226–233.
- Kramer, P. J., and T. T. Kozlowski. 1979. *Physiology of woody plants*. Academic Press, New York, New York, USA.
- Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safra-nyik. 2008a. Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452:987–990.
- Kurz, W. A., G. Stinson, G. J. Rampley, C. C. Dymond, and E. T. Neilson. 2008b. Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain. *Proceedings of the National Academy of Sciences of the United States of America* 105:1551–1555.
- Landhäusser, S. M., and V. J. Lieffers. 2002. Leaf area renewal, root retention and carbohydrate reserves in a clonal tree species following above-ground disturbance. *Journal of Ecology* 90:658–665.
- Landhäusser, S. M., and V. J. Lieffers. 2012. Defoliation increases risk of carbon starvation in root systems of mature aspen. *Trees* 26:653–661.
- Leblanc, D. 1990. Relationships between breast-height and whole-stem growth indices for red spruce on Whiteface Mountain, New York. *Canadian Journal of Forest Research* 20:1399–1407.
- Lebourgeois, F., G. Cousseau, and Y. Ducos. 2004. Climate-tree-growth relationships of *Quercus petraea* Mill. stand in the Forest of Bercé ("Futaie des Clos", Sarthe, France). *Annals of Forest Science* 61:361–372.
- Leonelli, G., B. Denneler, and Y. Bergeron. 2008. Climate sensitivity of trembling aspen radial growth along a productivity gradient in northeastern British Columbia, Canada. *Canadian Journal of Forest Research* 38:1211–1222.
- Lévesque, M., L. Walthert, and P. Weber. 2016. Soil nutrients influence growth response of temperate tree species to drought. *Journal of Ecology* 104:377–387.
- Lloyd, A. H., and C. L. Fastie. 2002. Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change* 52:481–509.
- Lopatin, E., T. Kolström, and H. Spiecker. 2006. Determination of forest growth trends in Komi Republic (northwestern Russia): combination of tree-ring analysis and remote sensing data. *Boreal Environment Research* 11:341–353.
- Loranty, M., S. Davydov, H. Kropp, H. Alexander, M. Mack, S. Natali, and N. Zimov. 2018. Vegetation indices do not capture forest cover variation in upland Siberian larch forests. *Remote Sensing* 10:1686.
- Lussier, J.-M., H. Morin, and R. Gagnon. 2002. Mortality in black spruce stands of fire or clear-cut origin. *Canadian Journal of Forest Research* 32:539–547.
- Macalady, A. K., and H. Bugmann. 2014. Growth-mortality relationships in piñon pine (*Pinus edulis*) during severe droughts of the past century: Shifting processes in space and time. *PLOS ONE* 9: e92770.
- Malone, T., J. Liang, and E. C. Packee. 2009. Cooperative Alaska Forest Inventory. PNW-GTR-785. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Mamet, S. D., K. P. Chun, J. M. Metsaranta, A. G. Barr, and J. F. Johnstone. 2015. Tree rings provide early warning signals of jack pine mortality across a moisture gradient in the southern boreal forest. *Environmental Research Letters* 10:084021.
- Manion, P. D. 1981. *Tree disease concepts*. Prentice-Hall Inc, Englewood Cliffs, New Jersey, USA.
- Mann, D. H., T. Scott Rupp, M. A. Olson, and P. A. Duffy. 2012. Is Alaska's boreal forest now crossing a major ecological threshold? *Arctic, Antarctic, and Alpine Research* 44:319–331.
- Masek, J. g., E. f. Vermote, N. e. Saleous, R. Wolfe, F. g. Hall, K. f. Huemmrich, F. Gao, J. Kutler, and T.-k. Lim. 2006. A Landsat surface reflectance dataset for North America, 1990–2000. *IEEE Geoscience and Remote Sensing Letters* 3:68–72.
- McDowell, N. G., et al. 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist* 178:719–739.
- McDowell, N. G. 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology* 155:1051–1059.
- McDowell, N. G., D. J. Beerling, D. D. Breshears, R. A. Fisher, K. F. Raffa, and M. Stitt. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology & Evolution* 26:523–532.
- McDowell, N. G., and S. Sevanto. 2010. The mechanisms of carbon starvation: How, when, or does it even occur at all? *New Phytologist* 186:264–266.
- Mekonnen, Z. A., W. J. Riley, J. T. Randerson, R. F. Grant, and B. M. Rogers. 2019. Expansion of high-latitude deciduous forests driven by interactions between climate warming and fire. *Nature Plants* 5:952–958.
- Melaas, E. K., M. A. Friedl, and Z. Zhu. 2013. Detecting interannual variation in deciduous broadleaf forest phenology using Landsat TM/ETM+ data. *Remote Sensing of Environment* 132:176–185.

- Melaas, E. K., D. Sulla-Menashe, J. M. Gray, T. A. Black, T. H. Morin, A. D. Richardson, and M. A. Friedl. 2016. Multisite analysis of land surface phenology in North American temperate and boreal deciduous forests from Landsat. *Remote Sensing of Environment* 186:452–464.
- Michaelian, M., E. H. Hogg, R. J. Hall, and E. Arsenault. 2011. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology* 17:2084–2094.
- Millar, C. I., R. D. Westfall, D. L. Delany, M. J. Bokach, A. L. Flint, and L. E. Flint. 2012. Forest mortality in high-elevation whitebark pine (*Pinus albicaulis*) forests of eastern California, USA; influence of environmental context, bark beetles, climatic water deficit, and warming. *Canadian Journal of Forest Research* 42:749–765.
- Najar, A., S. M. Landhäusser, J. G. A. Whitehill, P. Bonello, and N. Erbilgin. 2014. Reserves accumulated in non-photosynthetic organs during the previous growing season drive plant defenses and growth in aspen in the subsequent growing season. *Journal of Chemical Ecology* 40:21–30.
- O'Brien, M. J., S. Leuzinger, C. D. Philipson, J. Tay, and A. Hector. 2014. Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nature Climate Change* 4:710–714.
- Ogaya, R., A. Barbeta, C. Başnou, and J. Penuelas. 2015. Satellite data as indicators of tree biomass growth and forest dieback in a Mediterranean holm oak forest. *Annals of Forest Science* 72:135–144.
- Ogle, K., T. Whitham, and N. Cobb. 2000. Tree-ring variation in piñon predicts likelihood of death following severe drought. *Ecology* 81:3237–3243.
- O'sullivan, O. S., et al. 2017. Thermal limits of leaf metabolism across biomes. *Global Change Biology* 23:209–223.
- Perala, D. A. 1990. *Populus tremuloides* (Michx.) Quaking aspen. Pages 555–569 in R. M. Burns and B. H. Honkala, editors. *Silvics of North America: Hardwoods*. USDA Forest Service, Washington, D.C., USA.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2018. nlme: linear and Nonlinear Mixed Effects Models. R package version 3.1-131.1. <https://CRAN.R-project.org/package=nlme>
- R Development Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Regent Instruments Canada Inc. 2012. WinDENDRO: an image analysis system for tree-rings analysis. Regent Instruments Inc, Québec, Québec, Canada.
- Rogers, B. M., K. Solvik, E. Hogg, J. Ju, J. G. Masek, M. Michaelian, L. T. Berner, and S. J. Goetz. 2018. Detecting early warning signals of tree mortality in boreal North America using multiscale satellite data. *Global Change Biology* 24:2284–2304.
- Rohner, B., P. Waldner, H. Lischke, M. Ferretti, and E. Thürig. 2018. Predicting individual-tree growth of central European tree species as a function of site, stand, management, nutrient, and climate effects. *European Journal of Forest Research* 137:29–44.
- Rolland, C., and G. Lempérière. 2004. Effects of climate on radial growth of Norway spruce and interactions with attacks by the bark beetle *Dendroctonus micans* (Kug., Coleoptera: Scolytidae): a dendroecological study in the French Massif Central. *Forest Ecology and Management* 201:89–104.
- Roy, D. P., V. Kovalsky, H. K. Zhang, E. F. Vermote, L. Yan, S. S. Kumar, and A. Egorov. 2016. Characterization of Landsat-7 to Landsat-8 reflective wavelength and normalized difference vegetation index continuity. *Remote Sensing of Environment* 185:57–70.
- Sangüesa-Barreda, G., J. C. Linares, and J. J. Camarero. 2015. Reduced growth sensitivity to climate in bark-beetle infested Aleppo pines: connecting climatic and biotic drivers of forest dieback. *Forest Ecology and Management* 357:126–137.
- Seidl, R., et al. 2017. Forest disturbances under climate change. *Nature Climate Change* 7:395–402.
- Sevanto, S., N. G. McDowell, L. T. Dickman, R. Pangle, and W. T. Pockman. 2014. How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant, Cell & Environment* 37:153–161.
- Sheather, S. 2009. *A Modern Approach to Regression with R*. Springer-Verlag, New York, New York, USA.
- Silpi, U., A. Lacomte, P. Kasempasap, S. Thanyasawanyangkura, P. Chantuma, E. Gohet, N. Musigamart, A. Clément, T. Améglio, and P. Thaler. 2007. Carbohydrate reserves as a competing sink: evidence from tapping rubber trees. *Tree Physiology* 27:881–889.
- Stoltzfus, J. C. 2011. Logistic regression: a brief primer. *Academic Emergency Medicine* 18:1099–1104.
- Suarez, M. L., L. Ghermandi, and T. Kitzberger. 2004. Factors predisposing episodic drought-induced tree mortality in *Nothofagus* - site, climatic sensitivity and growth trends. *Journal of Ecology* 92:954–966.
- Torgersen, T. R., and R. C. Beckwith. 1974. Parasitoids associated with the large aspen tortrix, *Choristoneura conflictana* (Lepidoptera: Tortricidae), in interior Alaska. *Canadian Entomologist* 106:1247–1265.

- Trotter, R. T., N. S. Cobb, and T. G. Whitham. 2002. Herbivory, plant resistance, and climate in the tree ring record: Interactions distort climatic reconstructions. *Proceedings of the National Academy of Sciences of the United States of America* 99:10197–10202.
- Trugman, A. T., D. Medvigy, W. R. L. Anderegg, and S. W. Pacala. 2018. Differential declines in Alaskan boreal forest vitality related to climate and competition. *Global Change Biology* 24:1097–1107.
- Tucker, C. J. 1979. Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment* 8:127–150.
- Turner, D. P., W. B. Cohen, R. E. Kennedy, K. S. Fassnacht, and J. M. Briggs. 1999. Relationships between leaf area index and Landsat TM spectral vegetation indices across three temperate zone sites. *Remote Sensing of Environment* 70:52–68.
- Ung, C.-H., P. Bernier, and X. Guo. 2008. Canadian national biomass equations: new parameter estimates that include British Columbia data. *Canadian Journal of Forest Research* 38:1123–1132.
- USDA FS [U.S. Department of Agriculture Forest Service]. 2020. Forest Health Conditions in Alaska Reports & ADS Damage Maps. https://www.fs.usda.gov/detail/r10/forest-grasslandhealth/?cid=fs-sbdev2_038884
- van Mantgem, P. J., et al. 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323:521–524.
- Vermote, E., C. Justice, M. Claverie, and B. Franch. 2016. Preliminary analysis of the performance of the Landsat 8/OLI land surface reflectance product. *Remote Sensing of Environment* 185:46–56.
- Vicente-Serrano, S. M., et al. 2020. Linking tree-ring growth and satellite-derived gross primary growth in multiple forest biomes. Temporal-scale matters. *Ecological Indicators* 108:105753.
- Vicente-Serrano, S. M., J. J. Camarero, J. M. Olano, N. Martín-Hernández, M. Peña-Gallardo, M. Tomás-Burguera, A. Gazol, C. Azorin-Molina, U. Bhuyan, and A. El Kenawy. 2016. Diverse relationships between forest growth and the Normalized Difference Vegetation Index at a global scale. *Remote Sensing of Environment* 187:14–29.
- Wagner, D., L. DeFoliart, P. Doak, and J. Schneiderheinze. 2008. Impact of epidermal leaf mining by the aspen leaf miner (*Phyllocnistis populiella*) on the growth, physiology, and leaf longevity of quaking aspen. *Oecologia* 157:259–267.
- Wagner, D., J. M. Wheeler, and S. J. Burr. 2020. The leaf miner *Phyllocnistis populiella* negatively impacts water relations in aspen. *Tree Physiology* 40:580–590.
- Walker, X. J., and J. F. Johnstone. 2014. Widespread negative correlations between black spruce growth and temperature across topographic moisture gradients in the boreal forest. *Environmental Research Letters* 9:064016.
- Walker, X. J., M. C. Mack, and J. F. Johnstone. 2015. Stable carbon isotope analysis reveals widespread drought stress in boreal black spruce forests. *Global Change Biology* 21:3102–3113.
- Wang, T., A. Hamann, D. Spittlehouse, and C. Carroll. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLOS ONE* 11:1–17.
- Wiley, E., and B. Helliker. 2012. A re-evaluation of carbon storage in trees lends greater support for carbon limitation to growth. *New Phytologist* 195:285–289.
- Wiley, E., G. Hoch, and S. M. Landhäusser. 2017. Dying piece by piece: carbohydrate dynamics in aspen (*Populus tremuloides*) seedlings under severe carbon stress. *Journal of Experimental Botany* 68:5221–5232.
- Wilmking, M., G. P. Juday, V. A. Barber, and H. S. J. Zald. 2004. Recent climate warming forces contrasting growth responses of white spruce at tree-line in Alaska through temperature thresholds. *Global Change Biology* 10:1724–1736.
- Wilson, R., R. D'Arrigo, B. Buckley, U. Buentgen, J. Esper, D. Frank, B. Luckman, S. Payette, R. Vose, and D. Youngblut. 2007. A matter of divergence: tracking recent warming at hemispheric scales using tree ring data. *Journal of Geophysical Research-Atmospheres* 112:D17103.
- Wolken, J. M., D. H. Mann, T. A. Grant, A. H. Lloyd, T. S. Rupp, and T. N. Hollingsworth. 2016. Climate-growth relationships along a black spruce toposequence in interior Alaska. *Arctic, Antarctic, and Alpine Research* 48:637–652.
- Worrall, J. J., G. E. Rehfeldt, A. Hamann, E. H. Hogg, S. B. Marchetti, M. Michaelian, and L. K. Gray. 2013. Recent declines of *Populus tremuloides* in North America linked to climate. *Forest Ecology and Management* 299:35–51.
- Xie, Q., W. Huang, D. Liang, P. Chen, C. Wu, G. Yang, J. Zhang, L. Huang, and D. Zhang. 2014. Leaf area index estimation using vegetation indices derived from airborne hyperspectral images in winter wheat. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing* 7:3586–3594.
- Young, B., D. Wagner, P. Doak, and T. Clausen. 2010. Within-plant distribution of phenolic glycosides and extrafloral nectaries in trembling aspen (*Populus tremuloides*; Salicaceae). *American Journal of Botany* 97:601–610.

- Yukon Department of Energy, Mines, and Resources. 2020. Yukon Forest Health Report. Energy Mines and Resources, Government of Yukon, Forest Management Branch, Whitehorse, Yukon, Canada.
- Zhang, X., Y. Lei, Z. Ma, D. Kneeshaw, and C. Peng. 2014. Insect-induced tree mortality of boreal forests in eastern Canada under a changing climate. *Ecology and Evolution* 4:2384–2394.
- Zhao, J., H. Hartmann, S. Trumbore, W. Ziegler, and Y. Zhang. 2013. High temperature causes negative whole-plant carbon balance under mild drought. *New Phytologist* 200:330–339.
- Zhu, Z., S. Wang, and C. E. Woodcock. 2015. Improvement and expansion of the Fmask algorithm: cloud, cloud shadow, and snow detection for Landsats 4–7, 8, and Sentinel 2 images. *Remote Sensing of Environment* 159:269–277.
- Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer-Verlag, New York, New York, USA.

DATA AVAILABILITY

All relevant data are available through the Bonanza Creek LTER (<http://dx.doi.org/10.6073/pasta/4041316bc68a6d5f5f9252c9ef92fed4>, <http://dx.doi.org/10.6073/pasta/17dd18c0a4f0e9c807c0220dd519313d>, <http://dx.doi.org/10.6073/pasta/08d8211791b22ce66ba611c64cc30d0e>, <http://dx.doi.org/10.6073/pasta/8428afd5a949e52be0d78184df3d50ed>) and the International Tree-Ring Data Bank (<https://www.ncdc.noaa.gov/paleo-search/>; see files AK177 through AK184). R code associated with the statistics and figures is available on GitHub (https://github.com/meIBoyd/AK_aspen_mortality.git).

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3569/full>