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Impacts of climate and insect herbivory on productivity and physiology of trembling aspen (Populus tremuloides) in Alaskan boreal forests

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Abstract

Climate change is impacting forested ecosystems worldwide, particularly in the Northern Hemisphere where warming has increased at a faster rate than the rest of the globe. As climate warms, trembling aspen (*Populus tremuloides*) is expected to become more successful in northern boreal forests because of its current presence in drier areas of North America. However, large-scale productivity decline of aspen has recently been documented throughout the United States and Canada as a result of drought and insect outbreaks. We used tree ring measurements (basal area increment (BAI) and stable carbon isotopes ($\delta^{13}C$)) and remote sensing indices of vegetation productivity (NDVI) to study the impact of climate and damage by the aspen epidermal leaf miner (*Phyllocnistis populiella*) on aspen productivity and physiology in interior Alaska. We found that productivity decreased with greater leaf mining and was not sensitive to growing season (GS) moisture availability. Although productivity decreased during high leaf mining years, it recovered to pre-outbreak levels during years of low insect damage, suggesting a degree of resilience to *P. populiella* mining. Climate and leaf mining interacted to influence tree ring $\delta^{13}C$, with greater leaf mining resulting in decreased $\delta^{13}C$ when GS moisture availability was low. We also found that NDVI was negatively associated with leaf mining, and positively correlated with BAI and the $\delta^{13}C$ decrease corresponding to mining. This suggests that NDVI is capturing not only variations in productivity, but also changes in physiology associated with *P. populiella*. Overall, these findings indicate that the indirect effects of *P. populiella* mining have a larger impact on aspen productivity and physiology than climate under current conditions, and is essential to consider when assessing growth, physiology and NDVI trends in interior Alaska.

Introduction

Global temperatures have increased at an unprecedented rate in recent decades (IPCC 2013) contributing to increased drought stress and tree productivity decline in forested areas worldwide (Choat *et al* 2012, Williams *et al* 2013, Allen *et al* 2015). Warming-related declines in tree productivity (Beck *et al* 2011, Peng *et al* 2011; Girardin *et al* 2014, Hogg *et al* 2017) and radial growth sensitivity to moisture availability (Barber *et al* 2000, Walker and Johnstone 2014, Sullivan *et al* 2017) are prevalent in Arctic and Boreal regions of North America, where temperatures have increased at a rate nearly twice the global average in the last 30 years (IPCC 2013). Satellite remote sensing metrics of vegetation productivity have also detected boreal tree growth decline across large regions (Goetz *et al* 2005, Parent and Verbyla 2010, Beck and Goetz 2011, Baird *et al* 2012). The greatest changes in boreal ecosystems, however, are not expected to be from direct tree physiological responses to climate, but rather indirect impacts of climate change on disturbance regimes. In particular, many insect species experience shortened life cycles and increased survival in response to higher temperatures and longer growing seasons (GSs) (Dale *et al* 2001, Régnière *et al* 2012), resulting in severe and pervasive outbreaks that have led to widespread dieback of boreal trees (Berg *et al* 2006, Soja *et al* 2007, Kurz *et al* 2008, Kautz *et al* 2017). Incidence of both drought and insect infestation are expected to increase under continued climate change (Hinzman *et al* 2005, Gray 2008, Bentz *et al* 2009, Williamson *et al* 2009), and they may interact to influence tree productivity and mortality, more so than insects or drought alone (Gaylord *et al* 2013, Anderegg *et al* 2015).

Trembling aspen (*Populus tremuloides,* henceforth 'aspen') is a dominant deciduous tree in the North American boreal forest (Peterson and Peterson 1992). It is the most widespread poplar species in North America (Perala 1990) and is able to withstand a wide range of both climatic and biotic stressors (Van Cleve *et al* 1983, Lieffers *et al* 2001). However, mortality and dieback of aspen as a result of moisture stress and insect infestation has been observed throughout North America since the early 2000s (Brandt *et al* 2003, Hogg *et al* 2005, 2008, Michaelian *et al* 2011, Cahoon *et al* 2018, Itter *et al* 2019). In interior Alaska, widespread and severe herbivory by the aspen leaf miner (*Phyllocnistis populiella* Cham.) has been documented since its first record of outbreak in the early 2000 s (USDA Forest Service 2012). In 2007, at the peak of the *P. populiella* outbreak, over 300 000 ha of Alaskan forests were infested (USDA Forest Service 2012, Yukon Energy, Mines and Resources 2012). *Phyllocnistis populiella* feeds on leaf epidermal cells during the summer months (Condrashoff 1964), and decreases leaf photosynthesis and growth and development of aspen aboveground tissues (Wagner *et al* 2008, Wagner and Doak, 2013). While this insect has caused significant damage in interior Alaska, we lack an understanding of the extent to which *P. populiella* impacts aspen productivity and physiology in the context of climate variation.

The impacts of climate and insects on tree growth can be assessed through annual variation in tree radial growth (Fritts 1971, Barber *et al* 2000, Leland *et al* 2016) and chemical composition, such as stable carbon isotope ratios (δ^{13}C) (McCarroll and Loader 2004). While climate variables that limit tree productivity are often reflected in radial growth (i.e. Briffa *et al* 2008, Feliksik and Wilczyński 2009), damage by insect pests can also reduce radial growth (Tikkanen and Roininen 2001, Weidner *et al* 2010) and distort the climate-growth signal (Trotter *et al* 2002, van de Gevel *et al* 2017). Tree ring δ^{13}C reflects the balance between stomatal conductance and photosynthetic rate (Farquhar and Richards 1984), which are influenced by climate (Farquhar *et al* 1982, 1993). For example, if moisture is limiting then more ^{13}C is fixed in tissues because stomatal closure results in decreased diffusion of CO_2 and a reduction in discrimination against $^{13}CO_2$ during photosynthesis (McCarroll and Loader 2004). Insects can also directly influence tree ring δ^{13}C by consuming leaf epidermal cells and impairing stomatal regulatory function (Weidner *et al* 2010), or indirectly by increasing photosynthesis in remaining and less damaged leaves (Simard *et al* 2008). Analyzing radial growth in conjunction with tree ring δ^{13}C can provide a better understanding of how insects impact growth, physiology, and related tree dynamics.

Consistent with radial growth measurements, recent declines in the normalized difference vegetation index (NDVI), often referred to as 'browning', have been observed in boreal North American across multiple spatial and temporal scales (Goetz *et al* 2005, Guay *et al* 2014, Ju and Masek 2016, Sulla-Menashe *et al* 2018). There are a number of abiotic and biotic factors that could be contributing to browning (Parent and Verbyla 2010), but there is strong evidence that tree productivity decline in response to moisture stress is a significant driver, particularly among evergreen conifers (Lloyd and Bunn 2007, Beck *et al* 2011, Verbyla 2015). However, the contribution of deciduous species such as aspen to boreal forest 'browning' is largely unknown. In addition, assessing the association between NDVI and other tree ring metrics, such as δ^{13}C, may provide insight on growth dynamics other than radial growth that are captured in the NDVI signal (i.e. Leavitt *et al* 2008, Castillo *et al* 2015), and could be applied to assess changes in climate, insect infestation, or shifts in carbon allocation patterns that are not detectable in annual diameter increment.

Given that aspen radial growth has declined in regions of the boreal forest during insect infestation (Hogg *et al* 2002, 2005) and periods of moisture stress (Hogg *et al* 2008, Michaelian *et al* 2011, Chen *et al* 2017), our goal was to assess how climate and *P. populiella* leaf mining affect aspen productivity and physiology in the boreal forest of interior Alaska. We also sought to determine if variations in aspen productivity and physiology are reflected in NDVI time-series and how they contribute to boreal forest 'browning'. We tested the following hypotheses using a combination of leaf insect herbivory, climate, tree ring, and satellite measurements:

(1) Stem radial growth and tree ring δ^{13}C will be influenced by the interaction between moisture and *P. populiella* infestation. Specifically, when *P. populiella* damage is low, growth and δ^{13}C will reflect variations in moisture availability. When *P. populiella* damage is high, growth and δ^{13}C will be de-coupled from climate, such that growth will decrease and δ^{13}C increase (become enriched) regardless of moisture availability.

(2) Tree growth will remain low for multiple years following severe *P. populiella* mining.

(3) Summer NDVI will decline during *P. populiella* infestation and co-vary positively with radial growth and negatively with δ^{13}C, capturing the effects of moisture availability and *P. populiella* on aspen growth and physiology.

Methods

In August of 2016 we conducted field work at four sites (appendix S1; table S1 is available online at stacks.iop.org/ERL/14/085010/mmedia), where mining by *P. populiella* had been measured since 2004. Henceforth, 'mining' or 'leaf mining' refers only to *P. populiella* damage. Leaf mining was assessed annually, directly following the completion of *P. populiella* feeding. Specifically, at each site from 2004–2015, the percentage of leaf area mined (top and bottom surfaces) was estimated on seven proximal leaves of a single shoot for each of 29 to 41 trees (see Doak and Wagner 2015 for details) and averaged to the site level (see table S1 for site information).

Within each site we delineated a 15 m radius circular plot. Starting in the center of the plot we sampled the closest aspen (>5.0 cm in diameter and > 1.4 m in height) every 5, 10, and 15 m in each cardinal direction. For each tree, we measured diameter at breast height and obtained two orthogonal wood cores at the standard height of 1.4 m. We sampled 12 trees per site for a total of 48 trees across the four sites. We refer to sampled stems as trees but acknowledge that stems sampled at the same site could belong to the same clone and have accounted for this in our statistical methods (see appendix S1). Although we did not sample the exact trees that had been measured to calculate site-level leaf mining, site level herbivory was a good representation of average leaf mining damage at the tree level (see Results and appendix S2). We also obtained site-level measurements of elevation, slope, aspect, and calculated density (stems m^{-2} of trees >1.4 m in height) and basal area (m^2 ha^{-1} of trees >1.4 m in height) of all tree species.

We built individual tree basal area increment (BAI) chronologies for all trees that could be accurately cross-dated ($n = 47$). Annual carbon isotope composition from 2004–2015 was determined in 23 trees from two sites (BNZ and RP) and individual tree δ^{13}C chronologies were built ($n = 23$). These sites were representative of all four sites in terms of growth response to leaf mining (see appendix S3). We also built mean site-level chronologies of BAI for all sites and δ^{13}C for BNZ and RP. Primary analyzes were performed using individual tree BAI and δ^{13}C chronologies to conserve individual tree variability (see appendix S4 for site-level chronology results).

Annual GS climate moisture index (CMI) for each site was calculated using a combination of climate data from ClimateNA (Climate North America) (Wang *et al* 2016) and Fairbanks International Airport (FAI; National Centers for Environmental Information 2016) from 2004–2015. Site specific annual mean July–August NDVI was determined from 2004–2015 using NDVI derived from Landsat, the Moderate Resolution Imaging Spectroradiometer (MODIS), and the Advanced Very High Resolution Radiometer. We present Landsat NDVI results because of the higher spatial resolution and comparable results on the relationship between Landsat NDVI and tree ring measurements with other NDVI products (appendix S5). These measurements were used to assess the impacts of climate and *P. populiella* mining on aspen productivity, physiology, and NDVI trends. For detailed methods, refer to appendix S1.

Results

Climate and site characteristics

Across all sites, GS CMI was highest in 2014 (24.9 ± 7.72; mean ± 1 SE) and lowest in 2004 (−16.2 ± 3.20; figure 1) and was highly collinear among all sites (table S9). Average % site-level leaf mining was lowest in 2013 (1.95 ± 1.03%; mean ± 1 SE) and highest in 2007 (58.1 ± 3.35%; figure 1). Based on the trees sampled for herbivore damage, the greatest variability in leaf mining at the tree and stand level was during years of low mining (appendix S5), yet mining was still minimal across all leaves (i.e. 1.93 ± 3.66, mean % leaf mining ± SD for all trees surveyed in 2013). During years of high leaf mining, variation in % mining relative to the mean at both the tree and stand level was small compared to low mining years (appendix S2), such that mining was similar within and across trees at each site. Mean July–August Landsat NDVI across all sites was lowest in 2010 (0.68 ± 0.02; mean ± 1 SE) and highest in 2012 (0.79 ± 0.01; figure 1) and was highly correlated across all sites (table S6).

Aspen stem density was greater than that of other tree species (*Picea glauca*, *Betula neoalaskana*, and *Populus balsamifera*) at all sites (table S1). Similarly, aspen basal area was greater than that of other species at all sites except ED, where basal area of *B. neoalaskana* was highest (22.41 m^2 ha^{-1}). Stands varied in age, with the youngest stand (24 years) at roughly half the age of the oldest stand (52 years; table S1). Aspen productivity (mm^2 yr^{-1}) was positively related to tree ring δ^{13}C ($\beta_1 = 0.11$, $t = 5.33$, $df = 252$, $P < 0.05$), suggesting that an enrichment in δ^{13}C was associated with increased radial growth.

Impact of climate and leaf mining on productivity and δ^{13}C

As leaf mining increased BAI decreased (figure 2(a); table S10), with every 10% increase in mining resulting in a 10.22 mm^2 decrease in BAI (data not shown).

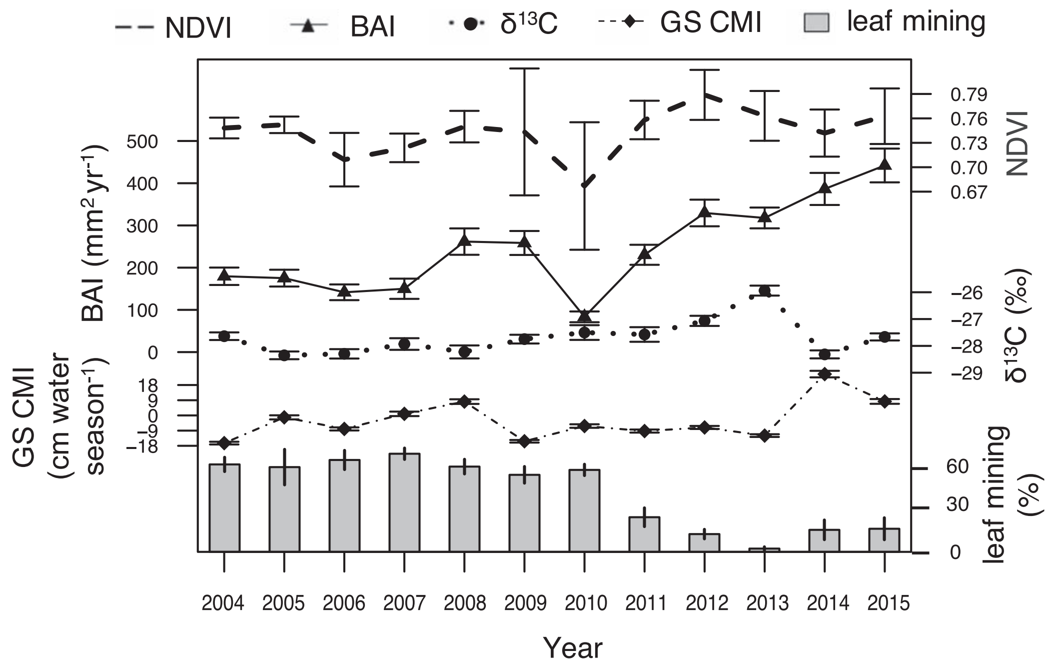

Figure 1. Mean July–August Landsat derived NDVI averaged across all sites ($n = 4$), average basal area increment (BAI) of all trees, average δ^{13}C (‰) of all trees from BNZ and RP, mean growing season climate moisture index (GS CMI; May–September) across all sites, and mean site-level % leaf mining averages across all sites from 2004–2015. Error bars show the standard error of the mean.

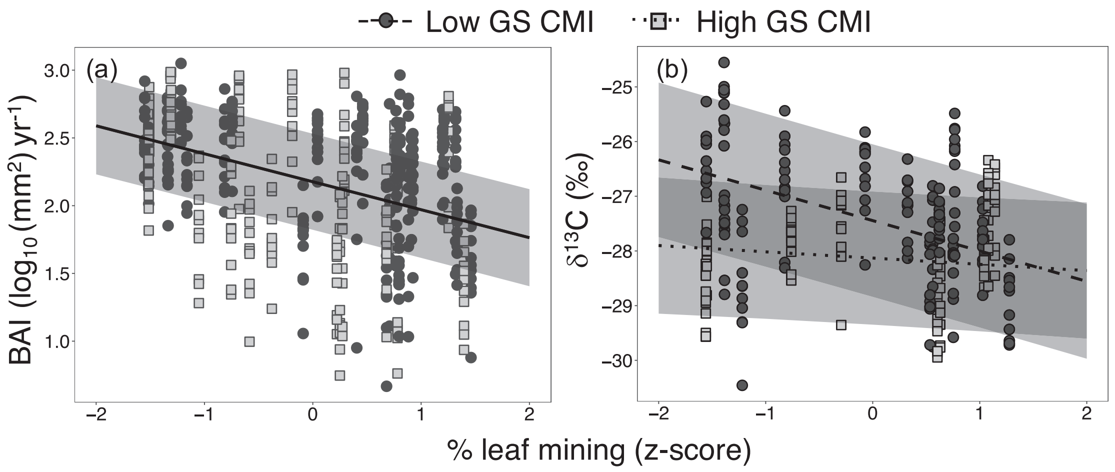

Figure 2. Results of hierarchical linear mixed effects models depicting the effect of (a) average % site-level leaf mining on log transformed basal area increment chronologies (BAI) of individual trees and (b) the influence of GS CMI and average % site-level leaf mining on δ^{13}C chronologies of individual trees. Covariates of average % site level leaf mining and GS CMI were scaled and centered to improve model interpretability. Points are years within a tree and are depicted as low (below average; dark grey circles) or high (above average; light grey squares) GS CMI. In (b), lines indicate relationship between δ^{13}C and % leaf mining and climate when GS CMI is high (dashed line; above average) and low (dotted line; below average). All lines represent final model fit, shading indicates 95% confidence intervals. For results of parameter estimates and AICc criterion see table S10 for (a) and table S11 for (b).

However, BAI was not influenced by GS CMI or the interaction between GS CMI and leaf mining (figure 2(a); table S10). Tree ring δ^{13}C was influenced by the interaction between GS CMI and leaf mining (table S10). When leaf mining was low tree ring δ^{13}C exhibited a typical response to moisture availability, such that δ^{13}C was more enriched when moisture was less available (figure 2(b)). As leaf mining increased tree ring δ^{13}C decreased when moisture availability was low (table S11; figure 2(b)), with every 10% increase in mining resulting in a 0.24‰ decrease in δ^{13}C (data not shown). When moisture availability was high, δ^{13}C did not exhibit an association with leaf mining (table S11; figure 2(b)).

Productivity prior to and after severe leaf mining

BAI was significantly lower during high leaf mining years (2004–2008) compared to years prior to the leaf

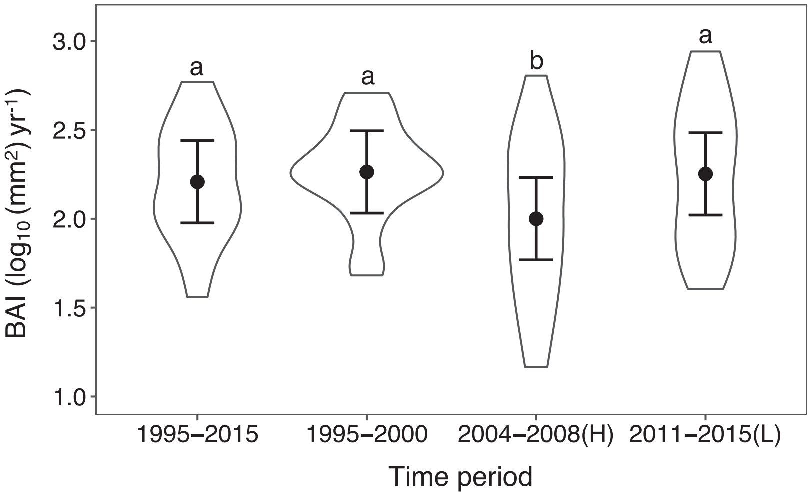

Figure 3. Least square mean log transformed basal area increment (BAI $\log_{10}$ (mm^2) yr^{-1}) of the whole time period considered (1995–2015), prior to the leaf miner outbreak (1995–2000), years of high leaf mining (2004–2008), and years of low leaf mining (2011–2015). Only trees that established prior to 1985 were included in the analysis. Points and error bars indicate least square means and 95% confidence intervals, and violin plots depict data distribution. Different letters denote significant difference in BAI between time periods based on Tukey-adjusted post-hoc pairwise comparison ($P < 0.05$).

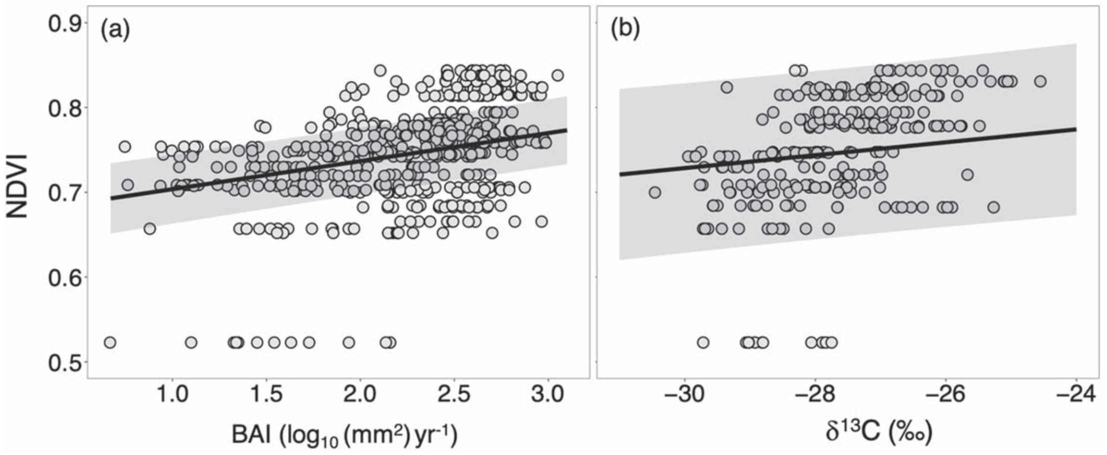

Figure 4. Results of hierarchical linear mixed effects models with mean July–August Landsat derived NDVI as the response variable and the fixed effect of (a) log transformed basal area increment (BAI) of individual tree chronologies and (b) δ^{13}C chronologies of individual trees. Black lines represent model fit, shading indicates 95% confidence intervals, and points are years within a tree. See table S8 for parameter estimates.

miner outbreak (1995–2000) and years of low leaf mining (2011–2015; figure 3; table S12). During low leaf mining years (2011–2015), BAI recovered to the same levels observed prior to the leaf miner outbreak (1995–2000; figure 3; table S12).

Relationships between NDVI, leaf mining, climate, and tree ring measurements

July–August Landsat NDVI was negatively associated with leaf mining and not related to GS CMI (*marginal* $R^2 = 0.11$, *conditional* $R^2 = 0.66$; table S7), and was positively associated with tree productivity (BAI) and δ^{13}C (figure 4; table S8). Tree productivity explained a slightly greater proportion of variance in Landsat NDVI than tree ring δ^{13}C (figure 4; table S8). All NDVI products exhibited a positive association between BAI and δ^{13}C. The strength of these relationships differed between products, with GIMMS$_{3g}$ exhibiting the strongest association with δ^{13}C when compared to relationships across all NDVI products and tree ring measurements (table S8; appendix S5).

Discussion

Our study on the direct and indirect impacts of climate on aspen productivity and physiology in interior Alaska suggests that productivity was primarily limited by *P. populiella* leaf mining and not moisture. The physiological response to moisture, as indexed by δ^{13}C, was disrupted by *P. populiella*, with increased mining resulting in decreased δ^{13}C at low moisture. Despite productivity strongly decreasing in association with severe leaf mining, tree productivity recovered to pre-infestation levels when leaf mining decreased. We also found that interannual variability in leaf herbivory, productivity, and physiology were captured by space-based measurements of summer NDVI. These findings highlight the importance of accounting for insect herbivory when analyzing aspen growth and physiology, and NDVI trends in interior Alaska.

Tree productivity is sensitive to leaf mining

Our findings indicate that during *P. populiella* infestation, insect damage negatively impacts aspen radial growth in interior Alaska, which is in agreement with studies in the southern boreal forest and aspen parkland on aspen growth during insect outbreaks (Hogg *et al* 2002, 2005, 2008, Chen *et al* 2018, Itter *et al* 2019). Contrary to our results, these studies also found that growth is sensitive to moisture availability during insect outbreaks, and in some cases dry conditions exacerbated the negative impact of insects on aspen productivity (i.e. Hogg *et al* 2002). As the mean annual temperature in Alaska has risen by approximately 1.7 °C in the last six decades (USGCRP 2014), we expected aspen productivity to be sensitive to moisture. However, we likely did not observe a productivity response to GS moisture availability as our study area is not as dry as regions of the boreal forest that have recently been examined (i.e. Hogg *et al* 2005, 2008, Michaelian *et al* 2011). Specifically, the lowest annual CMI (summed CMI over a 12 month period ending on July 31) documented at our study sites was -12.6 cm water year^{-1}. This is two times greater than the annual CMI observed during the 2001–2002 drought in Western Canada that resulted in aspen mortality and growth decline (Hogg *et al* 2008, Michaelian *et al* 2011). In addition, Cahoon *et al* (2018) found that radial growth of aspen in interior Alaska was not sensitive to precipitation during and 15 years prior to the *P. populiella* outbreak. Overall, our results suggest that aspen productivity is currently not moisture limited during *P. populiella* infestation. However, as temperatures continue to rise in interior Alaska (USGCRP 2014), the effect of moisture availability is likely to increase, as has been observed in drier areas of the boreal forest.

Tree ring δ^{13}C influenced by moisture availability and leaf mining

To our knowledge, this is the first study to investigate the influence of insect herbivory and climate on aspen tree ring δ^{13}C. We found that tree ring δ^{13}C was sensitive to moisture during the current GS, a signal that has also been observed in interior Alaska for other boreal species (Barber *et al* 2000, Walker *et al* 2015). However, leaf mining de-coupled the δ^{13}C-climate response. We observed a progressively depleted δ^{13}C signal with greater mining damage when moisture availability was low, which suggests that the insects dominate the δ^{13}C signal when leaf mining is moderate to severe. This isotope pattern is the opposite of what is expected during drought (McCarroll and Loader 2004) and is also opposite of what has been documented at the foliar level (Wagner *et al* 2008).

The decreased wood δ^{13}C with leaf mining that we observed could be due to post-photosynthetic fractionation during transport of metabolites from leaves to wood or during heterotrophic metabolism (Gessler *et al* 2009, Offermann *et al* 2011). Alternatively, the δ^{13}C of wood could reflect photosynthates produced in the early part of the GS (earlywood), which is isotopically lighter than latewood (Leavitt 1993, Livingston and Spittlehouse 1996, Kagawa *et al* 2006) and can dominate annual rings during pest or pathogen outbreaks (Fajvan *et al* 2008, Simmons *et al* 2014, Bert *et al* 2016). Tree ring δ^{13}C may also be reflective of photosynthates produced in leaves that were less heavily mined. Heavily mined leaves abscise earlier than those with less damage (Wagner *et al* 2008). A reduction in foliar biomass can reduce transpiration losses and increase water availability per unit leaf area, increasing stomatal conductance in remaining leaves (Reich *et al* 1993, Quentin *et al* 2011). Following a defoliation event, an upregulation of photosynthesis has also been documented in remaining leaves (Li *et al* 2012, Quentin *et al* 2012), and in some cases was only stimulated in more water-limited conditions (Kolb *et al* 1999, Geiger and Thomas 2005). If stomatal conductance or both stomatal conductance and photosynthesis increased in leaves remaining after premature leaf loss during *P. populiella* infestation, this would explain the δ^{13}C decrease associated with mining that we observed.

The rapid recovery of growth during years of low leaf mining, which were preceded by numerous years of severe and sustained *P. populiella* herbivory, is consistent with the third mechanism proposed above. While this recovery could be due to high photosynthetic rates in years following *P. populiella* damage, our δ^{13}C results suggest that this may be due to changes in allocation of photosynthates during infestation. Specifically, the decrease in tree ring δ^{13}C that we observed with greater mining may indicate that whole tree photosynthate production during *P. populiella* infestation may not decline (higher conductance and photosynthesis in less heavily mined leaves, as discussed above), but carbon allocation to radial growth decreases. Shifts in carbon allocation priorities have been documented during years of severe insect damage (Palacio *et al* 2012, Deslauriers *et al* 2015), particularly to non-structural carbohydrates (NSC) at the expense of radial growth (Wiley *et al* 2013, Piper and Fajardo 2014, Saffell *et al* 2014). As remobilization of stored carbon is necessary for trees to rapidly produce leaves in the beginning of the GS (Barbaroux *et al* 2003, Silpi *et al* 2007), an increase in allocation of carbon to NSC during *P. populiella* infestation explains the recovery in growth of aspen during years of low insect herbivory, and is consistent with lower BAI during infestation. However, with our current dataset we cannot decisively conclude that aspen increase allocation to NSC at the expense of radial growth during leaf miner infestation, and further research on this topic is warranted.

Our findings support the idea that aspen radial growth is resilient to leaf miner infestation since productivity recovered during low mining periods to levels observed prior to severe and sustained *P. populiella* mining. However, repeated insect outbreaks can reduce carbon reserves in roots of aspen (Landhäusser and Lieffers 2012) and NSCs used for maintenance, respiration, reproduction, and defense, which are particularly important during periods of drought (O'Brien *et al* 2014). Thus, after multiple leaf miner outbreaks or longer periods of insect infestation, carbon stores may become depleted and inadequate for re-foliation in years following outbreaks and recovery of lost radial growth. This is important to consider as climate change has and will continue to influence insect life cycles, abundance, and survival in the boreal forest.

NDVI reflects variations in leaf mining, productivity, and δ^{13}C

We detected a negative association between NDVI and leaf mining, and a positive correlation between NDVI and BAI. The latter is in agreement with other studies that have shown a positive association between radial growth and summer NDVI in the boreal forest (Lopatin *et al* 2006, Beck *et al* 2011, Berner *et al* 2011, Wu *et al* 2012). The negative association between NDVI and mining, and BAI and mining, emphasizes the importance of accounting for insect infestation when assessing NDVI trends in the boreal forest. Furthermore, we found that δ^{13}C was positively associated with July–August NDVI, suggesting a link between canopy condition and secondary productivity as described by BAI, and potentially between changes in allocation patterns of photosynthates during leaf miner infestation (i.e. allocation to NSC as discussed above). Specifically, with increased *P. populiella* mining we would expect to see greater leaf loss earlier in the GS (Wagner *et al* 2008) and a compensatory response of conductance and photosynthesis of remaining and/or less damaged leaves, resulting in both lower NDVI and more negative δ^{13}C in wood. Prior studies in the boreal forest have linked 'browning' to declining tree radial growth (Beck *et al* 2011, Berner *et al* 2011) and tree mortality events (Rogers *et al* 2018), but our results highlight the importance of also considering direct and indirect impacts of rising air temperatures on changes in physiology and allocation when interpreting the NDVI signal.

Conclusion

As temperatures and associated fire disturbances increase in boreal forests (Chapin *et al* 2008, Wendler and Shulski 2009, IPCC 2013), landscapes previously dominated by conifers may experience a shift to deciduous dominance (Goetz *et al* 2007, Huang *et al* 2010, Johnstone *et al* 2010). However, the response of deciduous species such as aspen to the direct and indirect impacts of climate warming in boreal forests, and their contribution to the NDVI signal, has been uncertain. Our findings suggest that under current climate conditions, *P. populiella* leaf mining has a larger impact than moisture availability on aspen productivity and physiology, yet productivity recovered tree to pre-infestation levels following severe *P. populiella* mining. However, with climate warming and drying, we may see a more direct effect of climate on growth, and in turn decreased resilience to *P. populiella* mining. Variations in both productivity and physiology due to leaf mining were reflected in mean July–August NDVI, highlighting the utility of summer NDVI for monitoring tree growth and insect dynamics at large scales, but also points to challenges in interpreting the NDVI signal if climate warming shifts productivity, allocation, and insect herbivory. Ultimately, our finding suggest that it is essential to account for insect herbivory in Alaskan boreal forests when assessing variability in aspen growth and physiology, and 'browning' trends as indicated by NDVI.

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