Insect-related tree mortality in south-central Alaska may be controlled by prior drought stress as indicated by $\delta^{13}C$ and $\delta^{18}O$ in tree rings

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Abstract

Increasing temperatures have resulted in reduced growth and increased tree mortality across large areas of the northern boreal forest. Following a recent spruce beetle (*Dendroctonus rufipennis*) outbreak in south-central Alaska, we examined whether trees showed evidence of temperature-induced drought stress prior to death by using tree-ring chronologies and $\delta^{13}C$ and $\delta^{18}O$ isotopic values in cellulose from paired live and dead trees. We also tested whether surviving trees differed from dead trees in their growth response and temperature sensitivity.

Our results indicate that trees killed by the beetle showed reduced radial growth up to 20 years prior to death, relative to surviving trees, and that this was true across age and DBH classes (n=48 pairs; $P<0.004$). A moving correlation between monthly mean temperature and live and dead tree-growth indices shows that whereas growth in surviving trees was only weakly correlated with temperature before the beetle outbreak, growth in the dead trees was positively correlated with spring-summer temperatures, particularly June mean temperature ($R=0.5$; $P<0.05$) for several decades before. Approximately 10 years prior to tree death, growth in the dead trees became decoupled from temperature. This is in contrast to $\delta^{13}C$ and $\delta^{18}O$ values in dead trees from the site that show a strong positive correlation between $\delta^{13}C$ and mean June maximum temperature ($R^2 = 0.35$; $P<0.001$), and with $\delta^{18}O$ later in the summer (June-July maximum temperature; $R^2 = 0.26$; $P<0.001$).

In the 10 years prior to tree death, the $\delta^{13}C$-temperature relationship became highly significant in trees killed by spruce beetle attack (June-July; $R^2=0.61$; $P<0.05$) (March-May; $R^2 = 0.73$; $P<0.01$) and the spring temperature signal also appeared in surviving live trees. Temperature-induced drought stress is the likely cause for the June-July temperature signals seen in the $\delta^{13}C$ and also explains the decoupling of temperature and growth in trees that were killed during the outbreak. The spring temperature signal is more complex and could be related to earlier melt, resulting in drier soil conditions early in the growing season and subsequent water stress in the trees that ultimately died.

Our $\delta^{13}C$ and $\delta^{18}O$ results indicate that surviving live and beetle-killed dead trees differ in their physiological response to temperature, and that divergence in the growth-temperature relationship can feed back to disturbance. Our results also indicate that trees that survive beetle outbreaks are less climatically sensitive than trees that die. This suggests that certain trees within a stand may be physiologically pre-disposed to mortality events by nature of their environmental response.

Background and Methods

Over 1.5M ha of forest have been killed by the spruce beetle (*Dendroctonus rufipennis*) in south-central Alaska during the recent outbreak (1990-2008). Above-average summer temperatures for several consecutive years are thought to have triggered the event, but in a region with relatively wet summers it remains unclear whether trees were drought-stressed prior to beetle attack. Using cores collected from live and dead white spruce (*Picea glauca*) at four sites affected by the spruce beetle (Fig. 1), we used ring-width chronologies and $\delta^{13}C$ and $\delta^{18}O$ in tree-ring cellulose to address the following questions:

1) Do trees killed by the spruce beetle show greater sensitivity to temperature in terms of growth and $\delta^{13}C$ than trees that survived the beetle attack?

2) Do trees show evidence of temperature-induced drought stress, as indicated by $\delta^{13}C$ and $\delta^{18}O$?

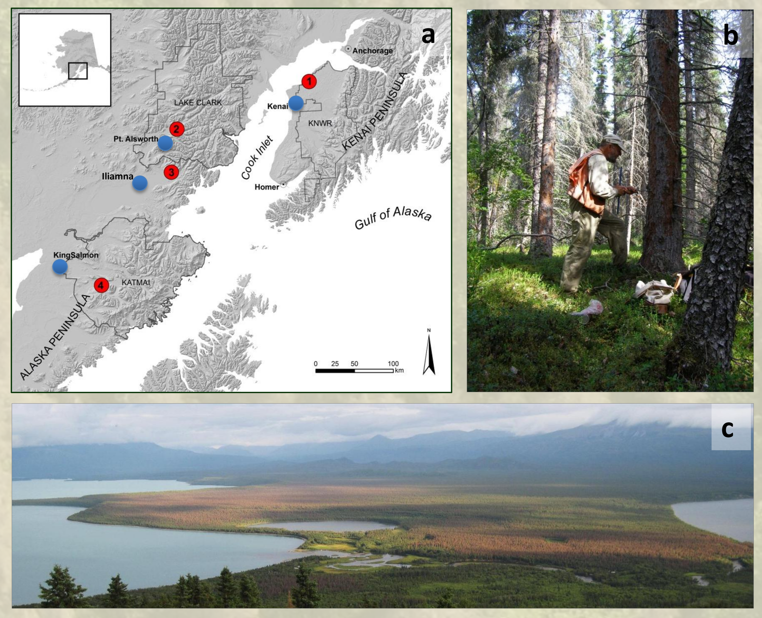

Fig. 1a. Study sites: 1) Bufflehead Rd; 2) Currant Cr.; 3) Pedro Bay; 4) Valley 10K Rd. **1b-c.** Views of Valley 10K Rd site on the Alaska Peninsula.

The study area encompasses two climatic zones in south-west and south-central Alaska. Mean annual temperature over most of the area is ~1 °C. Mean annual precipitation ranges from 375 mm-620 mm, with most falling as rain between July and October (Sherriff et al. 2011).

Study sites range in elevation from 75 m (Alaska Peninsula: Currant Cr and Valley 10K Rd) to 107 m (Kenai Peninsula: Bufflehead Rd). Infestation levels are moderate to high in all stands.

Sampled trees ranged from 26-62 cm in DBH and were between 109-246 years old. Cores and disks were cross-dated and measured using standard dendrochronological techniques (Cook and Kairiukstis, 1990). Ring-width chronologies were produced for the live and dead trees using the program ARSTAN.

For isotopic analysis, we analyzed 30 years from the Currant Creek (1980-2011) and Pedro Bay (1974-2004) sites, 35 years (1975-2010) from the Valley of 10K Rd site, and 45 years (1950-1995) from the Bufflehead Rd site. We pooled cores from 4-6 live and 4-6 dead trees at Currant Creek and Pedro Bay; we pooled 4 cores each from 4 live and 4 dead trees at Valley 10K; and we analyzed disks from 4 live and 4 dead trees at Bufflehead Rd.

All cores were sampled using micro-milling technology (Dodd et al. 2008) and processed to α-cellulose using the method outlined by Brendel et al. (2000), modified to include a rinsing step with sodium hydroxide to eliminate holocellulose (Gaudinski et al. 2005). All isotopic analyses were conducted at the University of Alaska Anchorage in the Environment and Natural Resources Institute stable isotope laboratory. $\delta^{13}C$ values were obtained from all sites, whereas $\delta^{18}O$ values were obtained only from the Pedro Bay, Valley of 10K and Bufflehead sites. All $\delta^{13}C$ series were corrected for the trend in atmospheric $\delta^{13}C$ values prior to interpretation.

Climate station data were obtained from the National Climatic Data Center (NCDC) and included stations located at Iliamna, Port Alsworth, King Salmon Airport and the Kenai Airport. All stations were checked for homogeneity and found to be homogeneous over the time period of interest.

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Reduced growth in beetle-killed trees prior to death

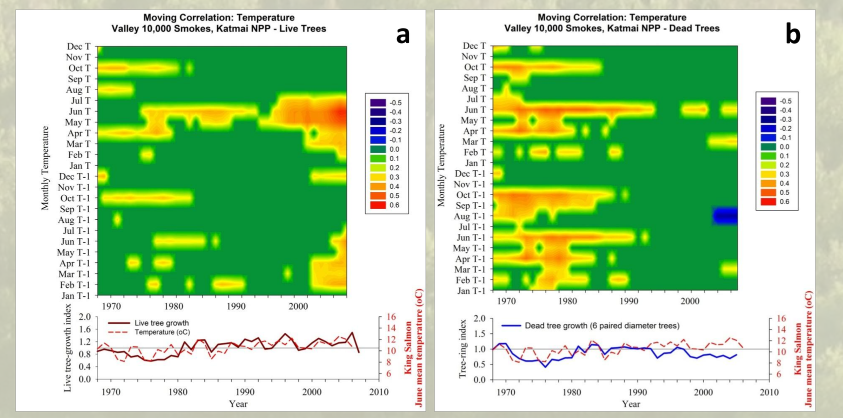

Fig. 2. Moving correlation between temperature and growth at the Valley 10K Rd site (Alaska Peninsula) using a 48-y window for year prior to growth and year of growth.

Live trees at our sites have responded positively to warming in recent decades (e.g., Fig. 2a, Fig. 3a), whereas beetle-killed trees have often responded negatively to warming prior to death, particularly at the southernmost site on the Alaska Peninsula (Fig. 2b). However, at a second site further north, both live and dead trees responded positively to warming (Fig. 3a-b), suggesting that growth was temperature- rather than water-limited. Dead trees nevertheless showed reduced growth prior to death. Our results indicate that across the Alaska Peninsula, trees killed by the beetle have shown reduced radial growth up to 20 years prior to death, relative to surviving trees, and that this reduction in growth has occurred across age and DBH classes (n=48 pairs; $P<0.004$; Fig. 4).

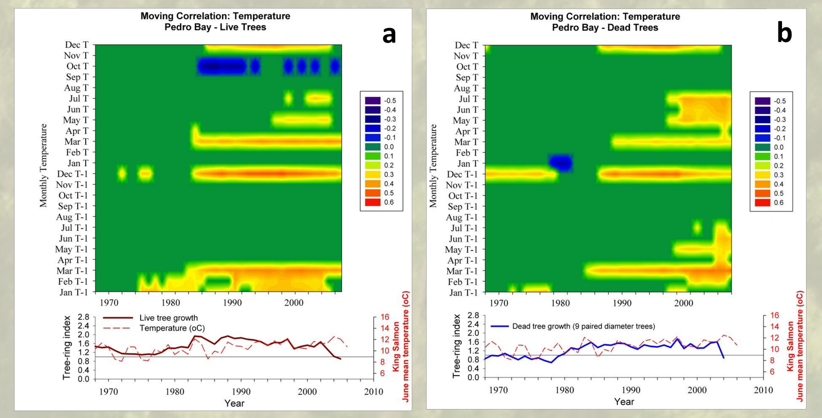

Fig. 3. Moving correlation between temperature and growth at the Pedro Bay (Alaska Peninsula) site using a 48-y window for year prior to growth and year of growth.

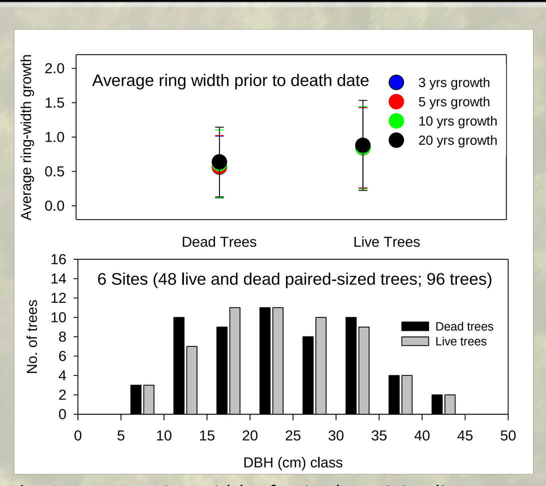

Fig. 4. Average ring width of paired surviving live trees and beetle-killed trees across six spruce beetle-infested sites on the Alaska Peninsula. Dead trees showed reduced growth prior to tree death.

$\delta^{13}C$ values indicate temperature sensitivity in beetle-killed trees

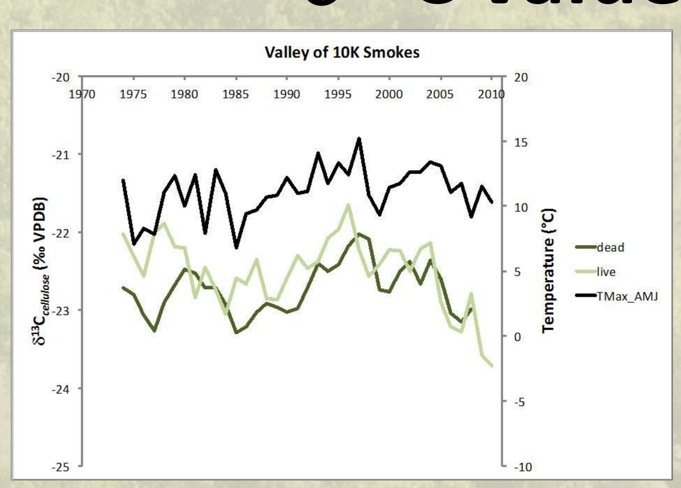

Fig. 5. Maximum April-June temperature and $\delta^{13}C$ chronologies from live and dead trees at Valley 10K Rd (Alaska Peninsula).

At the Valley of 10K Rd site on the southern Alaska Peninsula, $\delta^{13}C$ values in live and dead trees tracked maximum spring temperature (Fig. 5). However, $\delta^{13}C$ values in dead trees were more sensitive to (positively correlated with) temperature ($R^2 = 0.42$; $P<0.01$) than surviving live trees (Figs. 6-7), suggesting temperature-induced drought stress in the trees that died. Spring 'drought' could have occurred as trees initiated growth on late-thawing soils. Reduced water absorption and photosynthate production would have left a subset of trees water-stressed and susceptible to beetle attack (cf. Hard, 1987).

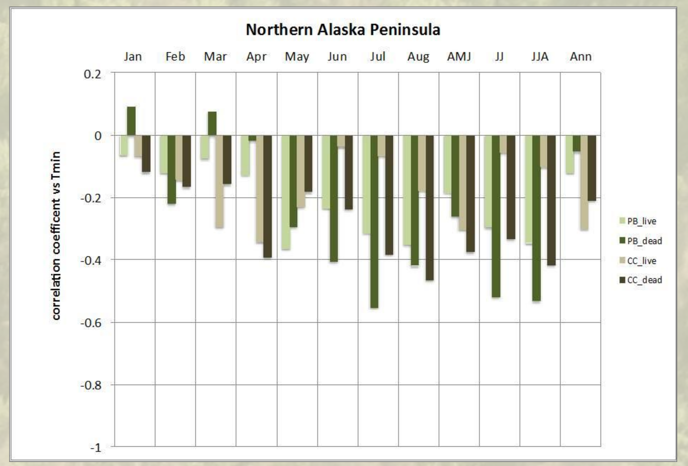

Fig. 8. Correlation coefficients and $\delta^{13}C$ chronologies from live and dead trees at Pedro Bay and Currant Creek (Lake Clark NP).

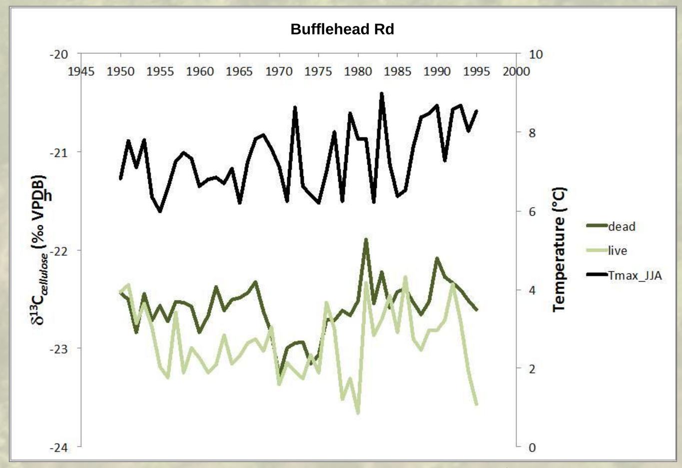

Fig. 9. Maximum June-August temperatures and $\delta^{13}C$ chronologies from live and dead trees at Bufflehead Rd (Kenai Peninsula).

At the Bufflehead Rd site on the Kenai Peninsula, $\delta^{13}C$ values in beetle-killed trees indicated temperature-induced drought stress associated with summer temperatures. As with the Valley 10K site, beetle-killed trees were more sensitive to temperature than surviving trees: $\delta^{13}C$ values in dead trees were enriched relative to live trees (Fig. 9) and were positively correlated with spring and summer temperatures ($R^2 = 0.30$; $P<0.01$; Fig. 10).

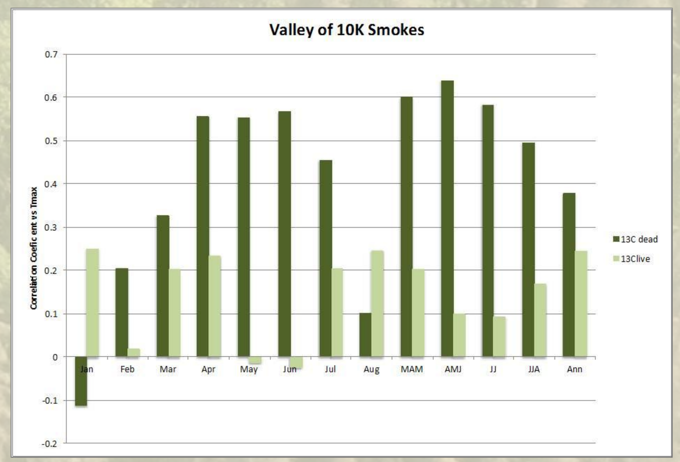

Fig. 6. Correlation coefficients and $\delta^{13}C$ chronologies from live and dead trees at Valley 10K Rd (Alaska Peninsula). Results indicate that beetle-killed trees are isotopically more temperature sensitive than survivors, suggesting temperature-induced water stress.

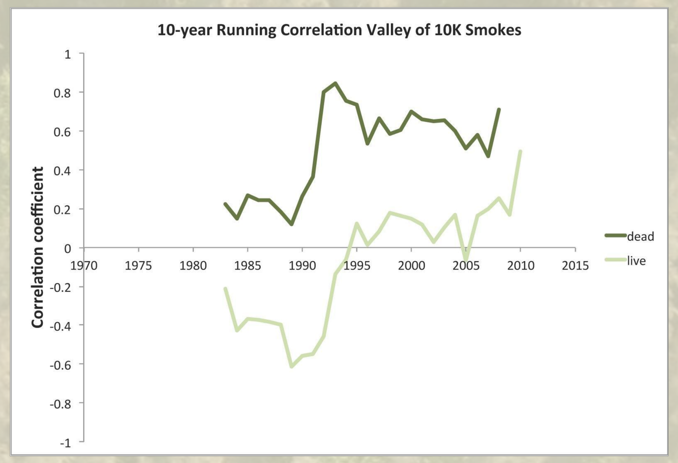

Fig. 7. 10-year running correlation of $\delta^{13}C$ chronologies from live and dead trees at Valley 10K Rd (Alaska Peninsula) with June-July maximum temperatures. Dead trees show an increased response to temperature starting 10-years prior to death ($R^2 = 0.73$; $P<0.01$).

At Pedro Bay (PB) and Currant Creek (CC), on the northern Alaska Peninsula, beetle-killed trees were more sensitive to temperature than surviving live trees. However, $\delta^{13}C$ values in dead trees were negatively correlated with minimum summer temperature ($R^2 = -0.18$; $P<0.05$; Fig. 8), suggesting that trees were not drought-stressed, but rather experienced wetter growing conditions, lower photosynthetic rates, or both, prior to death. In dead trees at both sites, $\delta^{13}C$ values were generally more enriched than in live trees. At Pedro Bay, $\delta^{13}C$ values correlated negatively with spring precipitation, suggesting that water availability at the start of the growing season may be critical to tree growth and survival.

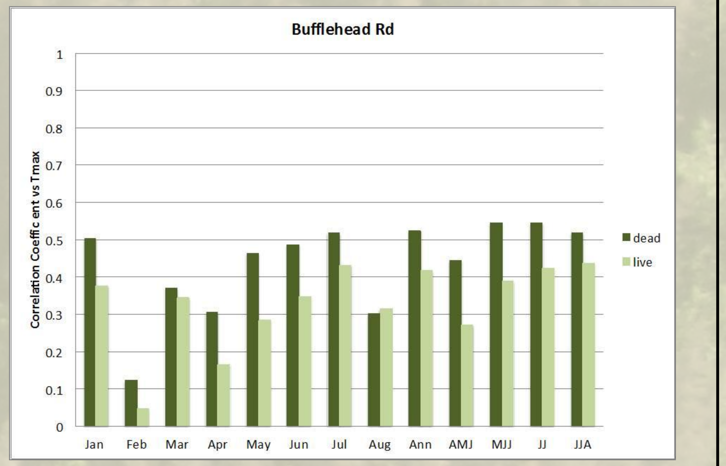

Fig. 10. Correlation coefficients and $\delta^{13}C$ chronologies from live and dead trees at Bufflehead Rd (Kenai Peninsula). Beetle-killed trees are isotopically more temperature sensitive than survivors.

Summary

1. Trees killed by the spruce beetle showed **reduced radial growth up to 20 years prior to death**, relative to surviving trees, across age and DBH classes.

2. At all sites, **$\delta^{13}C$ values in beetle-killed trees were more sensitive to spring-summer temperatures** than in surviving trees.

$\delta^{18}O$ values are sensitive to temperature and snow depth

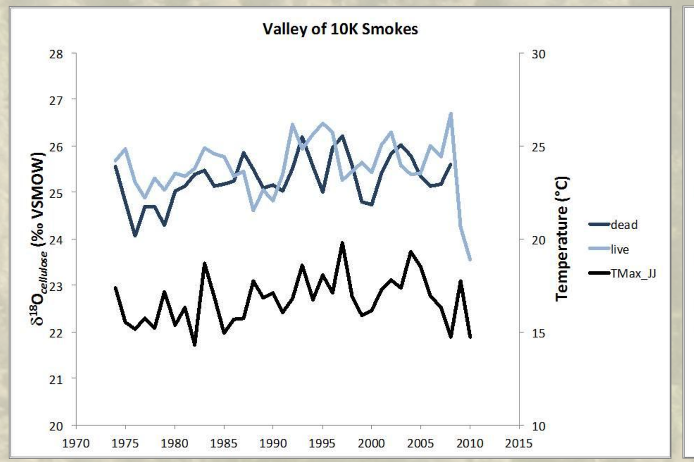

Fig. 11. Maximum June-July temperatures and $\delta^{18}O$ chronologies from live and dead trees at Valley 10K Rd (Alaska Peninsula).

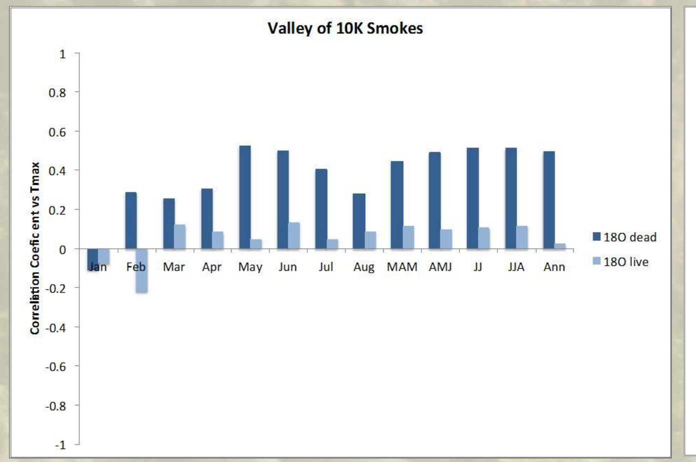

Fig. 12. Correlation coefficients between mean monthly maximum temperatures (Tmax) and $\delta^{18}O$ chronologies from live and dead trees at Valley 10K Rd (Alaska Peninsula).

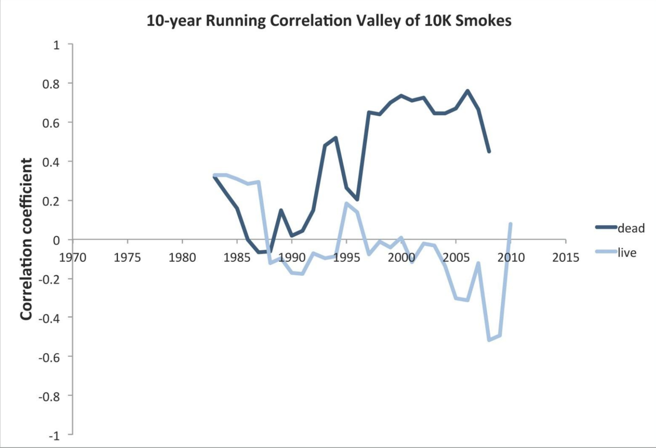

Fig. 13. 10-year running correlation of $\delta^{18}O$ chronologies from live and dead trees at Valley 10K Rd (Alaska Peninsula) with June-July maximum temperatures. Dead trees show an increased response to temperature starting 10-years prior to death.

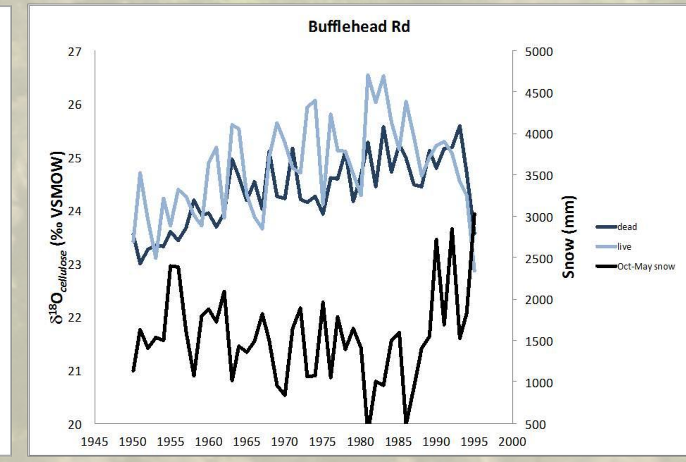

Fig. 14. Winter (Oct-May) snow depth and $\delta^{18}O$ chronologies from live and dead trees at Bufflehead Rd (Kenai Peninsula).

At the Valley of 10K Rd site, $\delta^{18}O$ values in beetle-killed trees were positively correlated with maximum spring and summer temperatures ($R^2 = 0.26$; $P<0.01$; Figs. 11-12), suggesting evaporative enrichment due to water stress. Surviving trees were much less sensitive to temperature than the trees that died. A 10-year running correlation of $\delta^{18}O$ values showed increased temperature sensitivity in dead trees in the 10 years prior to death (Fig. 13). This is in agreement with $\delta^{13}C$ values from beetle-killed trees that showed an increased sensitivity to temperature in the 10 years prior to death (Fig. 7), as well as with ring-width data that show decreased growth in beetle-killed trees 10-20 years prior to death in response to warmer temperatures (Figs. 2 and 4). -- At Pedro Bay, $\delta^{18}O$ chronologies from live trees indicate a response to late winter precipitation ($R^2 = 0.14$; $P<0.1$; data not shown), comparable to results from Bufflehead Rd (Fig. 14). We have not yet analyzed $\delta^{18}O$ in the cores from the dead trees.

At Bufflehead Rd, the strongest signal in the $\delta^{18}O$ values was with winter (Oct-May) snowfall (Fig 14), rather than with spring-summer temperature as with Valley 10K Rd (Fig. 11). In addition, it was the surviving trees rather than beetle-killed trees that showed the strongest correlation with snowfall ($R^2 = 0.29$; $P<0.01$). Live trees had enriched $\delta^{18}O$ values (Fig. 14) that were also weakly correlated with summer (June-August) precipitation ($R^2 = 0.17$; $P<0.01$; data not shown), suggesting that trees that can access both winter and summer precipitation may be better able to survive a beetle outbreak.

Summary (cont.)

3. Positive correlations between $\delta^{13}C$ and spring-summer temperature in dead trees indicated **temperature-induced drought stress** at two of four sites. Hydraulic failure in the xylem resulting from blue-stain fungi is also a possibility.

4. A negative correlation between $\delta^{13}C$ and minimum summer temperature in dead trees suggested **wetter growing conditions, lower photosynthetic rates, or both** at the remaining two sites.

5. A positive correlation between $\delta^{18}O$ and spring-summer temperature in dead trees suggested drought stress (Valley 10K Rd), whereas the correlation between $\delta^{18}O$ and snow depth in live trees suggested the importance of snow as a water source (Bufflehead Rd). The **isotope-climate relationship appears to be strongest in the spring**, suggesting that the timing of growth, in addition to water availability, determines which trees may survive a beetle attack.

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