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Wood δ^{13}C, δ^{18}O and radial growth responses of residual red pine to variable retention harvesting

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Summary Variable retention harvests are used to enhance the development of structural complexity in managed forests by retaining living trees and other structural legacies from the pre-harvest ecosystem. While harvesting should increase resource availability to residual trees, greater crown exposure may also increase environmental stress, which makes it difficult to predict growth in different structural environments. We used stable carbon isotope ratios (δ^{13}C) of annual rings from red pine trees (*Pinus resinosa* Ait.) as an index of intrinsic water use efficiency (iWUE), the ratio of photosynthetic carbon assimilation (A) to stomatal conductance (g_s), to better understand how differences in physiological performance relate to growth responses following harvests that left residuals dispersed, aggregated between small (0.1 ha) gaps or aggregated between large (0.3 ha) gaps. Stable oxygen isotope ratios (δ^{18}O) were used as an index of g_s to investigate the drivers behind changes in iWUE. Retention harvesting did not appear to affect δ^{13}C or δ^{18}O at the stand scale when compared to unharvested control stands, but there was a significant, negative correlation between residual tree δ^{13}C and plot basal area in the second and third years after harvesting that suggests declining iWUE as overstory competition increases. Residual tree δ^{18}O was similar across treatments and basal areas. Trees in variable retention harvests showed small but positive increases in radial growth from the pre-treatment to post-treatment measurement periods, while radial growth declined in unharvested control stands. There were no significant differences in radial growth among retention treatments. Our results suggest residual red pine in relatively open environments benefit from greater A but do not show evidence of changes in g_s that would indicate altered water relations.

Keywords: forest management, intrinsic water use efficiency, Pinus resinosa, stable isotopes.

Introduction

Structural complexity benefits forest ecosystems by promoting biodiversity, sustaining key ecosystem processes and maintaining ecological resilience in the face of changing environmental conditions (Franklin et al. 1997, Lindenmayer and Franklin 1997, Palik et al. 2002, Drever et al. 2006), but complexity in managed forests is often lower than in unmanaged forests (Franklin et al. 2002). Variable retention harvest systems maintain structural elements within harvested stands to sustain or accelerate the development of structural complexity in managed forests (Franklin et al. 1997). There are, however, many unresolved questions about how different spatial patterns of overstory retention influence stand development and forest productivity (Halpern et al. 1999, Palik et al. 2003).

Overstory density reductions can increase soil moisture availability (Sucoff and Hong 1974), and studies in *Pinus ponderosa* (Dougl. ex Laws.) forests indicate density reductions that leave residual trees dispersed relatively evenly can reduce moisture stress by increasing soil moisture availability, leading to an increase in photosynthetic carbon assimilation rates (A) associated with increased stomatal conductance (g_s; McDowell et al. 2003, Skov et al. 2004, McDowell et al. 2006). Increased evaporative demand associated with greater crown exposure following harvesting, however, could also lead to stomatal closure, which could limit A, and has been suggested as a cause for crown dieback in isolated trees following retention harvesting (Bladon et al. 2006, 2007). Evidence of lower moisture stress in edge and interior trees indicates the potential for different responses between dispersed residuals and trees in aggregates (Bladon et al. 2007). Increased light availability to the lower crown and enhanced nitrogen mineralization rates could also lead to elevated A and growth following harvesting (Aussenac and Granier 1988), even in the absence of any apparent change in residual tree water relations (Hartmann et al. 2008).

Stable carbon isotope ratios ($\delta^{13}C$) of tree rings or foliage can be used to evaluate mechanisms for residual tree growth increases or decreases following harvesting because $\delta^{13}C$ is correlated with leaf-level physiological processes. Discrimination against ^{13}C that occurs during photosynthesis is proportional to the partial pressure of CO_2 inside the leaf (c_i; Farquhar et al. 1982). Since the balance between A (CO_2 demand) and g_s (CO_2 supply) is largely responsible for changes in c_i, tree ring or foliar $\delta^{13}C$ should be positively correlated with A/g_s, the intrinsic water use efficiency (iWUE), as long as atmospheric $\delta^{13}C$ and atmospheric CO_2 concentrations are similar across the trees and years being compared (Farquhar et al. 1982, 1989).

Several authors suggest analyzing oxygen isotope ratios ($\delta^{18}O$) of plant tissue in tandem with $\delta^{13}C$ to provide further insight about the gas exchange parameters contributing to changes in $\delta^{13}C$ (Farquhar and Lloyd 1993, Saurer et al. 1997, Scheidegger et al. 2000, Barbour et al. 2002). In well-mixed environments, oxygen isotope enrichment in leaf water should be proportional to $1 - e_a/e_i$, where e_a is water vapor pressure in the atmosphere and e_i is water vapor pressure inside the leaf (Craig and Gordon 1965, Dongmann et al. 1974, Farquhar and Lloyd 1993, Barbour 2007), and the original isotopic signature of leaf water is dependent upon the isotopic composition of source water in the soil (DeNiro and Epstein 1979, Farquhar et al. 1998). This suggests leaf water $\delta^{18}O$ should have an inverse relationship with stomatal conductance (g_s) when compared across samples from environments with similar evaporative demand and soil water $\delta^{18}O$, and that $\delta^{18}O$ should increase as evaporative demand increases due to declines in e_a/e_i (Dongmann et al. 1974, Farquhar et al. 2007). Oxygen in leaf water is eventually assimilated into plant tissues, so these relationships should also be reflected in wood or foliage (DeNiro and Epstein 1979, Farquhar et al. 1998).

We used analyses of $\delta^{13}C$, $\delta^{18}O$ and annual growth from tree rings to test competing hypotheses about residual tree responses to harvesting. Our overall objective was to quantify how spatial pattern of residual tree retention, i.e., dispersed or aggregated, influenced physiological response and growth. We expected either (i) a decrease in $\delta^{13}C$ and $\delta^{18}O$ accompanied by an increase in growth if responses to retention harvesting are driven by increased gas exchange associated with increased soil moisture availability, (ii) an increase in $\delta^{13}C$ and $\delta^{18}O$ along with a decrease in growth if responses to retention harvesting are driven by stomatal closure in response to increased evaporative demand or (iii) an increase in both $\delta^{13}C$ and growth with little change in $\delta^{18}O$ if responses to retention harvesting are driven by increased A in response to greater light or soil nitrogen availability.

Materials and methods

The study took place on the Chippewa National Forest in northern Minnesota, USA. The study sites were part of the

Red Pine Retention Study, an ongoing experiment testing the impacts of variable retention harvest treatments on the development of structural complexity in red pine (*Pinus resinosa* Ait.) forests (Palik and Zasada 2003, Palik et al. 2005). The Red Pine Retention Study has a split-plot, randomized complete block design with four overstory retention treatments applied to whole stands and two understory competition control treatments applied to half of each stand. The treatments were fully replicated across four treatment areas (blocks) in 70–80-year-old stands that averaged 16 ha in size. Three treatment areas were directly adjacent to one another, and the fourth treatment area was located ∼8 km to the north.

All overstory treatments reduced stand basal areas from 35 to 45 $m^2 ha^{-1}$ to ∼16 $m^2 ha^{-1}$ with residual trees dispersed, aggregated between small (0.1 ha) gaps, aggregated between large (0.3 ha) gaps or left as unharvested controls. Average basal areas in control stands were 36 $m^2 ha^{-1}$. Understory treatments included a mechanical understory release, in which all woody trees and shrubs under 6.4 cm diameter at breast height (d.b.h.) were cut, and an untreated understory control. Understory release treatments were conducted in the spring of 2003 after harvesting and repeated each spring throughout our study period. Stands were located on deep, well-drained sands consisting of mixed, frigid Aquic Udipsamments, frigid Lamellic Udipsamments and frigid Typic Udipsamments (Richardson 1997).

Increment cores were collected from trees at 10 study points in each stand during the fourth growing season after harvesting. Five study points were located in the understory release side of each stand, with the remaining five points in the understory control side. Cores were collected from the three red pines closest to each point and the diameter of all trees >2.5 cm diameter at 1.4 m in height (d.b.h.) was measured in a 0.08-ha circular plot around each study point and used to calculate plot basal area. The upper end of basal areas represented by our plots (50–60 $m^2 ha^{-1}$) is slightly higher than the 35–45 $m^2 ha^{-1}$ typically reported for red pine stands of similar ages in the region (Gilmore et al. 2005, Zenner and Peck 2009), but similar to values reported for old, unmanaged stands (summarized in Stearns and Likens 2002), and within the variability reported for similar plot sizes within red pine stands (Zenner and Peck 2009). Further, our basal area values represent the variability between small (0.08 ha) neighborhood environments rather than average values for entire stands.

Only healthy trees in dominant or codominant canopy positions were selected for coring. Four cores were removed from each tree at breast height (1.4 m) and placed in plastic holders. Two cores from each tree were sanded and temporarily mounted for measurement of annual ring widths using a binocular microscope and sliding stage micrometer. Cores were not cross-dated, but increment cores from several of the stands included in this study that were cross-dated using the method described by Yamaguchi (1991) and verified with the software program COFECHA (Holmes 1983) did not

suggest significant dating errors during the years immediately before and after treatment (Powers et al. 2009).

After ring-width measurements, two groups of growth rings representing the 3 years immediately prior to treatment and the 3 years immediately following treatment were cut from each increment core under a microscope. Rings from the three trees at each study point were bulked and ground to pass a 20 mesh screen on a Wiley mill before being pulverized to fine powder on a ball mill. Pre- and post-treatment samples were separately milled for each study point. The carbon isotope ratio of whole wood samples was determined using a Costech Elemental Combustion System 4010 connected to a continuous-flow isotope ratio mass spectrometer (Deltaplus, Thermo Finnigan, Bremen). Oxygen isotope ratios were determined for the same samples at the Washington State University Stable Isotope Core Laboratory using a pyrolysis elemental analyzer (TC/EA, Thermo Finnigan, Bremen) connected to a continuous-flow isotope ratio mass spectrometer (Delta PlusXP, Thermo Finnigan, Bremen). While cellulose is often isolated for isotopic analyses, several recent studies have found both whole tissue and cellulose show similar trends in $\delta^{13}C$ and $\delta^{18}O$ (Borella et al. 1998, Barbour et al. 2001, Cernusak et al. 2005, Powers et al. 2008), so only whole wood was analyzed in this study.

Annual ring widths were used to calculate the percent radial growth change (%GC) following harvesting using the formula:

$$\%GC = [(M_2 - M_1)/M_1] \times 100\%$$

where M_1 is the 3-year mean of radial growth preceding harvesting and M_2 is the 3-year mean of radial growth following harvesting (Nowacki and Abrams 1997). While changes in isotopic data could be analyzed in a similar manner, we chose to report raw pre-treatment and post-treatment isotope ratios since changes in $\delta^{13}C$ and $\delta^{18}O$ between pre-treatment and post-treatment could be influenced by changes in source air or source water isotopic signatures in addition to any treatment effects. Growth change data, $\delta^{13}C$ data and $\delta^{18}O$ data from each study point were averaged across the understory release and understory control side of each stand, and these stand averages were used in statistical analyses. Carbon and oxygen isotope ratios were analyzed using repeated-measures, split-plot analysis of variance (ANOVA) with overstory treatment as the whole plot variable, understory treatment as the split-plot factor, treatment area as a blocking variable and measurement period (pre- or post-harvest) as the repeated measure. Growth change data were analyzed using split-plot ANOVA, with overstory treatment as the whole plot factor, understory treatment as the split-plot factor and treatment area as a blocking variable. Normal probability plots of error residuals and plots of residuals against predicted values were used to check ANOVA and regression assumptions. Tukey's honest significant difference was used to rank treatment levels when an ANOVA F-test indicated significant differences.

Previous studies suggest isotopic effects associated with harvesting may take several years to manifest in tree rings (McDowell et al. 2003, 2006), so we also collected individual rings representing the 3 years prior to harvesting (years bulked) and each of the 3 years of growth following treatment (years collected and analyzed separately) from each of our sample trees in one of our four treatment blocks to look for any lagged isotopic responses. These rings were processed, samples from the three trees at each plot were bulked and the samples were analyzed for $\delta^{13}C$ and $\delta^{18}O$ using the same methods described above, except that the individual post-treatment years were analyzed separately rather than bulked.

Regression models were used to evaluate relationships between the isotopic composition of tree rings from individual study points ($\delta^{13}C$ and $\delta^{18}O$) and plot basal area for the pre-treatment period, and each of the 3 years following harvesting. Since the plot-scale data had a hierarchical structure (plots within substands representing understory treatments within stands representing different overstory treatments), we performed a preliminary analysis using mixed-effects regression models to evaluate the potential for spatial autocorrelation between plots within the same understory treatment (substand) or overstory treatment (stand). Models were evaluated using AICC scores, a variant of Akaike's Information Criterion, where a lower AICC score indicates a given model explains more variability in the response variable (Burnham and Anderson 2002). Regression models between annual ring $\delta^{18}O$ and $\delta^{13}C$ were also used to evaluate the leaf-level processes contributing to variability in $\delta^{13}C$ across the plot basal area gradient (Saurer et al. 1997, 2000, Barbour et al. 2002). Normal probability plots of error residuals and plots of residuals against predicted values were used to check regression assumptions, and transformations were applied as necessary.

Tree height has a well-documented, positive relationship with $\delta^{13}C$ (Samuelson et al. 2003, McDowell et al. 2005, He et al. 2008) that could contribute to any relationship between $\delta^{13}C$ and plot basal area if sample tree height also varies with basal area. We analyzed the relationship between the average height of our three sample trees at each sample point with plot basal area using regression models to investigate any potential confounding variable between height and basal area in our isotopic analyses. Average height of the three trees at a given sample point was used rather than individual heights because tree ring samples from the three trees were bulked rather than analyzed separately. Regression diagnostics were conducted as described above.

Results

Treatment effects (stand scale)

Carbon isotope ratios varied between measurement periods ($P < 0.001$), and there was a significant time by understory interaction ($P = 0.035$) but no change in $\delta^{13}C$ associated with
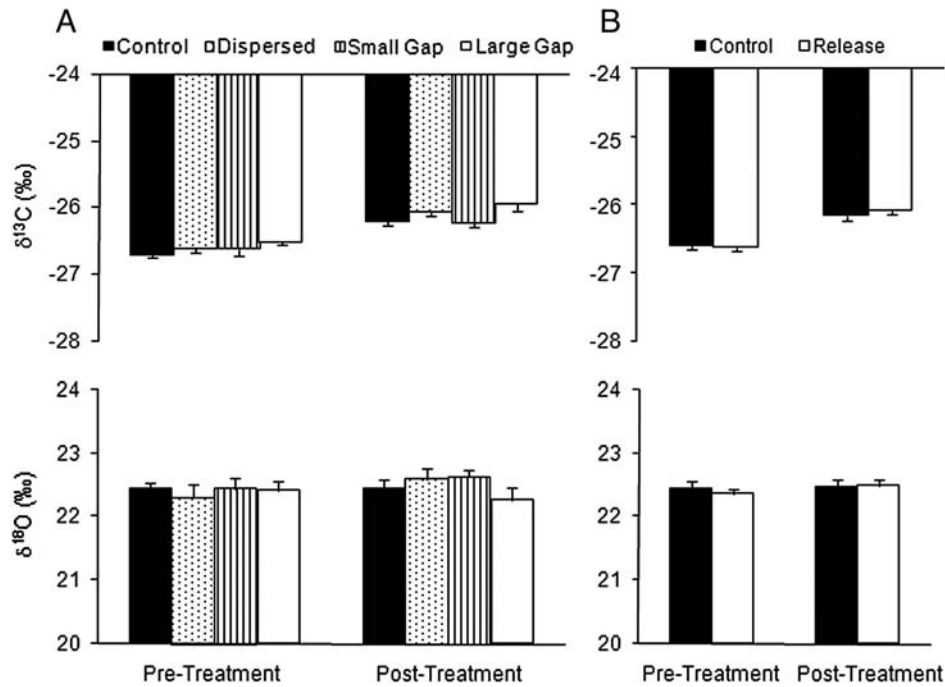
Figure 1. Stable carbon isotope ratios ($\delta^{13}C$) and oxygen isotope ratios ($\delta^{18}O$) of wood from overstory *P. resinosa* trees before and after variable retention harvesting (A) and with or without understory competition control treatments (B). Retention treatments included an unharvested control, dispersed retention, aggregated retention between small (0.1 ha) gaps and aggregated retention between large (0.3 ha) gaps. Understory treatments included an untreated control and cutting all woody vegetation under 6.4 cm d.b.h. (understory release). Error bars represent one standard error.
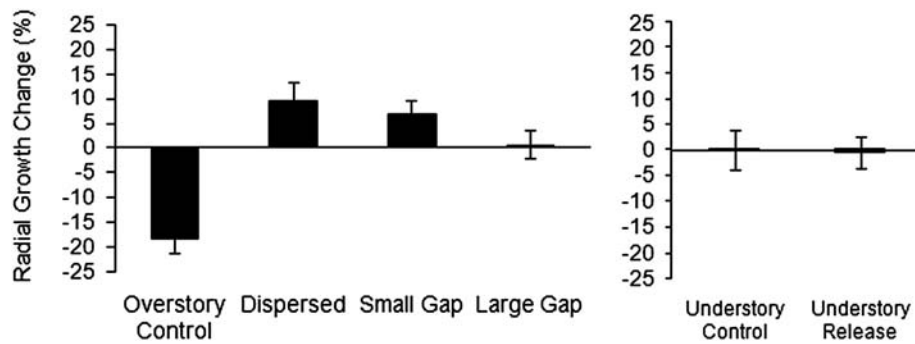

Figure 2. Radial growth change of overstory *P. resinosa* trees in response to variable retention harvesting and understory competition control treatments. Variable retention treatments included an unharvested control, dispersed retention, aggregated retention between small (0.1 ha) gaps and aggregated retention between large (0.3 ha) gaps. Understory treatments included an untreated control and cutting all woody vegetation under 6.4 cm d.b.h. (understory release). Error bars represent one standard error.

overstory treatment or the overstory treatment by understory treatment interaction (Figure 1). Post-treatment $\delta^{13}C$ was enriched by about 0.5‰ compared to pre-treatment values. The change in $\delta^{13}C$ from pre-treatment to post-treatment was greater in understory release treatments than in understory controls, but similar among overstory treatments. There were no significant differences in $\delta^{13}C$ among overstory treatments or understory treatments within either measurement period. There were no significant differences in wood $\delta^{18}O$ associated with overstory treatment, understory treatment or their in-

teraction either before or after treatment, and there were no changes in $\delta^{18}O$ between pre-treatment and post-treatment periods (Figure 1).

Significant differences in %GC were associated with overstory treatment ($P < 0.001$), but not understory treatment or the overstory treatment by understory treatment interaction (Figure 2). Radial growth change was 20–30% greater in variable retention treatments than overstory controls, but there were no significant differences in %GC among variable retention treatments. Increases in growth following variable

Table 1. AICC values for competing models describing the relationship between stable isotope ratios of tree rings and the basal area of plots that contained those trees.

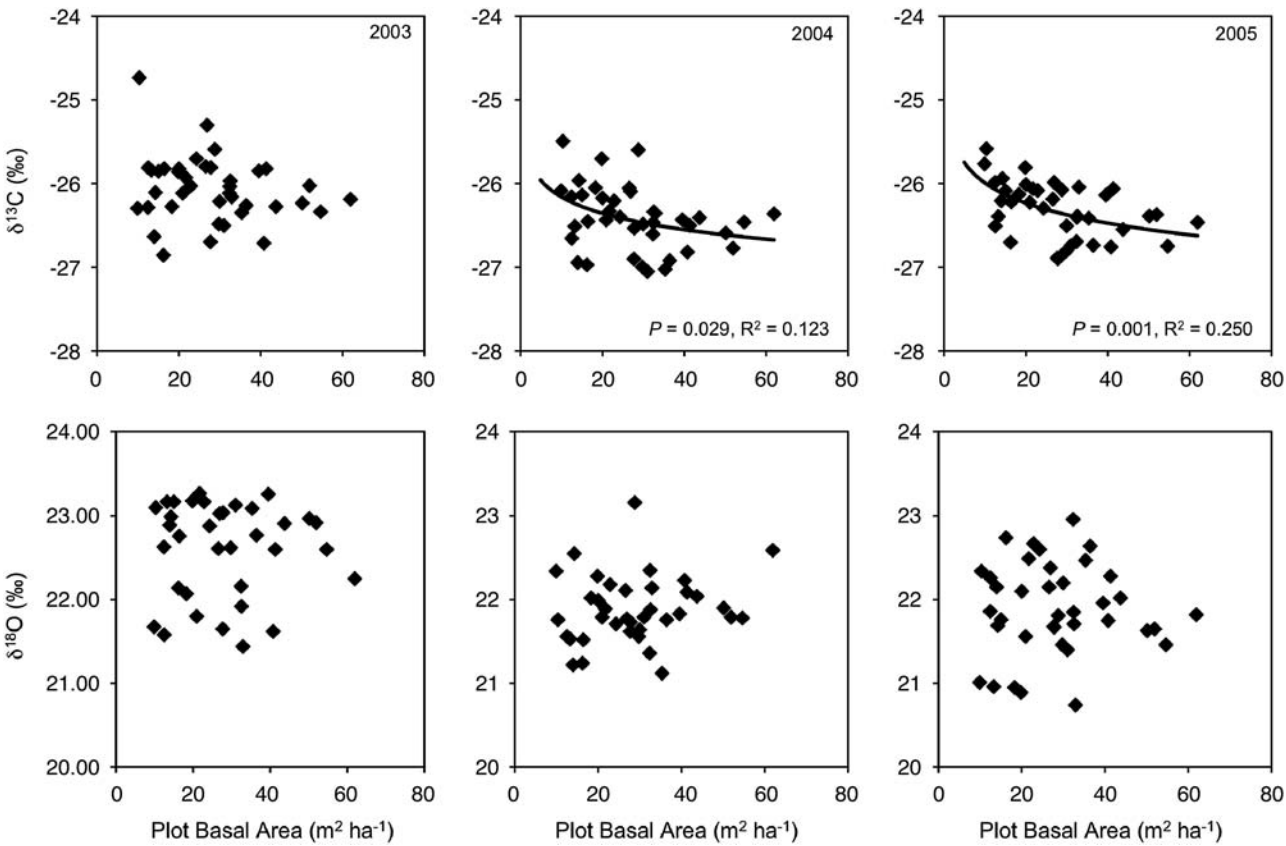| Dependent variable	Measurement interval	Plot basal area within substand within stand	Plot basal area within stand	Plot basal area
$\delta^{13}C$	Pre-treatment	22.8	22.8	22.8
$\delta^{13}C$	2003	44.6	43.2	43.2
$\delta^{13}C$	2004	40.5	39.3	38.2
$\delta^{13}C$	2005	25.1	22.9	21.4
$\delta^{18}O$	Pre-treatment	45.7	44.1	43.3
$\delta^{18}O$	2003	67.7	67.7	65.4
$\delta^{18}O$	2004	48.1	46.1	44.8
$\delta^{18}O$	2005	88.8	88.8	93.5

Figure 3. Relationships between stable carbon ($\delta^{13}C$) or oxygen ($\delta^{18}O$) isotope ratios of annual tree rings from residual overstory trees and the basal area of plots those rings were collected from for the first 3 years following variable retention harvesting in *P. resinosa* stands. Significant relationships are indicated with regression curves.

retention harvesting were modest but considerable when compared with the growth reductions observed over the same time period in the unharvested control stands.

Stable isotope–overstory basal area relationships (plot scale)

Simple regression models without random intercept or error terms accounting for correlation between plots in the same substand or stand explained the most variability in the relationship between tree ring stable isotope signatures and plot basal area in nearly all cases (Table 1), so these models were used for our final analysis. Annual ring $\delta^{13}C$ was not significantly related to plot basal area for the first year after treatment ($P = 0.175$), but had a significant, negative logarithmic relationship with basal area for the second ($P = 0.029$) and third ($P = 0.001$) year after treatment (Figure 3). The proportion of variability in $\delta^{13}C$ explained by plot basal area also increased from 5% for the first year after treatment to 12% for the second year after treatment, and 25% for the third year after treatment. Annual ring $\delta^{18}O$ was not significantly
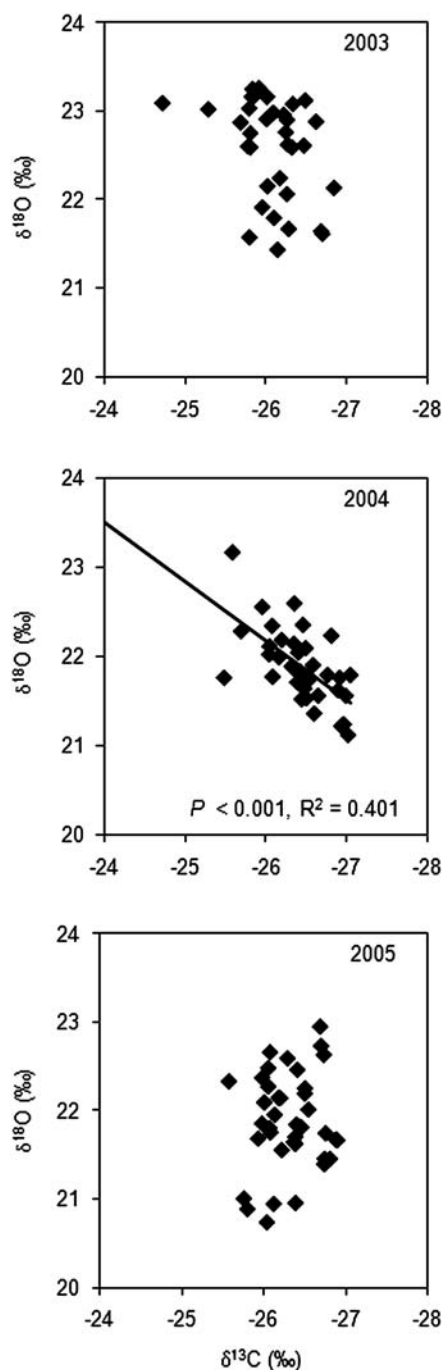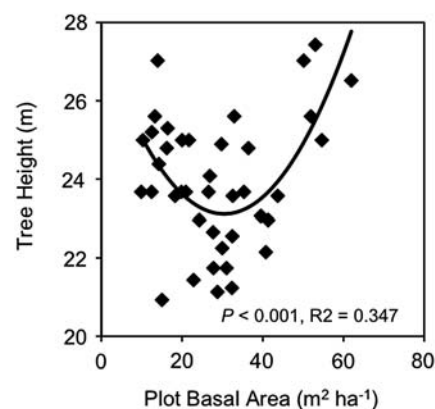
Figure 5. Relationship between average sample tree height and the basal area of plots that contained those trees.

also a significant, second-order polynomial relationship between average sample tree height and plot basal area ($P < 0.001$), with greater average tree heights in plots with low or high basal area than in plots with intermediate basal areas (Figure 5).

Discussion

These results indicate that variable retention harvest treatments increased growth in residual red pine, but there were no changes in $\delta^{13}C$ or $\delta^{18}O$ to suggest the growth increase was driven by altered water relations. There was evidence that iWUE decreased as overstory competition increased, but the relationship was not apparent when dispersed residual trees were compared to aggregated residuals or trees in unharvested controls across entire stands. The results also suggest understory release treatments were associated with a slight increase in iWUE in residual trees.

While there were no significant effects of overstory treatment on residual tree $\delta^{13}C$ when averaged across the 3 years following harvesting, the development of significant, negative relationships between annual ring $\delta^{13}C$ and plot basal area during the second and third years after harvesting suggests residual overstory trees did show a treatment response. This relationship indicates a decline in c_i consistent with either a decrease in g_s or an increase in carbon assimilation rates in environments characterized by low residual basal areas (Farquhar et al. 1982, 1989). Thus, the $\delta^{13}C$ results could support either Hypothesis 2 or 3, but provide little evidence for any large increase in g_s within the treatment stands (Hypothesis 1).

In our study, the lower end of basal areas (10–20 $m^2 ha^{-1}$) represents environments on aggregate edges or in the dispersed retention treatment, while plots in the upper end of the basal area gradient (40–60 $m^2 ha^{-1}$) were in unharvested stands. Thus, there is some evidence of either an increase in g_s or a decline in A as overstory competition increases from the most open environments created by retention harvesting

Figure 4. Relationships between stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope ratios of residual overstory trees for the first 3 years following variable retention harvesting in *P. resinosa* stands. Significant relationships are indicated with regression lines.

related to basal area for any of the three post-treatment years (Figure 3). There were no significant relationships between either $\delta^{13}C$ or $\delta^{18}O$ and plot basal area during the pre-treatment period ($P = 0.200$ and $P = 0.547$, respectively). Annual ring $\delta^{18}O$ was significantly, positively related to $\delta^{13}C$ during the second year after treatment ($P < 0.001$), but not during the first or third year after treatment (Figure 4). There was

to the closed canopy environments typical of undisturbed forest interior conditions. An increase in g_s along the overstory competition gradient would be consistent with Hypothesis 2 and the findings of Bladon et al. (2006, 2007), who reported greater water stress in isolated residual trees than forest edge or interior trees. However, there were no significant correlations between annual ring $\delta^{18}O$ and plot basal area that would suggest differences in g_s and $\delta^{18}O$ was generally not well correlated with $\delta^{13}C$, which indicates that the variability in $\delta^{13}C$ across the basal area gradient was largely driven by differences in A (Barbour et al. 2002). This is consistent with Hypothesis 3, which predicted that retention harvesting would increase A as a result of greater light availability to the lower crown or increased nitrogen mineralization rates. The absence of large changes in $\delta^{18}O$ could also indicate that any increase in evaporative demand following harvesting was offset by a corresponding increase in soil moisture availability (Hartmann et al. 2008). Differences in internal conductance may also contribute to trends in $\delta^{13}C$ (Warren and Adams 2006, Seibt et al. 2008), so further studies may be necessary to determine whether the trends in $\delta^{13}C$ we observed were driven by changes in A or g_s.

The increasing model fits and significance from post-treatment years 1–3 suggest that physiological acclimation to variable retention harvesting was a gradual process. This lagged response is consistent with the delayed growth releases commonly reported following overstory density reductions in conifers (Latham and Tappeiner 2002, McDowell et al. 2003, Bebber et al. 2004, Bevilacqua et al. 2005, McDowell et al. 2006) as well as studies that used stable isotopes to evaluate physiological responses to thinning treatments (McDowell et al. 2003, 2006). This lagged response may be tied to physiological acclimation to gap creation at the leaf level, which can be a slow process, driven by changes in leaf morphology that manifest themselves over one or more cohorts of foliage (Jones and Thomas 2007, Gauthier and Jacobs 2009) as leaves adjust to new within-canopy light gradients (Ellsworth and Reich 1993). This gradual acclimation process could explain why our plot-level data showed increasing evidence of physiological responses to retention harvesting in the second and third year after harvesting while our stand-scale data (which analyzed the 3-year post-treatment period as a single, bulked sample) did not suggest any treatment effects.

The decrease in $\delta^{13}C$ associated with increasing basal area we found does not appear to be related to hydraulic constraints associated with trends in sample tree height. If changes in $\delta^{13}C$ across the basal area gradient were driven by differences in sample tree height, we would expect the greatest $\delta^{13}C$ in plots with the greatest tree heights since increased hydraulic pathway length can reduce leaf-specific hydraulic conductance, which limits g_s, reduces c_i and increases $\delta^{13}C$ (Samuelson et al. 2003, McDowell et al. 2005, Ryan et al. 2006). Sample tree heights, however, were as high or higher in the plots with the highest basal areas as in any other portion of the basal area gradient, so we would expect high

$\delta^{13}C$ values in these high basal area plots if trends in $\delta^{13}C$ were driven by tree size. Instead, $\delta^{13}C$ was lowest in our high basal area plots. While we cannot rule out tree size effects without more direct testing, our results indicate the stable isotope trends we observed were most likely driven by leaf-level physiological differences associated with different neighborhood environments.

The increase in radial growth observed in variable retention treatments compared to unharvested controls is consistent with a number of studies that reported greater growth along forest edges or following harvesting than in unharvested, interior forest conditions (Deal and Tappeiner 2002, Deal et al. 2002, McDonald and Urban 2004, Roberts and Harrington 2008). Although our stand-scale analyses did not provide direct evidence for the mechanisms responsible for growth increases following retention harvesting, evidence of greater A in environments with lower basal areas during the second and third years after harvesting suggests radial growth increases were likely associated with increased carbon assimilation rather than alternative explanations such as changes in carbon allocation. The pattern of overstory retention did not appear to have a large impact on residual tree growth when averaged across stands, which differs from predictions that growth should be lower in aggregated residuals than dispersed residuals (Halpern et al. 1999) and findings that within-stand structural variability following variable retention harvesting impacts residual tree responses on an individual tree basis (Roberts and Harrington 2008, Powers et al. 2009).

The finding that understory release treatments were associated with a greater increase in $\delta^{13}C$ from pre-treatment to post-treatment measurement periods than understory controls suggests understory competition control increased iWUE in overstory trees. Nitrogen availability can increase following understory release treatments (Burgess and Wetzel 2000, Boucher et al. 2007), and elevated nitrogen availability could increase A due to the strong relationship between foliar nitrogen concentrations and photosynthetic capacity (Evans 1983, 1989, Reich et al. 1995). An increase in A would explain the increase in $\delta^{13}C$ we observed in stands that received understory release treatments. The lack of significant differences in $\delta^{18}O$ across understory treatments suggests there was little difference in g_s or evaporative demand, which supports an assimilation-based explanation for the increase in $\delta^{13}C$ associated with understory release treatments.

Our findings suggest that increased A, rather than reduced g_s, may partly explain why isolated residual trees sometimes exhibit greater iWUE than forest edge or interior trees following variable retention harvesting, and also indicate that residual trees in environments with high levels of overstory competition show less pronounced responses to retention harvesting than more isolated individuals. Physiological responses to partial canopy disturbances appear to be gradual in red pine, and full acclimation likely takes longer than the 3 years of post-treatment data collected in this study. Although physiological responses were less pronounced in en-

vironments with greater residual tree basal areas, growth responses indicate variable retention harvest treatments did provide a release for residual trees regardless of the spatial pattern of overstory retention that was used. These initial responses indicate variable retention harvests that create different neighborhood environments could promote functional complexity within stands, while maintaining similar levels of residual tree growth and productivity among stands with different residual structures.

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