

Cross-scale interactions affect tree growth and intrinsic water use efficiency and highlight the importance of spatial context in managing forests under global change

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Summary

1. We investigated the potential of cross-scale interactions to affect the outcome of density reduction in a large-scale silvicultural experiment to better understand options for managing forests under climate change.
2. We measured tree growth and intrinsic water-use efficiency (iWUE) based on stable carbon isotopes ($\delta^{13}\text{C}$) to investigate impacts of density reduction across a range of progressively finer spatial scales: site, stand, hillslope position and neighbourhood. In particular, we focused on the influence of treatments beyond the boundaries of treated stands to include impacts on downslope and neighbouring stands across sites varying in soil moisture.
3. Trees at the wet site responded with increased growth when compared with trees at the dry site. Additionally, trees in treated stands at the dry site responded with increased iWUE while trees at the wet site showed no difference in iWUE compared to untreated stands.
4. We hypothesized that water is not the primary limiting factor for growth at our sites, but that density reduction released other resources, such as growing space or nutrients to drive the growth response. At progressively finer spatial scales we found that tree responses were not driven by hill-slope location (i.e. downslope of treatment) but to changes in local neighbourhood tree density.
5. *Synthesis.* This study demonstrated that water can be viewed as an agent to investigate cross-scale interactions as it links processes operating at coarse to finer spatial scales and vice versa. Consequently, management prescriptions such as density reductions to increase resistance and resilience of trees to climate change, specifically to drought, need to consider cross-scale interactions as specific magnitude and mechanisms of growth responses can only be predicted when multiple scales are taken into account.

Key-words: climate change, cross-scale interactions, dendrochronology, density reduction, plant–climate interactions, plant–plant interactions, stable isotope analysis

Introduction

Global climate change, especially as reflected in increased drought events, is projected to affect ecosystems and valuable services at multiple scales and processes (Garcia *et al.* 2014). A main challenge in planning for global change is to identify the scales over which ecosystem processes will be impacted. Global-scale processes such as CO₂ fertilization or temperature increase affect water-use efficiency and biomass-allocation patterns (Keenan *et al.* 2013; Reich *et al.* 2014).

Regional processes such as drought and species migration affect plant growth, mortality and disturbance patterns (Raffa *et al.* 2008; McDowell *et al.* 2011). Local processes such as competition or physical damage affect plant growth and mortality patterns (D'Amato & Puettmann 2004; Holzwarth *et al.* 2013). Just as, or even more important, factors at different scales interact, for example, global and regional impacts can be moderated through decoupling of the environment at finer, local scales. For example, regional warming can be moderated by local topographic features (Daly, Conklin & Unsworth 2010) or site quality (Lévesque *et al.* 2014), and plant interactions (De Frenne *et al.* 2013; Spasojevic *et al.* 2014).

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Separately assessing these impacts and the spatial scales over which they operate may lead to mismatches of potential management interventions with processes that affect ecosystem services such as water yield and carbon sequestration (Peters *et al.* 2004; Morris *et al.* 2014). Examining factors at only one spatial scale in isolation can lead researchers and managers to miss important options or potential synergies. It also ignores cross-scale interactions, where processes at one scale, like regional climate, interact with processes at another scale, such as plant competition (Peters, Bestelmeyer & Turner 2007). Cross-scale interactions can be especially important when considering climate change as they give rise to nonlinear or threshold responses that can overwhelm the effects of processes at other scales (Peters *et al.* 2004; Raffa *et al.* 2008).

Plant density strongly influences the intensity and importance of processes that act at fine spatial scales, such as competition. Consequently, natural resource managers have commonly managed density by regulating plant spacing through seeding and planting or reducing post-establishment plant density by thinning operations (Puettmann, Coates & Messier 2012). By managing competition, thinning has been used to achieve a variety of objectives such as to increase tree growth and vigour (Waring & Pitman 1985; Breda, Granier & Aussenac 1995), understorey species richness and adaptive capacity (Neill & Puettmann 2013), diversifying overstorey structure (Bauhus, Puettmann & Messier 2009) or reducing canopy fuel loads (Allen *et al.* 2002). The primary effect of density reduction in forests is to increase the amount of resources (water, light, nutrients, growing space) available for residual vegetation (Breda, Granier & Aussenac 1995; Boyden *et al.* 2012). In response to increased resource availability, trees will adjust crown architecture, and leaf, sapwood and root areas to capture these resources (Aussenac 2000). Tree responses not only depend on the amount and spatial heterogeneity of residual available resources right after treatment but also vary over time. Density reduction through thinning has been proposed in temperate and boreal forests as an option to reduce the effects of climate change on forests, specifically drought, through its impact of increasing available resources, especially water (Kohler *et al.* 2010; Chmura *et al.* 2011; D'Amato *et al.* 2013; Park *et al.* 2014).

Douglas-fir forests managed for commodity production and other ecosystem services provide an ideal opportunity to study the influence of density reduction at multiple spatial scales in the context of adaptation to climate change. Douglas-fir has a broad natural distribution and is widely planted in many different ecosystems, including outside its natural range, in a correspondingly wide range of climate conditions (Chen, Welsh & Hamann 2010; Chmura *et al.* 2011; Lévesque *et al.* 2013; Lavender & Hermann 2014). Additionally, in forests where Douglas-fir is a dominant species, an abundance of research exists on potential management options in uncertain future climates; for a review, see Chmura *et al.* (2011).

Retrospective studies on effects of density reduction, other disturbances and climate variability on trees often use dendrochronology. Additionally, isotopic analysis of tree-ring

cellulose allows more detailed investigations of climate and growing condition influences on plant physiological performance over time. Specifically, stable carbon isotope analysis ($\delta^{13}\text{C}$) from tree rings, combined with dendrochronology, has become a common tool used to retrospectively investigate impacts of climate and forest management on the intrinsic water-use efficiency (iWUE) of trees (McDowell *et al.* 2006; Brooks & Coulombe 2009; Brooks & Mitchell 2011). Using $\delta^{13}\text{C}$ to calculate iWUE facilitates comparisons of the physiological responses to changing resources over time among trees growing at different sites (McCarroll & Loader 2004; Lévesque *et al.* 2013). In general, changes in iWUE indicate a shift in the physiological balance between photosynthesis and stomatal conductance, and are often caused by changes in moisture availability. Thus, isotopic records in tree ring chronologies indicate physiological responses to moisture conditions at the time the carbon was fixed (McCarroll & Loader 2004).

We initiated the current study to investigate multi-scale processes to understand the mechanisms responsible for tree responses to density reductions. In a previous study on Douglas-fir in western Oregon, Ruzicka, Puettmann & Olson (2014) identified that trees within and downslope of treated stands showed higher post-treatment growth than trees in untreated stands and downslope of gaps. In this study, we follow up using changes in growth and iWUE to examine if cross-scale interactions provide insight into management options that reduce the impact of climate change on forests. Our analysis is based on a hierarchy of scales, where we first examine coarse-scale patterns, that is, basic information about growth differences across three sites, which varied in local climate. We then examined progressively finer scale processes to investigate potential cross-scale interactions, starting with a comparison of tree growth in treated and untreated stands within sites. Lastly, to understand responses at the stand scale, we examined finer grained interactions from hillslope location to the local neighbourhood scale.

Materials and methods

Our study utilized sites established as part of the Density Management and Riparian Buffer Study of western Oregon, USA (DMS; Cissel *et al.* 2006; Ruzicka, Puettmann & Olson 2014) (Fig. 1). We chose three DMS study sites (Keel Mountain, North Soup, OM Hubbard) to represent a climate gradient (wet, intermediate, dry respectively; Table 1). All three sites experience a Mediterranean climate with cool wet winters and warm dry summers. Average precipitation ranged from 1417 to 1968 mm year⁻¹, mostly occurring from November through April. Keel Mountain was the wettest site experiencing, on average, the most precipitation and lowest growing season vapour pressure deficit (VPD) while OM Hubbard was the driest with the lowest yearly rainfall and highest VPD. The three sites in this study were composed of several stands, over 200 ha in area, and approximately 200 km apart from each other. Forests on all sites were dominated by conifer species, primarily Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) with a smaller component of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western redcedar (*Thuja plicata* Donn ex D. Don), which were more prevalent at Keel

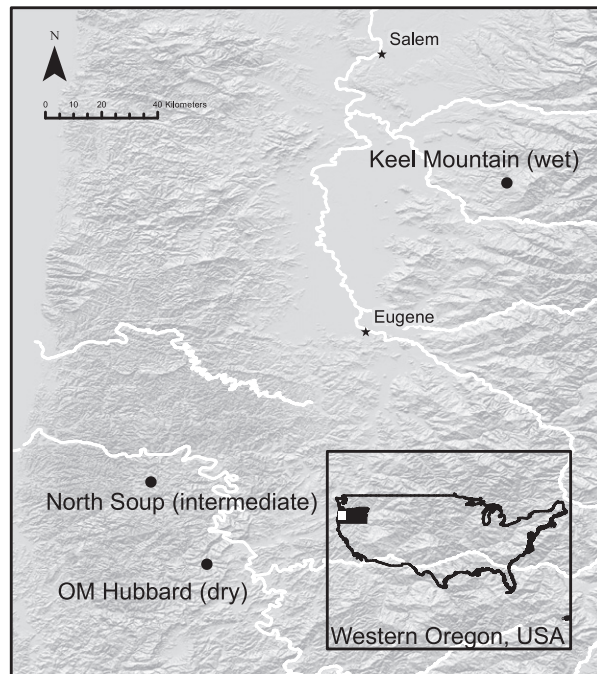


Fig. 1. Location map.

Mountain in the western Cascade Range (Fig. 1). Soils were primarily humic ultisols and inceptisols with high infiltration rates typical of western Oregon. The soils at OM Hubbard contain a higher clay content than the other two sites. The study plan by Cissel *et al.* (2006) contains a complete DMS overview including detailed site histories and descriptions.

The upland treatments (density reduction through thinning and gap creation) covered large areas (20–49 ha), creating the different stands used in this study. OM Hubbard and Keel Mountain were treated in 1997 while North Soup was treated in 1998. We examined two different tree densities within the variable density treatment area: (i) areas thinned to a residual density of 100 trees per hectare (thinned) with adjacent riparian stands located downslope of thinned areas (downslope thinned); and (ii) 0.4-ha circular gaps in which all trees were harvested in the gap with adjacent riparian stands below the gaps (downslope gap). An unthinned stand was also included as a reference or control stand (unthinned). All thinning preferentially removed smaller trees, except for minority conifer species and hardwoods, which were retained for structural and species diversity.

At all sites, we collected data from overstorey trees in plots that were part of 13 pre-established trans-riparian transects (Cissel *et al.*

2006; Anderson, Larson & Chan 2007), aligned perpendicular to headwater streams. Riparian buffer widths ranged from 16 to 32 m as measured from the middle of the stream channel. The buffer was designed with a 15 m minimum width, but could be wider to accommodate local conditions of riparian vegetation and topography. The first and second plot centres were 4.5 and 14 m from the stream centre, respectively, and typically were located in the riparian buffer (downslope thinned, downslope gap and unthinned stands). The third and fourth plots (thinned and unthinned stands) were 22.7 and 41 m upslope of the stream centre respectively. From June to August 2011, we selected and recorded locations of the three co-dominant and apparently healthy Douglas-fir closest to plot centres. The number of sample trees by treatment were 9 (three per site) in thinned stands, 14 (six wet, three intermediate and five dry) in downslope of thinned 21 (six wet, seven intermediate and eight dry) in downslope of gaps, and 32 (12 wet, 13 intermediate and 7 dry) in unthinned stands. Unequal sample sizes resulted because we excluded some trees due to an inability to cross-date cores or other sampling problems. The majority of excluded trees were downslope gap and thinned stands at the dry (6) and intermediate (14) sites. For four transects, the ridge top was less than 41 m from the stream centre, limiting measurements to three plots. In addition, one plot in the control stand at Keel Mountain did not have any Douglas-fir, resulting in a total of 36 plots. Our final sample size was 76 trees over three sites.

For each tree, we measured diameter at breast height and distance from treatment edge (downslope stands only), which was defined as the closest cut stump. To estimate the change in local competition, we counted the number of trees and stumps within 11.5 m of each tree. We measured slope distance, not horizontal distance, to capture the physical length of soil between trees and the treatment edge. Trees in riparian buffers were between 2 and 30 m downslope of stand edges.

We collected one 7-mm increment core to the pith and three 12-mm cores to capture at least 30 annual rings, one from each cardinal direction. Each core was sanded until rings and early latewood boundaries were clearly visible. We measured ring width using an optical scanner with 2400 DPI resolution and loaded into WinDendro to measure early, late and annual ring width. Tree rings were cross-dated visually using pointer years and statistically using the cross.date function in the dplR program library (Bunn 2010). After cross-dating to ensure intra- and inter-tree accuracy, we averaged the four cores from each tree together by year into a raw ring width chronology for each tree. We converted raw tree ring widths to basal area increment (BAI) for earlywood, latewood and annual ring growth (Phipps 2005) after subtracting the width of the bark from the final tree diameter (Larsen & Hann 1985). For both BAI and isotope analysis we sampled rings from 5 years pre-treatment to 12 years post-treatment for each tree in our analysis.

Table 1. Characteristics and treatment conditions for three western Oregon, USA study sites

	Keel Mountain (wet)	North Soup (intermediate)	OM Hubbard (dry)
Latitude	44°31' 41.0"	43°33' 57.0"	43°17' 30.0"
Longitude	122°37' 55.0"	123°46' 38.0"	123°35' 00.0"
Elevation (m)	654–756	176–411	436–783
*Mean annual precip. (mm)	1968	1735	1417
*Mean growing season vapour pressure deficit (kPa)	1.23	1.5	1.64
Treatment start	December 1997	August 1998	September 1997
Stand age at treatment	44	48	39

*Weather data from PRISM Climate Group <http://www.prism.oregonstate.edu/explorer/> for the study time period.

For $\delta^{13}\text{C}$ measurements, we separated early and latewood from the three 12-mm cores from each tree along ring boundaries established in the dating process using a grinding bit in a handheld rotary tool, which transformed the wood tissue to a fine powder. We combined the powdered samples from the replicate cores for each tree by year and then extracted to α -cellulose (Leavitt & Danzer 1993). The stable isotope lab at Oregon State University College of Earth, Oceanic, Atmospheric Sciences in Corvallis, OR determined the values of $\delta^{13}\text{C}$ in tree ring cellulose. Samples were combusted to CO_2 in a Carlo Erba NA1500 elemental analyzer then introduced into a DeltaPlusXL isotope ratio mass spectrometer. Measurement precision was better than 0.1‰ as determined by repeated measures from sample replicates. We could not analyse some samples due to insufficient sample size to accurately measure for isotope composition or sample corruption. Sample corruption occurred for few trees with very narrow growth rings that were ground using a ball mill where iron filings were accidentally introduced to the sample. The final sample size was 1347.

We reported $\delta^{13}\text{C}$ values relative to the Pee Dee Belemnite standard where the ratio of ^{13}C to ^{12}C atoms in a sample (R_{sample}) was compared with the ratio of the standard (R_{standard}) in eqn (1):

$$\delta^{13}\text{C} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \quad \text{eqn 1}$$

We analysed only latewood for $\delta^{13}\text{C}$ because latewood provides a more robust indicator of the growing conditions for a particular year and because it provides a record of the growing conditions for the water-limited season in a Mediterranean climate. Earlywood potentially retains the isotopic signature of photosynthesis carried out in the previous growing season and winter, and from other non-structural carbohydrates stored for longer periods (McCarroll & Loader 2004).

ISOTOPE THEORY

Intrinsic water-use efficiency is defined as the ratio of photosynthesis and stomatal conductance (A/g_s) and can be estimated using $\delta^{13}\text{C}$. First, we calculated discrimination ($\Delta^{13}\text{C}$) against the heavier isotope to remove year-to-year variation of $\delta^{13}\text{C}$ in the atmosphere using equating 2: (Farquhar, O'leary & Berry 1982)

$$\Delta^{13}\text{C} = \frac{\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{cell}}}{1 + \delta^{13}\text{C}_{\text{cell}}} \quad \text{eqn 2}$$

where $\delta^{13}\text{C}_{\text{air}}$ and $\delta^{13}\text{C}_{\text{cell}}$ are the $\delta^{13}\text{C}$ values of the atmosphere and cellulose samples. We obtained $[\text{CO}_2]$ and $\delta^{13}\text{C}_{\text{air}}$ concentrations from the National Oceanic and Atmospheric Administration Cooperative air sampling network, Midway Island station for the years 1991–2011 (<http://www.esrl.noaa.gov/gmd/ccgg/flask.php>). To account for seasonal changes in the concentration of CO_2 and $\delta^{13}\text{C}$ we converted monthly data to seasonal averages corresponding to the seasonal climate averages associated with early and late periods of carbon fixation (April–June and late July–September; Barnard, Brooks & Bond 2012; Beedlow *et al.* 2007). $\Delta^{13}\text{C}$ is regulated by the ratio of internal $[\text{CO}_2]$ to atmospheric $[\text{CO}_2]$ (c_i/c_a) as described by eqn (3) (Farquhar, Ehleringer & Hubick 1989):

$$\Delta^{13}\text{C} = a + (b - a) \left(\frac{c_i}{c_a} \right) \quad \text{eqn 3}$$

where a is the fractionation from diffusion through the stomata (4.4‰) and b is the fractionation by rubisco (~27‰). $i\text{WUE}$ is then estimated using the atmospheric concentration of CO_2 (c_a) and the

difference in diffusivity of CO_2 and water in air (1.6) in eqn (4): (Farquhar, Ehleringer & Hubick 1989)

$$i\text{WUE} = \frac{A}{g_s} = \frac{(c_a - c_i)}{1.6} \quad \text{eqn 4}$$

Isotopically derived values of $i\text{WUE}$ from tree rings facilitate comparisons of long-term trends because the carbon in latewood is integrated over the period of latewood formation, averaging $i\text{WUE}$ over the late growing season (McCarroll & Loader 2004). Year-to-year values of $i\text{WUE}$ can then be compared to indicate different physiological responses to water availability or changing growing conditions. Implicit in these models are assumptions that mesophyll conductance remains constant and non-limiting in leaves throughout the study (Seibt *et al.* 2008), and any fractionation events in the trunk or in phloem are consistent (Offermann *et al.* 2011) in terms of their effects on $\delta^{13}\text{C}$ in tree rings. For most studies, these assumptions appear to be valid (Cernusak *et al.* 2013; Cernusak & English 2015). Additionally, climatological studies have identified that a juvenile effect may influence the $\delta^{13}\text{C}$ in tree rings in young trees due to respiration of carbon and/or tree height (McCarroll & Loader 2004). However, the respired CO_2 influence is confined to young seedling within 1 m of the forest floor (Buchmann, Brooks & Ehleringer 2002), and Monserud & Marshall (2001) found no influence of height on tree ring carbon isotope discrimination for Douglas-fir. Trees in our study were taller than 25 m at the onset of the study so beyond any juvenile effect. Additionally, our study design comparing treated and control stands from the same cohort would account for any age influences over time.

DATA ANALYSIS

We used a hierarchical framework for data analysis at multiple scales. The results of analysis at coarse scales were used to inform the analysis at finer scales. Data analysis in this framework allowed us to explore variation found at coarse scales in the search of a more parsimonious explanation for patterns observed at each scale.

The first and largest scale analysed was at the site level which was done to assess site differences in tree growth and $i\text{WUE}$. Trees growing in the unthinned riparian stands were used for this analysis to avoid any treatment effects ($n = 32$). Two-way, repeated measures ANOVA was used to investigate inherent site differences in five metrics: annual ring growth, or BAI, earlywood and latewood BAI, latewood $i\text{WUE}$ and ratio of earlywood to annual ring width (earlywood proportion). A random error structure was included to account for our nested design (plots within transects) and an autoregressive covariance structure to model the autocorrelation present due to repeated measures by year. The five models (annual BAI, earlywood BAI, latewood BAI, latewood $i\text{WUE}$ and earlywood proportion) were fitted using the `lme` function from the `nlme` package (Pinheiro *et al.* 2011) and computed in R 3.1.1 (R Core Team 2012). The function `varIdent` was used to allow for different variances in sample size between sites (Zuur *et al.* 2009). The Bonferroni method was used for multiple comparisons to obtain correct P -values when computing contrasts.

The second scale analysed for this study was at the stand level. Multiple stands were created at each site using the treatments described in the methods (thinned, downslope thinned, downslope gap, unthinned). A two-way, repeated measures ANOVA was used to investigate stand differences among sites after treatment in four metrics: annual ring growth (BAI), earlywood BAI, latewood BAI and latewood $i\text{WUE}$. The interaction between stand and site was included in the model. The four [annual ring growth (BAI), earlywood BAI,

latewood BAI and latewood iWUE] models were fitted using the lme function from the nlme package (Pinheiro *et al.* 2011) and computed in R 3.1.1. The models were fit using the same error structures as the site-level variables. Contrasts between stands within each site and between sites were calculated using the testInteractions function from the phia package (De Rosario-Martinez & Fox 2013). The Bonferroni method was used for multiple comparisons to obtain correct *P*-values when computing site contrasts.

Analysis at the stand scale not only highlighted the difference between stands among sites but also suggested that finer scale processes might better explain differences at the stand scale. A previous study at our sites (Ruzicka, Puettmann & Olson 2014) described effects from upslope thinning treatments extended about 15 m from the edge into the stands downslope of thinning. We focused the next investigations on the stands downslope of thinning and gaps to test for possible cross-scale interactions that influence stand-level responses. The finer scales analysed for this study used only trees ($n = 35$) downslope of thinned and gap stands to investigate differences between these stands.

Trees in the thinned and downslope thinned and gap stands were divided into groups; trees that grew within 15 m from the edge of the treated stand, and those that did not. A type II ANOVA was used to compare differences in post-pretreatment-normalized growth between the two groups. A zero value in the difference would indicate no change in growth after treatment. An interaction between hillslope location (stand edge and not edge) and site was included to examine if any difference between hillslope locations was based on the sites. The model was fitted using the aov function in the base R 3.1.1.

The interaction of the factors acting at hillslope and local neighbourhood scales was investigated to determine why some trees in downslope of thinned and gap stands responded with increased growth and others did not. The annual ring BAI growth difference (post minus pre) for trees in the downslope thinned and gap stands were analysed using a mixed effect model with site and the proportion of trees removed during treatment as well as the interaction thereof. The proportion of trees cut from the local neighbourhood in the thinning process was arcsine square root transformed to improve model fits when using a proportion. Similar to the site and stand level, the model was fit using the lme and varIdent functions in R.

The final investigation was to determine if the response of trees at the local scale was related to changes in the tree's iWUE. The trees were divided into two groups; trees within 15 m that responded with increased growth to density reduction from treatments and those that did not. A type II ANOVA was used to compare the difference (post-pretreatment) in latewood iWUE between the two groups. An interaction was included to examine if any difference was based on the site. The model was fit using the aov function in R 3.1.1 (R Core Team 2012). The assumptions of normality and homogeneity of variances was tested graphically for all ANOVA tests at the hillslope location and local scale. Additionally, *P*-values from tests done at the hillslope

location and local scale were corrected using the false discovery rate to account for multiple tests (Verhoeven, Simonsen & McIntyre 2005).

Results

Site-scale differences (e.g. precipitation, growing season VPD: Table 1) were reflected in growth and iWUE of unthinned trees (Table 2, Fig. 2). Annual ring BAI and latewood BAI was lower at drier sites in the unthinned riparian stands. Trees growing at the wet site (Keel Mountain) had the highest average annual growth, while trees at the dry site (OM Hubbard) had the lowest (Table 2). Earlywood BAI growth was not significantly different among the three sites (Table 2). In contrast, trees growing at the dry site had significantly less latewood BAI growth with almost 60% of diameter growth completed before the seasonal summer drought lead to a shift to latewood production (Brix 1972) (Table 2). Tree iWUE was also higher at the dry and intermediate sites but only the intermediate site was significantly higher than the wet site (Table 2). Latewood iWUE at the dry site was not significantly different from the other two sites as a result of two trees at that site having the lowest average iWUE from all trees in this study (Fig. 2). We did not find any special circumstances that may have influenced these trees. However, when these two trees were removed from the analysis trees, the dry site had significantly higher iWUE than trees on the wet site but not significantly different from intermediate site trees (data not shown). No trees were removed for the analysis presented in Fig. 2 and Table 2.

Stand-level differences indicated a cross-scale interaction with the site scale as trees responded differently to stand-level treatments at each site (Fig. 3). Annual BAI increased significantly more after thinning at the wet site compared to trees in the thinned stand in the dry site (Table 3). Similar patterns were found when examining earlywood and latewood BAI individually (data not shown). Trees in stands downslope of gaps showed an increase in growth after treatment at the intermediate site compared to trees at the wet and dry stands (Table 3). The variation in the magnitude of thinned-stand responses as well as the site differences in stands downslope of treatments, suggested that cross-scale interactions at finer spatial scales likely affected tree growth.

Trees in the thinned stand at the dry site increased in iWUE after thinning (Fig. 4), which is the opposite of expectations if water resources available to individual trees had

Table 2. Site differences in unthinned Douglas-fir basal area increment (BAI) and intrinsic water-use efficiency. Type III repeated measures ANOVA was used to determine differences between sites for all five comparisons

Site	BAI (total ring) (mm ²)	Earlywood BAI growth (mm ²)	Latewood BAI growth (mm ²)	Proportion of earlywood	Latewood iWUE (μmol mol ⁻¹)
Wet	3759a* (457)	1821a (284)	1916a** (220)	0.47a** (0.02)	103a** (2)
Intermediate	2887ab (645)	1397a (398)	1554ab (313)	0.46a** (0.03)	112b** (2)
Dry	2378b* (739)	1445a (466)	904b** (354)	0.60b** (0.03)	107ab (3)

Mean annual values for each site (standard error) are indicated in each column. Significant contrasts among the sites are indicated by stars (* $P < 0.1$, ** $P < 0.05$) after Bonferroni correction while values with the same letters are not different.

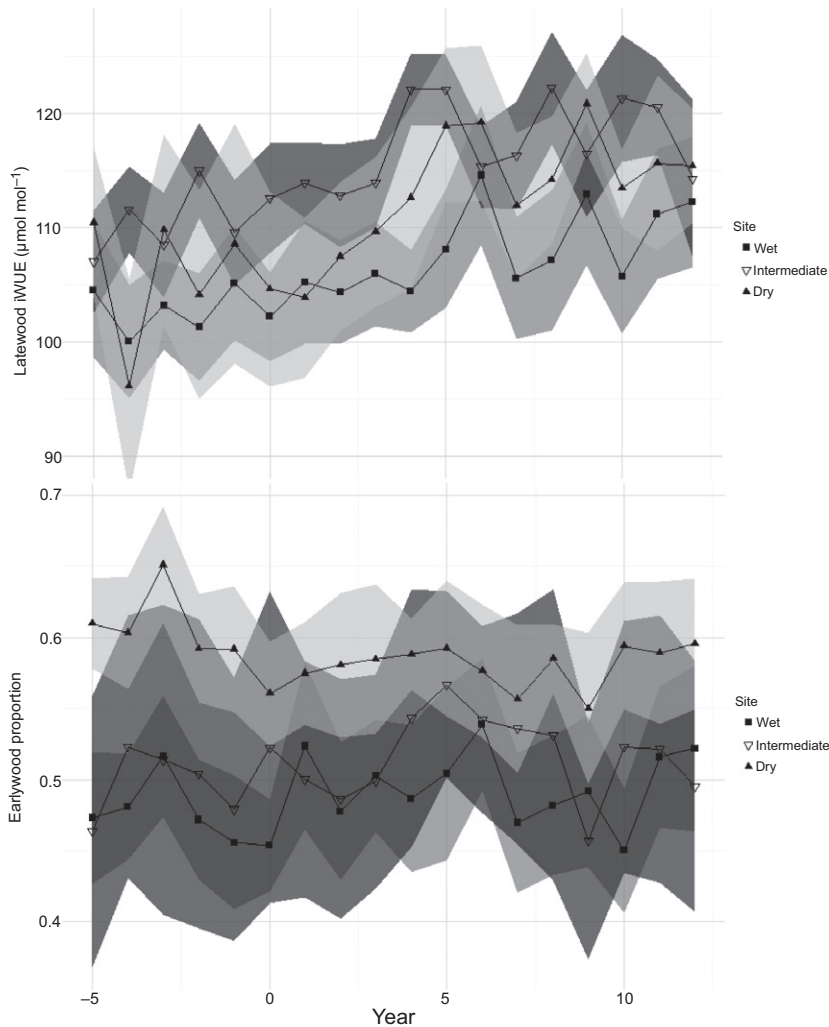


Fig. 2. Latewood intrinsic water-use efficiency (iWUE) and the proportion of earlywood (as part of total ring basal area increment (BAI)) by year for Douglas-fir trees growing in untreated stands of three western Oregon, USA study sites.

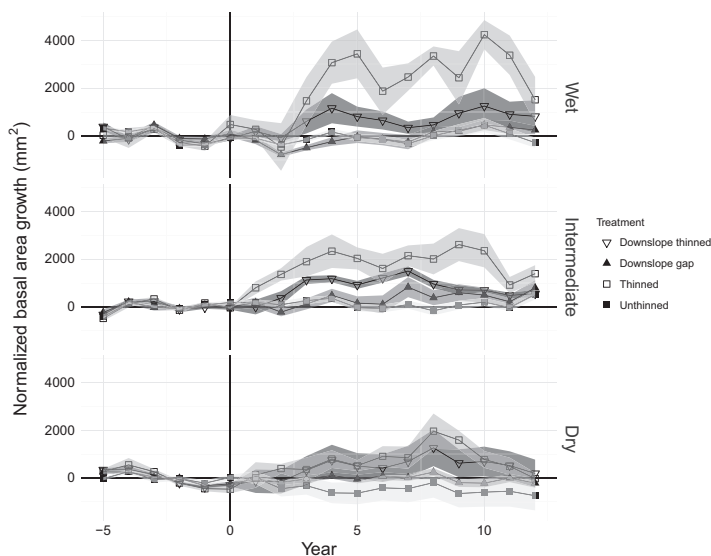


Fig. 3. Stand-level annual basal area increment (BAI) growth by year for Douglas-fir trees within three western Oregon, USA study sites. Growth was normalized by post minus pretreatment to account for inherent differences in tree growth (see Methods). Error bars represent standard errors. A value of zero for growth would indicate no difference from the pretreatment average. Year zero represents the year that density reduction treatments were applied.

increased after thinning. Trees downslope of the thinned stands at the intermediate site also had a significantly higher iWUE than trees at the same hillslope locations on the wet site but not the dry site (Table 4). An increase in iWUE along

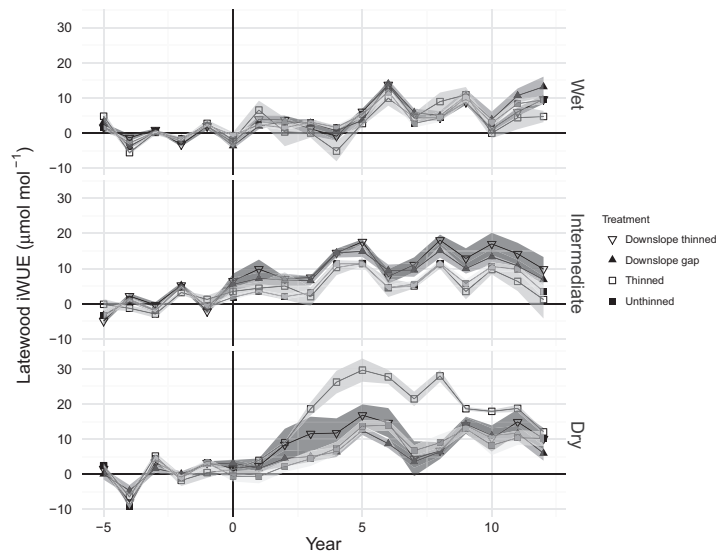
with an increase in growth in response to thinning indicated that the photosynthetic rate increased relative to stomatal conductance (increased A/g_s). Remarkably, the iWUE for trees on the wet site for all treatment stands was unchanged after

Table 3. Mixed model Type III repeated measures ANOVA results for the difference across sites in annual basal area increment (BAI) for Douglas-fir stands among three western Oregon, USA study sites

Stand X Site	Wet BAI (mm ²)	Intermediate BAI (mm ²)	Dry BAI (mm ²)
Thinned	2871.6aB** (364.5)	1933.7abB* (183.7)	787.6b**A (166.10)
Downslope thinned	798.5aA (166.8)	971.6aA (110.7)	1382.8aB* (122.82)
Downslope gap	104.9aA (81.6)	626.3aA (152.4)	−181.4aA (50.7)
Unthinned	52.4aA (73.1)	194.2aA (87.2)	55.1aA (58.2)

Mean values (standard error) indicate the average change in BAI after treatment for trees within stands. Values were normalized using the pre-treatment means; thus, a zero value would indicate no change in growth after treatment. Significant contrast differences are indicated by stars (* $P < 0.1$, ** $P < 0.05$) after Bonferroni correction. Significant differences between stands within a site are indicated by different capital letters (A,B, column comparisons), while significant differences among sites are indicated by different lower case letters (a,b, row comparisons).

Fig. 4. Stand-level latewood intrinsic water-use efficiency (iWUE) by year for Douglas-fir trees within three western Oregon, USA study sites. iWUE was normalized by post minus pretreatment to account for inherent differences in tree physiology (see Materials and methods). Error bars represent standard errors. A value of zero for iWUE would indicate no difference from the pretreatment average. Year zero represents the year density reduction treatments were applied.

**Table 4.** Mixed model Type III repeated measures ANOVA contrasts indicating within treatment difference in latewood intrinsic water-use efficiency (iWUE) for Douglas-fir stands among three western Oregon, USA study sites

Stand X Site	Wet iWUE (μmol mol ^{−1})	Intermediate iWUE (μmol mol ^{−1})	Dry iWUE (μmol mol ^{−1})
Thinned	4.54aA (1.11)	6.99aA (0.98)	22.27b**B** (1.22)
Downslope thinned	5.93aA (0.65)	14.01b*A (0.95)	11.52aA (1.23)
Downslope gap	7.49aA (0.83)	11.98aA (0.63)	8.54aA (0.67)
Unthinned	6.28aA (0.48)	8.29aA (0.46)	10.26aA (0.69)

Mean values (standard error) indicate the change in latewood iWUE after treatment for trees within stands. Values were normalized using the pre-treatment means; thus, a value of zero would indicate no change in iWUE after treatment. Significant contrast differences are indicated by stars (** $P < 0.05$, * $P < 0.1$) after Bonferroni correction. Significant differences between stands within a site are indicated by different capital letters (A,B, column comparisons), while significant differences among sites are indicated by different lower case letters (a,b, row comparisons).

density reduction. Together these two lines of evidence suggested that increased water from density reduction was not driving the growth increase of trees in this study. iWUE would likely have decreased after density reduction if an increase in water availability led to the increased growth, that is, stomatal conductance would have increased more relative to the rate of photosynthesis (decreased A/g_s) indicating that water was less limiting to tree growth. There is no evidence to suggest that treatment differences in iWUE were due to changes in local climate as the sites varied in sync and the relative climate differences between sites stayed the same.

For trees downslope of the thinning treatments, only trees within 15 m of the edge increased in BAI in response to

upland density reduction. However, our experimental design was not set up to test if the edge effect was related to distance from the edge or if the responses were only related to changing local density, that is, there was no density reduction in riparian areas so the density did not change beyond the treatment areas. When averaged across sites, a significant edge effect was evident as trees within 15 m of density reduction treatments responded with increased BAI ($P = 0.027$). However, when compared between sites, edge growth response was marginally greater but not statistically different in edge trees at the wet and intermediate sites compared to the dry site where the edge response was more variable. It is likely that the variability between and within stands indicates

that resources were not released uniformly across a stand after density reduction. Higher variability observed in the edge response at the hillslope location scale, especially at the dry site, suggested that interactions with finer spatial scales can explain the apparent edge effect (Fig. S2, Supporting Information).

At the local scale, trees in the downslope of thinned and gap stands responded with increased BAI to greater density reduction in the local neighbourhoods ($P = 0.004$). The effect was consistent at all three sites with no significant difference or interaction between them (Fig. 5). In general, a similar number of trees were removed from each site (trees per hectare target thinning) but the mean tree size was smaller at the time of thinning at the dry site (average DBH was 27 cm, 25.4 cm and 19.4 cm at the wet, intermediate and dry site respectively).

The effect of the cross-scale interaction between stand and local neighbourhood was reflected by variability in tree physiological response. Trees that increased growth within the 15-m edge showed a highly variable iWUE response to upland forest management. iWUE generally increased in trees downslope of thinned and gap stands that responded at the intermediate and dry sites, with more dramatic increases at the intermediate site and more variability at the dry site although the differences or the site interaction were not significant (data not shown). This result provided further evidence that changes in water availability after density reduction were not the primary driver of the growth response in trees.

Discussion

In summary, by using a hierarchical analysis framework, our results indicated that impacts of global climate change can be influenced by local conditions, as cross-scale interactions control the growth response to density reduction. Density at the local neighbourhood scale overrode treatment effects at the larger scales. Conversely, factors acting at the regional scale (site) moderated the magnitude of growth response at the

stand scale. This suggests a cross-scale interaction, where patterns observed at larger scales (stand) were mediated by patterns observed at small-scale conditions (local neighbourhood, Fig. 6).

Our study is an example of how viewing forests as complex adaptive systems can provide insights into ecosystem processes (Messier *et al.* 2015), for example, by highlighting and emphasizing cross-scale, hierarchical interactions. Specifically, it provided support for the importance of assessing cross-scale interactions to understand ecological processes, such as tree growth. This is especially important in an era of climate change, when mitigation strategies at the global scale are not likely to be effective, thus placing more emphasis on managing at fine scales, for example, stand levels or smaller in forestry operations (Puettmann, Coates & Messier 2012). Our study adds to the growing body of evidence that suggests that this approach has merit, as it shows that impacts of large-scale phenomena, such as climate change, can be mediated by fine-scale processes, such as competition or facilitation (De Frenne *et al.* 2013; Spasojevic *et al.* 2014). In this study, we identified that multiple processes interact across scales to affect the response of trees to density reduction. Site-scale differences influenced the magnitude of the growth response of different stands to treatment with a larger growth response in trees at wet sites. However, local neighbourhood density was the primary driver behind the larger scale patterns when investigating whether or not a downslope tree responds with increased growth to upslope density reduction (Fig. 6).

Cross-scale interactions may also act at scales beyond those used in our study. Douglas-fir obtains maximum size and competitive advantage with cool wet winters followed by relatively cool dry summers typical of the Pacific Northwest (Waring & Franklin 1979). Due to widespread planting, however, Douglas-fir growth can also be compared across very different climate patterns. For example, modelling studies have hypothesized that Douglas-fir in New Zealand grow faster because of lower summer evaporative demand and higher summer moisture availability compared to sites in the Pacific

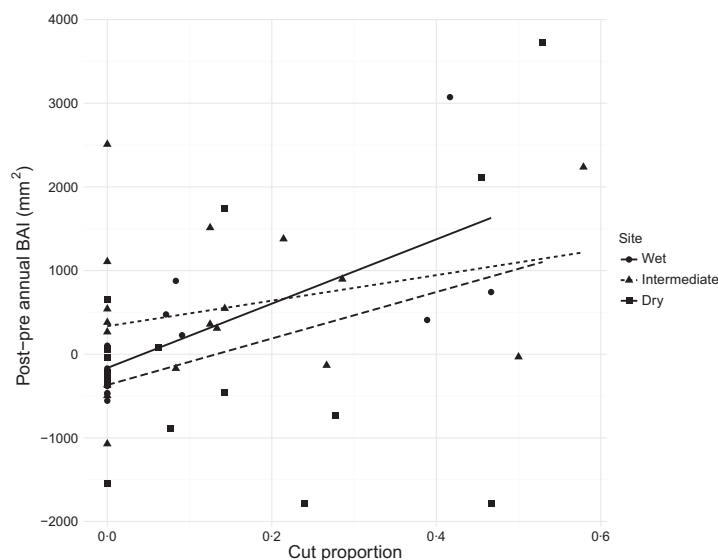


Fig. 5. Difference in post minus pretreatment entire ring basal area increment (BAI) for individual trees growing downslope of the thinned and gap stands plotted over the proportion of trees removed from local neighbourhoods.

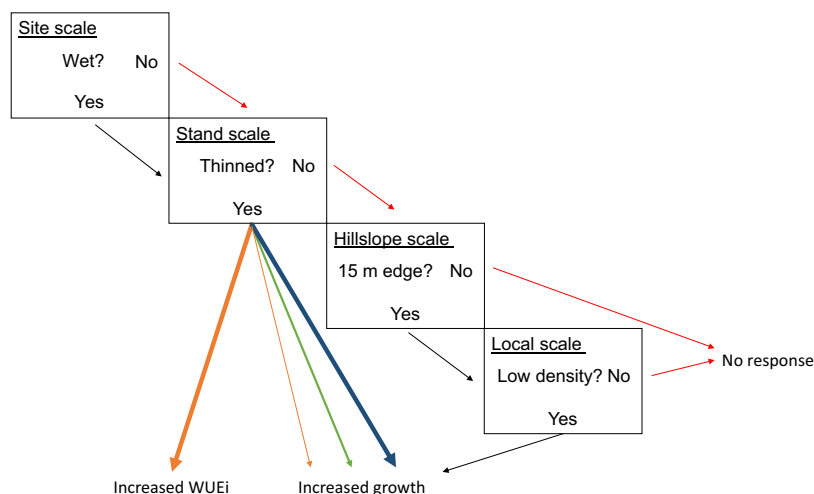


Fig. 6. Conceptual model for cross-scale interactions examined in our study from the largest scale in the upper left. Site-scale differences in growth impact the magnitude of the growth response of different stands to density reduction. Local neighbourhood density can override larger scale processes when investigating tree response to density reduction. Arrow width represents the magnitude of the cross-scale interaction for the response of Douglas-fir intrinsic water-use efficiency (iWUE) or growth. The dry site (orange arrow) responded to thinning with increased water-use efficiency. The wet site (blue arrow) responded to thinning with the greatest growth increase followed by the intermediate site (green arrow) and dry site. Multiple site trajectories of 'yes' responses are shown by black arrows. [Colour figure can be viewed at wileyonlinelibrary.com]

Northwest (Waring *et al.* 2008). In Europe, planted Douglas-fir grow faster at a mesic, continental site with summer rains than in a Mediterranean climate with a summer moisture deficit (Lévesque *et al.* 2013). The presence of cross-scale interactions suggest that results from our study, in a region with seasonal moisture patterns of a Mediterranean climate may not apply to these areas where Douglas-fir was introduced or even to other regions where Douglas-fir is found naturally (e.g. the Rocky Mountains). Higher summer moisture availability in many other regions (Waring *et al.* 2008) would likely modify the patterns found in this study, suggesting caution when extrapolating our results to other regions in the world without accounting for differences in amount and seasonal timing of water availability.

Our study suggested that even within the Pacific Northwest, sensitivity of Douglas-fir growth response to density reduction varies along a fairly narrow range of site conditions compared with the natural (and even more so, the anthropogenic) distribution of the species. In our study, trees on different sites appeared to have established different sensitivities to local climate. Trees growing at the dry site likely will experience more stress and less growth with changes, such as lower precipitation in the winter and spring because the majority of their diameter growth occurred in the spring prior to summer dry periods.

Our results supported general findings that report differences in growth rates and iWUE along a climate gradient at regional Pacific Northwest and sub-continental western North American scales (Nakawatase & Peterson 2006; Littell, Peterson & Tjoelker 2008). In general, trees growing at drier sites had a lower growth and higher iWUE (higher $\delta^{13}\text{C}$) when compared with trees on wetter sites (Panek & Waring 1997; Roden *et al.* 2005). Also, higher iWUE in trees on drier sites is relatively consistent when examined at continental scales for Douglas-fir (Chen, Welsh & Hamann 2010). In the Pacific Northwest,

photosynthesis in the winter and early spring contribute a large amount of carbon to tree reserves (Waring & Franklin 1979) and substantial water can be stored in tree trunks of Douglas-fir for use during the seasonal summer drought (Phillips *et al.* 2003). Trees may have also responded to extreme summer droughts by closing stomata and thus decoupling growth from regional climate measures (Panek & Waring 1997). Our results highlight that Douglas-fir can be locally adapted to site-level conditions through these and other ecophysiological mechanisms such as leaf morphology or crown architecture (Ausse-nac 2000). Earlier genetic studies suggested that Douglas-fir was adapted to environmental conditions at even smaller spatial scales, for example, on north vs. south slopes of the same ridge (Hermann & Lavender 1968). We identified cross-scale interactions (Fig. 6) that indicate site-scale adaptations should be taken into account when examining changes in growth or iWUE at fine spatial scales because these responses can vary depending on regional water regimes (Littell, Peterson & Tjoelker 2008; Chen, Welsh & Hamann 2010).

Density reduction typically increases growth rates in residual trees because of an increase in available resources with larger increases at better sites (Ausse-nac 2000). An increase in growth from density reduction without a change in iWUE at the intermediate and wet sites in our study suggested that photosynthesis and stomatal conductance increased in tandem (Farquhar, Ehleringer & Hubick 1989). On these sites, we speculate that the availability of resources that increase photosynthesis (light and nutrients) increased proportionally to resources that increase stomatal conductance (water). In contrast, trees in the treated stand at the dry site showed increased earlywood, latewood and entire ring growth and higher iWUE after treatment, indicating that impacts of an increase in available growing space or other resources that would favour photosynthesis was greater than impacts of increased water availability (Brooks &

Mitchell 2011). Contrary to expectations, our results indicated that density reduction at dry sites did not result in increased growth due to higher water availability in the late summer, rather growth responses appeared to be driven by an increase in other resources such as light or nutrients (McDowell *et al.* 2003, 2006). This notion is supported by other studies which showed increased iWUE in Douglas-fir due to nitrogen addition that likely increased photosynthesis relative to stomatal conductance (Brooks & Coulombe 2009; Brooks & Mitchell 2011). Our results also question whether an increase in absolute growth after density reduction on the dry site has resulted in higher tree vigour, that is, trees being further away from a tipping point, for example, drought-related mortality (Reyer *et al.* 2015).

Our findings also show how cross-scale interactions can help interpret confusing or contradictory findings. For example, when diameter growth in stands was averaged across our sites, trees downslope of treatment responded with increased growth, while trees in stands downslope of gaps did not. In our previous work, we had hypothesized that mechanisms for this included an expansion of understorey plants in the gaps as they were competing for nutrients, especially nitrogen, with the trees growing at the treatment edge (Ruzicka, Puettmann & Olson 2014). A more detailed investigation at finer spatial scales coupled with information about iWUE presented in the current study failed to support that hypothesis. Instead, our results suggested that competition in areas with high local neighbourhood tree densities may override any potential impacts from uphill treatment or gap creation. In this study, the hillslope scale (distance from treatment edge) was likely a proxy for competitive processes operating at the local neighbourhood scale. Other studies have also found that processes such as habitat availability operating at forest edges are dependent on the spatial scale examined (Donovan *et al.* 1997), as well as at cross-scale interactions which can lead to the apparent variability in responses when investigating edge effects (Ries *et al.* 2004). The importance of a small-scale variability has been shown in previous studies at DMS sites, as gap creation increased the amount and variability of nitrogen at the edges of gaps (Thiel & Perakis 2009). This increased small-scale variability in nutrient availability has been hypothesized as a factor for understorey responses that depended on small-scale processes operating at gap edges (Fahey & Puettmann 2008). Our study reported variability not just acting at fine scales (e.g. hillslope location or neighbourhoods), but that variability was influenced by larger scale factors, as it differed among sites and trees on the dry site had a more variable response than trees on the wet site.

Competition and other plant interactions influence plant establishment and growth at small spatial scales (i.e. local plant neighbourhoods; D'Amato & Puettmann 2004). Our study suggested a cross-scale interaction between competition operating at the local scale and the growth response downslope of treated and created gap stand edges. Although competition was reduced in the overstorey in stands after density reduction and near the edge, not all edge trees experienced the same change in local conditions. Even if they did, our

study suggested that trees would exhibit slightly different patterns of growth and iWUE after treatment depending on cross-scale interactions with site. Gap creation and density reduction create spatial heterogeneity in resource availability driven by residual plant structure, substrate and associated plant responses (Boyden *et al.* 2012). For example, regional-scale patterns in regeneration and understorey plant diversity after density reduction varied based on local competitive neighbourhoods and cross-scale interactions between overstorey cover and understorey competition (Burton, Ganio & Puettmann 2014; Dodson, Burton & Puettmann 2014). Other studies have also found that response to climate gradients can change based on interactions at different spatial scales or plant processes (Galván, Camarero & Gutiérrez 2014). Potential mechanisms for this disparity are rooted in local genetic adaptation (Hermann & Lavender 1968) and changes in resource availability over space and time as plants adjust to different growing conditions (Aussenac 2000).

Conclusions and management implications of cross-scale interactions

Our study identified a hierarchy of cross-scale interactions that reflect the changes in growth and iWUE following density reduction. Variability and patterns at each spatial scale investigated in our study has been driven by cross-scale interactions with the other spatial scales examined. There is great value in placing a project area and organisms under management consideration within the context of the larger landscape (Fig. 6). It was likely that unexplained variability in tree response to changes in neighbourhood density, especially at different sites, was at least partially due to factors measured at very fine scales, such as microclimate, soil resource availability and genetics not investigated, in this study.

Management actions to create a robust, climate-smart landscape need to examine the processes affected at multiple spatial and temporal scales. Our study identifies several potential avenues where cross-scale interactions can be utilized for management actions. Managers can prioritize stands for treatment based on different management goals and current conditions. Wet sites can be targeted for density reduction if increased growth and vigour of trees is the primary objective. Trees in dry or dense stands may respond at lower levels of residual density compared to wet stands. Management techniques used to create structural heterogeneity will need to account for changes in the local neighbourhoods of individual trees to understand stand-level responses (Dodson, Ares & Puettmann 2012). Local density controls can be used to create a mosaic of different conditions that vary over spatial scales. In addition, tree responses are not constant but change over time. For example, D'Amato *et al.* (2013) showed the initial beneficial responses reversed over time, that is, compared to unthinned stands, eventually trees in treated stands became more susceptible to drought, likely due to their increased crown size and leaf area.

Finally, the finding that cross-scale interactions are important in understanding vegetation response suggests that the inference scope for studies of tree response to density

reductions need to be placed into a larger spatial context (Raffa *et al.* 2008). Inference made on studies using single stands or averaging across regions cannot be simply extrapolated to global scales (Heffernan *et al.* 2014), other regions of the world (Soranno *et al.* 2014) or easily downscaled to local management options without the context of multiple interacting scales (Peters *et al.* 2004).

Authors' contributions

K.R., K.P. and J.B. conceived and designed the study, and wrote the manuscript; K.R. collected and analysed the data with feedback from K.P. and J.B.

Acknowledgements

Our research was supported by the American Recovery and Reinvestment Act, the United States Forest Service, Pacific Northwest Research Station, the United States Environmental Protection Agency, the Bureau of Land Management and the Edmund Hayes Silvicultural Fellowship. This manuscript has been subjected to the Environmental Protection Agency's (EPA) peer and administrative review, and it has been approved for publication as an EPA document. Mention of trade names or commercial products does not constitute endorsement or recommendation for use. Dede Olson and Paul Anderson helped with study design and site selection. We thank Paul Puettmann and Fritz Kraetcher for help with data collection. We also thank the EPA team at the ISIRF facility for expert advice and lab help for cellulose extraction. Numerous undergraduate students also helped with isotope sample preparation. We thank Louisa Evers, Dave Woodruff and two anonymous reviewers for reviews and helpful suggestions.

Data accessibility

Data, including location, growth and iWUE data are located at ScholarsArchive@OSU <https://doi.org/10.7267/N9QJ7F7B> (Ruzicka, Puttemann & Brooks 2017).

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Received 5 July 2016; accepted 3 January 2017

Handling Editor: Frank Gilliam

Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Basal area increment by year for the entire ring, earlywood and latewood for Douglas-fir trees growing in the unthinned stands at three western Oregon, USA study sites.

Fig. S2. Boxplots of post-pretreatment entire ring BAI for Douglas-fir trees downslope of the thinned and gap treatments in three western Oregon, USA study.