Examining the influences of tree-to-tree competition and climate on size-growth relationships in hydric, multi-aged *Fraxinus nigra* stands

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ABSTRACT

Most research on tree-tree competition and size-growth relationship (SGR – a stand-level metric that infers the relative efficiency with which different sized trees utilize available resources) has focused on upland systems. It is unclear if inferences from these studies extend to wetland forests. Moreover, no study to date has thoroughly investigated the relationship between individual tree-tree competition and SGR. To fill these research gaps, we conducted a dendrochronological study examining the relationship of tree-tree competition, SGR, and climate in late-successional *Fraxinus nigra* (black ash) wetland forests in northern Minnesota, USA. We took advantage of a detailed, stem-mapped dataset of 1670 trees in five late-successional, multi-aged stands to explore the following research questions: (1) how do competitive interactions, particularly size symmetry, influence individual-tree growth; (2) do late-successional *F. nigra* stands display inverse asymmetric SGR; and (3) do short-term variations in drought influence SGR in *F. nigra* wetland forests? Using neighborhood competition indices, which characterize the growth of individual trees based on the size, number, and distance of competitors, we examined the nature and strength of individual tree-tree interactions. Additionally, we used SGR to determine how tree size and individual tree contributions to stand productivity relate to changes in stand growth and competitive interactions during stand development. At the individual tree level, we found evidence of size-asymmetric competition, with larger trees disproportionately suppressing the growth of smaller trees. However, tree size was a stronger predictor of growth than competition at all sites. At the stand level, our multi-aged *F. nigra* sites showed consistent patterns of inverse size-asymmetric SGR (i.e., smaller individual trees growing at disproportionately higher rates relative to larger trees), which is generally consistent with previous observations of mature upland forests and supports the hypothesis that large trees decline in relative growth as stands age. While seemingly counter-intuitive, the simultaneous presence of size-asymmetric individual tree-level competition and stand-level inverse asymmetric SGR suggests declines in large tree production efficiency. Drought effects on SGR, as expressed by PDSI, while sometimes evident, appeared weak on both relatively mesic and extremely wet sites. Our findings, which are consistent with previous studies of both *F. nigra* wetlands and upland forests, demonstrate that the combined results of individual-tree competition models and stand-level SGR can provide deeper insights into growth and competition in *F. nigra* and other forest types.

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1. Introduction

Trees differentiate in growth rate and size during stand development, with implications for long-term patterns of forest productivity, structural characteristics, and mortality (Oliver and Larson, 1996). Differences in individual tree growth rates and sizes within forest stands may reflect a number of factors including microsite characteristics, such as water availability (Greenwood and Weisberg, 2008). In closed canopy stands in the absence of disturbance, the degree of heterogeneity in growth rates and size can be greatly influenced by tree-tree interactions, in particular, competition (Long et al., 2004; Oliver and Larson, 1996).

Retrospective studies of competition in forests have used neighborhood competition indices, which characterize the growth of individual target trees based on the size and, in some cases, the distance of competitors (Biging and Dobbertin, 1995; Canham et al., 2006, 2004; Larocque, 2002). Incorporating information about the relative distance of competitors is hypothesized to improve growth predictions in complex uneven-aged stands (Inoue et al., 2008), although the results of previous research using distance-dependent indices are inconsistent (Busing and Mailly, 2004). Competition indices can be used to supplement traditional measures of stand density in order to better describe the nature of tree-tree interactions, including size symmetry (Biging and Dobbertin, 1995; Canham et al., 2006, 2004; Larocque, 2002). When light is a limiting resource, as in closed canopy stands, tree-tree competition often demonstrates partial size asymmetry, with larger trees disproportionately suppressing the growth of smaller individuals (Schwinning and Weiner, 1998). In contrast, competition for soil resources, which are more diffuse and difficult to preempt, is more size-symmetric (Schwinning and Weiner, 1998), with access of individual trees to resources directly proportional to size (Larocque, 2002). If not offset by mortality, size-asymmetric interactions can increase growth rate variability within stands over time (Binkley, 2004), whereas size-symmetric competition evenly reduces individual tree growth below potential levels (Weiner and Thomas, 1986). Size-asymmetric competition may become increasingly symmetric later in stand development (Masaki et al., 2006), possibly as a result of increasingly scarce soil resources. In drought-limited forests, competition may also become inverse size-asymmetric, disproportionately impacting larger individuals (Biondi, 1996).

The onset of competition among trees early in stand development is typically understood to coincide with peak net stand-level growth and leaf-area (Long et al., 2004). Declining net stand-level growth following canopy closure contrasts with individual tree wood production, which typically increases with age (Long et al., 2004; Stephenson et al., 2014). Changes in stand growth and competitive interactions during stand development have been examined in terms of size-growth relationship (SGR), to aid in understanding the association between tree size and individual tree contributions to stand productivity (Castagneri et al., 2008; Metsaranta and Lieffers, 2010; Pretzsch and Biber, 2010). SGR is a stand-level metric that infers from tree sizes and growth rates the relative efficiency with which trees of differing sizes utilize available resources (Castagneri et al., 2012). In addition to long-term trends, SGR may provide insights into the effects of short-term fluctuations in stresses, such as extreme temperatures, drought, or low site quality on growth inequality (Castagneri et al., 2012; Pretzsch and Dieler, 2010). Similar to the patterns of size-symmetry used to characterize competition effects on individual trees, SGR is considered asymmetric when larger trees in a stand grow at relatively higher rates, symmetric when trees of all sizes grow at relatively similar rates, and inverse asymmetric when smaller trees grow at relatively higher rates (Castagneri et al., 2012).

In mature stands, several studies have found evidence of inverse size-asymmetric SGR, with smaller trees growing at higher rates than larger trees (Binkley et al., 2006; Castagneri et al., 2012; Pretzsch and Biber, 2010), supporting the hypothesis that large trees decline in relative growth as stands age (Binkley et al., 2006). However, research to date suggests inverse size asymmetry does not necessarily emerge in unmanaged mature stands (Bradford et al., 2010; Doi et al., 2010; Metsaranta and Lieffers, 2010; Nord-Larsen et al., 2006), may only occur in non-clonal species (Binkley et al., 2006), or is only stable in stands with multilayered structures (Castagneri et al., 2012). Inverse size-asymmetric SGR may stem from a size-related decline in the efficiency of large

trees or from a decline in individual tree competition for light or other resources (Pretzsch and Biber, 2010), although no study to date has thoroughly investigated the relationship between individual tree competition and stand-level SGR.

Furthermore, most research on tree-tree competition and SGR has focused on upland systems. It is unclear if inferences from these studies extend to wetland forests. Seasonal inundation in wetland forests poses particular challenges to tree growth (Kreuzwieser and Rennenberg, 2014). Although nutrient inputs during flood events may offset stress (Odum, 1985), saturated soil conditions can reduce productivity (Megonigal et al., 1997), while impairing tree nutrient status by restricting rooting depth (Baker et al., 2001). The few studies examining competitive dynamics in wetland systems show varying results. For example, even-aged *Taxodium distichum* L. (swamp cypress) stands display size-density and self-thinning relationships similar to those in upland forests (Keim et al., 2010), while Minnesota *Fraxinus nigra* Marsh (black ash) wetland forests show no evidence of competition based on an analysis of neighborhood basal area (Benedict and Frelich, 2008). In general, tree growth is thought to be less affected by drought in more hydric environments, due to the greater reliability of available water (Dudek et al., 1998). However, in a harsh floodplain environment in Quebec, *F. nigra* exhibited a lagged growth response to drought, with the seasonality of the drought determining whether the response was negative or positive (Tardif and Bergeron, 1993). No analysis to date has looked at the influence of drought on SGR in hydric forests.

We retrospectively investigated the relationship of tree-tree competition, SGR, and climate in northern Minnesota wetland forests dominated by *F. nigra*, an important tree species in northeastern North America currently threatened by the invasive insect, emerald ash borer (*Agrilus planipennis*, EAB; MacFarlane and Meyer, 2005). We took advantage of a detailed, stem-mapped dataset of 1670 trees in five late-successional, multi-aged *F. nigra* stands to answer the questions: (1) how do competitive interactions, particularly individual-level size symmetry, influence individual-tree growth; (2) do late-successional *F. nigra* stands display inverse asymmetric SGR; and (3) do short-term variations in drought influence SGR in *F. nigra* wetland forests? We expected competition to be primarily size-symmetric, particularly at wetter sites where higher abiotic stress would increase soil resource limitation. Given advanced stand age and moderate shade tolerance of *F. nigra*, we further expected to find inverse-size asymmetric SGR (i.e., disproportionately faster growth of smaller trees), especially at more severely flooded sites and sites with more shade-tolerant competitor species. Lastly, given a hydrological regime characterized by ponding and minimal sediment transport, we expected drought to increase both individual large tree growth and SGR by reducing abiotic stress. Our overarching goal was to test whether the combined results of individual-tree competition models and stand-level SGR could provide deeper insights into growth and competition in *F. nigra* forests.

2. Material and methods

2.1. Site description

We examined five late-successional, multi-aged, *F. nigra*-dominated forest stands, located on dispersed study sites in northeastern Minnesota (Fig. 1). Climate is continental, with the majority of precipitation occurring from May through September (PRISM Climate Group, 2015).

Soil varies from loam and sandy loam derived from glacio-fluvial or lacustrine parent materials to clay and silty clay derived from glacio-lacustrine material (USDA Natural Resources
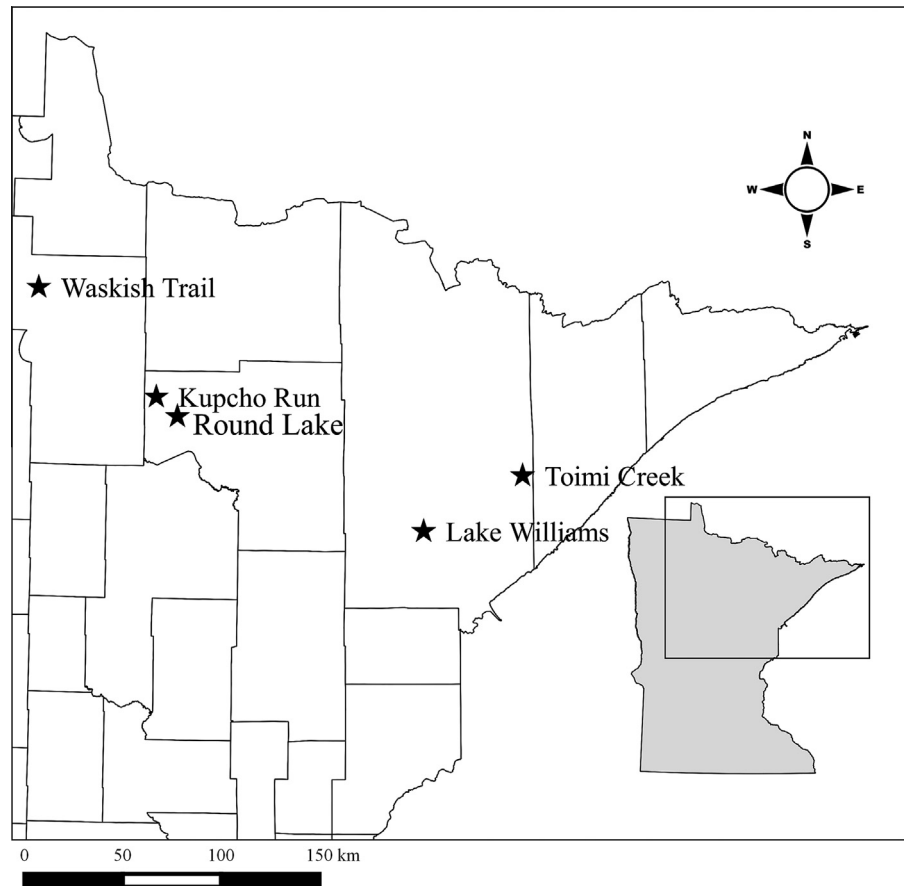
Fig. 1. Map depicting location of the five *Fraxinus nigra* study sites in northern Minnesota USA: Kupcho Run (KR), Lake Williams (LW), Round Lake (RL), Toimi Creek (TC), and Waskish Trail (WT).

Conservation Service, 2013). A confining layer of clay results in poor soil drainage and ponding during the early part of the May to September growing season, with water levels declining to below the ground surface typically by mid-July on all but the wettest sites (USDA Natural Resources Conservation Service, 2013). Precipitation (especially snowmelt) and evapotranspiration are largely responsible for water table fluctuations, with only minimal shallow subsurface flow occurring (Slesak et al., 2014). Ponding duration is highest at Lake Williams, followed by Toimi Creek, Round Lake, Waskish Trail, and Kupcho Run. Due to soil and slight topographical differences, variations in ponding duration were not linked to variations in mean annual rainfall (Table 1).

Fraxinus nigra was the dominant tree species an all sites, averaging 77.30 ± 2.7 percent of basal area across the five study sites (Table 1). Other tree species varied by site. The most common tree species other than *F. nigra* were *Tilia americana* L. (American basswood) and *Abies balsamea* L. (balsam fir) at Kupcho Run, *Betula alleghaniensis* Britton (yellow birch) and *Thuja occidentalis* L. (northern white cedar) at Lake Williams, *Ulmus americana* L. (American elm) and *A. balsamea* at Round Lake, *T. occidentalis* and *B. alleghaniensis* at Toimi Creek, and *A. balsamea* and *Picea glauca* (Moench) Voss (white spruce) at Waskish Trail (Table 1).

2.2. Field data collection

We installed one 71.7 × 71.7 m (0.5 ha) plot per stand. Within each plot, we assessed all living trees ⩾10 cm diameter at breast height (DBH) and recorded their species, DBH, status (live or dead), and Cartesian coordinates (x and y). We collected a single increment core to pith when possible from all trees at 1.3 m above the ground, for a total of 1670 cored live trees. While Visser (1995) recommends collecting a second core per tree at 90 deg from the first to obtain an accurate estimate of growth, the large number of sampled trees, given our desire to quantify population-level growth, made this infeasible. We also sampled 147 standing snags but opted to exclude them, as only 42 yielded measurable increment cores, species identification was problematic, and uncertain preservation rates meant that extant deadwood could not serve as a reliable sample of conditions beyond the most recent decades.

2.3. Sample preparation

Increment cores were prepared for analysis using standard dendrochronological techniques (Speer, 2010). Finished cores were measured for annual ring width using a Velmex measuring stage and visually cross-dated using the pointer-year method. We validated cross-dating in the COFECHA program (Holmes, 1983). To account for radial asymmetry (Visser, 1995), we scaled growth records by the ratio of the summed ring widths to the estimated mean inside-bark radius of the tree (Frelich, 2002), except where heart rot precluded obtaining full cores. We used bark thickness equations for Lakes States trees published in Dixon and Keyser (2008) to estimate diameter inside bark. For the analysis of competition, raw ring widths were converted to basal area increment (BAI) in the dplR package (Bunn, 2008) for R (R Core Team, 2013). For the analysis of growth asymmetry, we converted raw ring widths to annual biomass increment. We used biomass allometric equations in Perala and Alban (1993) for all species, which

Table 1
Summary statistics for live trees ⩾10 cm diameter at breast height (DBH) in five multi-aged *Fraxinus nigra* stands.

Measure	Species	Site					Mean
		Kupcho Run	Lake Williams	Round Lake	Toimi Creek	Waskish Trail	
TPH × species	FRNI	482	656	414	614	426	518.4
	ABBA	28	2	24	50	142	49.2
	ULAM	20	0	66	0	22	21.6
	THOC	0	28	0	78	0	21.2
	BEAL	0	74	0	28	0	20.4
	PIGL	38	0	0	2	18	11.6
	TIAM	50	0	4	0	0	10.8
	QUMA	34	0	8	0	2	8.8
	ACRU	0	12	0	0	0	2.4
Total TPH		664	774	516	776	610	668
TPH% *F. nigra*		73	85	80	79	70	77.3
Total BA		27.4	25.8	33.2	29.4	23.7	27.9
BA% *F. nigra*		69.1	90.2	95.2	77.9	83.7	84
QMD		23.0	20.6	28.6	22.0	22.2	23.3
Maximum diameter (cm)		58.1	54.5	59.4	58.0	50.0	56.0
Average tree age (yr)		75.4	94.3	113.7	122.5	117.6	104.7
Mean Precipitation (mm)		677	720.5	686.7	853.5	699	727.3
Ponding duration (5 longest)		1	5	3	4	2	

Note: TPH = trees per hectare, BA = basal area, QMD = quadratic mean diameter. Species codes are as follows: FNRI = *Fraxinus nigra*, ABBA = *Abies balsamea*, ULAM = *Ulmus americana*, THOC = *Thuja occidentalis*, BEAL = *Betula alleghaniensis*, PIGL = *Picea glauca*, TIAM = *Tilia americana*, QUMA = *Quercus macrocarpa*, ACRU = *Acer rubrum*. Mean values include standard errors.

were developed in Minnesota for trees spanning the range of diameters in our samples. The analysis of competition used BAI instead of biomass increment for consistency with other studies (Fraver et al., 2014; Larocque, 2002; Wykoff, 1990); the relationship between BAI and biomass was strongly linear ($R^2 = 0.97$).

2.4. Analysis

2.4.1. Individual tree growth and competition

We examined several distance-dependent (competitor trees weighted by distance from the target tree) and distance-independent competition indices (CIs) in order to further characterize the nature of competition in these stands (Table 2). We were particularly interested in whether competition was size-symmetric or asymmetric and distance-dependent or independent, and consequently restricted our analysis to fairly simple CI formulae based on available DBH and distance information. In the context of this paper, our uses of the terms size symmetry, size asymmetry, and inverse size asymmetry are equivalent to Schwinning and Weiner's (1998) perfect size symmetry, partial size asymmetry, and partial size symmetry, respectively. Index 1 is simply the sum of competitor diameters within a given radius (Table 2).

Indices 1 and 2 do not consider target tree diameter and can thus be viewed as size-symmetric. Indices 2–5 include information about competitor size and distance relative to the target tree and correspond to Indices 9–12 in Rouvinen and Kuuluvainen (1997). Index 3 is Hegyi's (1974) size-asymmetric index. Index 4 is also size-asymmetric but weights tree-tree distance heavily. Index 5 squares the size ratio, which weights competitors that are larger than the target tree more heavily. Index 6 is a distance-independent version of index 5. We also tested Lorimer's (1983) and Wykoff's (1990) distance-independent indices, both of which are size-asymmetric but involve less intensive field data collection and have proven effective in describing the nature of competition in a variety of forest conditions (Fraver et al., 2014). As with the other CIs, we calculated Lorimer's (1983) and Wykoff's (1990) indices based on focal tree neighborhoods rather than stand-level basal area or sums of diameters. A key step in using distance-dependent CIs is selecting a maximum search radius for potential competitors (Biging and Dobbertin, 1995). While recent authors have used a nonlinear, maximum-likelihood approach to estimate weighting factors for competitor size, distance, and maximum distance (e.g., Canham et al., 2004), we opted to test these factors using different CIs and search radii to characterize the nature of

Table 2
Summary of diameter-based competition indices.

Index	Type	Size symmetry	Equation	Source
CI-1	Distance dependent	Symmetric	$CI_i = \sum_{j=1}^{n} d_j$	Author adapted[a]
CI-2	Distance dependent	Symmetric	$CI_i = \sum_{j=1}^{n} \frac{d_j}{L_{ij}}$	Rouvinen and Kuuluvainen (1997)
CI-3	Distance dependent	Asymmetric	$CI_i = \sum_{j=1}^{n} \frac{\left(\frac{d_j}{d_i}\right)}{L_{ij}}$	Hegyi (1974)
CI-4	Distance dependent	Asymmetric	$CI_i = \sum_{j=1}^{n} \frac{\left(\frac{d_j}{d_i}\right)}{L_{ij}^2}$	Rouvinen and Kuuluvainen (1997)
CI-5	Distance dependent	Asymmetric	$CI_i = \sum_{j=1}^{n} \frac{\left(\frac{d_j}{d_i}\right)^2}{L_{ij}}$	Rouvinen and Kuuluvainen (1997)
CI-6	Distance independent	Asymmetric	$CI_i = \sum_{j=1}^{n} \left(\frac{d_j}{d_i}\right)^2$	Author adapted[a]
Lorimer	Distance independent	Asymmetric	$CI_i = \sum_{j=1}^{n} \frac{d_j}{d_i}$	Lorimer (1983)
Wykoff	Distance independent	Asymmetric	$CI_i = \sum_{j=1}^{n} (d_j)^2 * 0.00007854$	Wykoff (1990)

Note:
Indicated is whether competitors are weighted by distance and treated as symmetric or asymmetric in terms of diameter, equations, and in original publications where applicable. Symbols are as follows: CI_i is the competition index (*CI*) for the individual target tree (*i*); d_j is the diameter (*d*) of a given competitor (*j*); d_i is the diameter of target tree (*i*), L_{ij} is the distance (*L*) between target (*i*) and competitor (*j*). Indices are calculated for (*j* = 1) where (*j* ≠ *i*).

[a] Adapted by authors based on indices in Rouvinen and Kuuluvainen (1997).

competition (Aakala et al., 2013). This approach uses more traditional linear modeling that facilitates multi-model inference using information-theoretic approaches (Burnham and Anderson, 2003). We initially constructed a model of log-transformed 20-yr average BAI (1991–2010) vs. CIs pooled across all sites, with CIs calculated based on search radii varying from 5 to 10 m in 1 m increments. We chose a 20-yr average because a previous study suggested shorter growth windows are more easily perturbed by climatic factors (Busing and Mailly, 2004). We modeled growth only for target trees ⩾10 m from plot edge to avoid bias from unmeasured competitors. We found a search radius of 7 m was optimal (using pooled data) in terms of having the lowest value of Akaike's information criteria in bivariate regression with BAI (AIC, Akaike, 1974).

2.4.2. Size-growth relationship

We followed Metsaranta and Lieffer's (2010) approach for characterizing size-growth relationships given its computational ease, ability to handle missing data over previous years, and straightforward interpretation. Briefly, this approach (hereafter referred to as "SGR") estimates the slope of the regression between present-year proportional growth increment (individual-tree biomass increment relative to total stand biomass increment) and preceding-year proportional tree size (individual-tree biomass relative to total stand biomass), both of which are center log ratio-transformed (Aitchison, 1986). This transformation first relativizes within-tree growth and then applies a log transformation over all trees (Aitchison, 1986), yielding a linear relationship between increment and size over long time periods (Metsaranta and Lieffers, 2010). A value of 1 indicates size-symmetry; values above and below 1 indicate size-asymmetry and inverse size-asymmetry, respectively (Metsaranta and Lieffers, 2010). We confirmed SGR linearity through exploratory analysis (data not shown). We opted to use total aboveground biomass increment instead of volume, which has been used in previous studies (e.g., Metsaranta and Lieffers, 2010), due to the availability of local biomass equations (Perala and Alban, 1993), as well as the potential to account for shifts in aboveground growth allocation over time and for varying wood density among species. We calculated the index for the 1951–2010 period, as sample depth (number of trees) declined sharply in the 1940s. The index was calculated separately for *F. nigra*, as well as for all species pooled to allow for examinations of species-specific and population-level trends in SGR.

2.4.3. Climate

We examined the relationship between annual variations in drought and SGR for each site. We standardized 60-yr SGR chronologies at each site by fitting a 20-yr cubic spline with a wave cutoff of 0.5. We used Palmer's drought severity index (PDSI, Palmer, 1965) as an indicator of historical water availability. An integrated measure of precipitation and potential evapotranspiration, PDSI has been widely used in dendro-climatological studies to represent moisture stress (Speer, 2010). Positive PDSI values indicate above-average moisture; negative values indicate moisture deficits. We obtained monthly PDSI records for the northern Minnesota study area from the National Climatic Data Center (National Oceanic and Atmospheric Administration, 2015). We also investigated SGR relationships with mean monthly precipitation and maximum temperature records (PRISM Climate Group, 2015).

2.4.4. Statistical modeling

Our analyses included two organizational levels: individual tree-tree interactions and stand-level SGR. For the analysis of individual tree-level growth, sites were analyzed independently to examine within-site patterns, while we used the pooled dataset of trees across all sites to model the general performance of the various CIs. In both cases, we examined the relationship between

F. nigra growth and tree size and competition, with average 20-yr BAI (1992–2011) as the response variable. Non-*F. nigra* species were too scarce to separate competitors by species. To address the fact that tree response to competition may vary with size (Biondi, 1996; Canham et al., 2006), we included an end-year DBH × CI interaction term in the full models. Square root and natural log transformations of BAI were applied when necessary to meet regression assumptions. Based on plots of raw data and model residuals, it was unnecessary to transform Wykoff's (1990) index. All other CIs, as well as DBH, were natural log transformed. We centered and scaled variables to place DBH and CI on comparable scales and reduce multicollinearity.

We began the analysis of individual tree growth by building candidate models based on expectations regarding the nature of tree-tree competition in multi-aged *F. nigra* stands. Our analyses were structured to distinguish among competitive (negative CI effect), neutral (low AIC support for models excluding CI), or facilitative (positive CI effect) tree-tree effects on growth. For each CI, we began with a global model including the main effects of size and CI, plus an interaction term to allow for the possibility that growth response to competition may vary with tree size (as above). Based on the global model, we also derived models to evaluate the main effects of CI and DBH both together and as univariate predictors. Models with the lowest AIC values were considered the best approximating models in a given set, and we compared strength of evidence for a given model based on its difference from the top model in a given set (ΔAIC). Candidate models within ΔAIC ⩽ 2 were considered as having a similar level of support for being the best approximating model in a set (Burnham and Anderson, 2003). We further compared models using Akaike's (1974) weights and weight ratios to construct confidence sets of models with an evidence ratio within 1/8 of the highest-weight model (Burnham and Anderson, 2003). For clarity, we only present the top within-site models included in the confidence set at each site. Similarly, among the pooled data models, we also restrict our presentation to confidence set models. We also present intercept-only null models for purposes of comparison, in which BAI is solely a function of mean growth rate and spatial autocorrelation. Given adjacency of trees within sites, we compared models both excluding and accounting for spatial autocorrelation of recent individual-tree growth. Spatially autocorrelative models involved fitting an exponential variogram to model residuals to adjust regression estimates. This approach helps control for microsite heterogeneity or shared history of minor disturbances that may result in adjacent trees showing similar growth rates, regardless of biotic interactions (Puettmann et al., 2009). Analysis of individual-site growth models was performed using generalized least-squares (GLS) regression.

In contrast to individual-tree-level growth, for the stand-level metric, SGR, each site was treated as representing a single sample unit. We examined within-site differences in SGR in terms of type (calculated separately for *F. nigra* vs. all species combined), year, and year × type interaction. We constructed a null intercept-only model, a global model incorporating main effects and the interaction for each site, and simpler models of main effects and bivariate relationships. We used AIC as described above to assess strength of evidence for each alternative. Spatial autocorrelation was not a potential confounding factor in these analyses, as it was with individual tree competition. However, because SGR represented time-series (1951–2010) data as opposed to a single, periodic average, there was a possibility that temporal autocorrelation could influence estimates. Autocorrelation function, partial autocorrelation, and model residuals plots suggested SGR was an AR (1) process (SGR in the present year is positively correlated with SGR of the previous year), which we modeled in the residual variance using generalized least squares (GLS) modeling. We performed GLS modeling using the gls function in the nlme package (Pinheiro et al.,

2012) for R (R Core Team, 2013). Pooled data models included a random site effect to stratify autocorrelation estimates; these models were performed using the lme function in nlme.

The relationships between SGR and climate variables were examined using bootstrapped response function analysis in the R package bootres (Zang and Biondi, 2013). This procedure reduces the dimensionality of multivariate monthly climate records through principle components analysis (PCA), followed by regression of principle components (PC) on a given chronology (Speer, 2010). Significance is then determined through a bootstrapped randomization test with 1000 iterations. Given delays between precipitation and hydrological responses, combined with known lagged *F. nigra* climate-growth responses (Tardif and Bergeron, 1993), we extended the analysis window from January of the preceding year through the end of the current-year growing season (September).

3. Results

3.1. Individual tree growth and competition

Basal area increment (BAI) over the 1992–2011 period for *F. nigra* subsampled for the individual-tree growth models averaged 409.8 ± 12.3 mm^2 yr^{-1} for all sites and was highest at Kupcho Run (618.2 ± 136.5 mm^2 yr^{-1}) and Round Lake (638 ± 167 mm^2 yr^{-1}), intermediate at Waskish Trail (405.9 ± 12.33 mm^2 yr^{-1}) and Lake Williams (420.1 ± 79.6 mm^2 yr^{-1}), and lowest at Toimi Creek (293.7 ± 45.5 mm^2 yr^{-1}). Diameter at breast height (DBH) for the *F. nigra* subsample averaged 22.2 ± 15 cm for all sites and was highest at Round Lake (30.6 ± 4.5 cm), followed by Waskish Trail (22.8 ± 3.5), Toimi Creek (20.7 ± 2.6 cm), Kupcho Run (20.5 ± 3.3), and Lake Williams (19.8 ± 2.5). We tested for but found no evidence of facilitation.

There was evidence that tree size significantly influenced *F. nigra* growth at all sites, while the most parsimonious models found that CI was an important predictor of individual tree growth at all sites but Lake Williams (Table 3). End-year DBH was a significant, positive predictor of past growth within the confidence set of all sites except Waskish Trail (Table 3).

Furthermore, DBH had a larger standardized partial regression coefficient than either CI or interaction terms in models for Kupcho Run, Lake Williams, and Round Lake (Table 3).

The nature of competition, as evidenced by the selection of different competition indices to predict growth, varied among sites
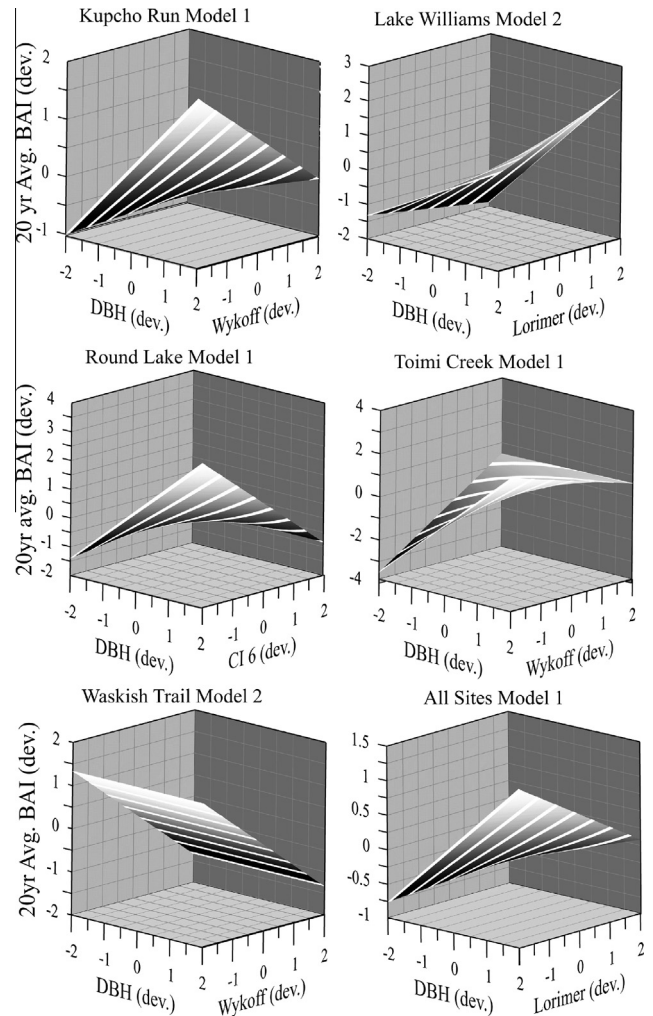
Fig. 2. Response surfaces for the most highly supported *Fraxinus nigra* growth model in the confidence set for 5 multi-aged *F. nigra* stands. In the case of Lake Williams, the second-best supported model is displayed for illustration; the best-supported model at Lake Williams was a simple function of DBH. Basal area increment increases from bottom to top on the Y axis. The X axis displays DBH with standard deviation (dev.), while the Z axis displays competition index (CI) with standard deviation (dev.). Variables were centered and standardized following transformations. BAI for Kupcho Run, Round Lake, and Toimi Creek was square-root transformed. All other response and predictor variables were log-transformed.

Table 3
Summary of null and confidence set models for individual sites (ΔAIC $\leqslant 8$), showing relative support for both null and most probable model by competition index (CI) across sites.

Site	Model	DBH	CI	DBH × CI	AIC	ΔAIC	Relative likelihood	Weights	Evidence ratio
KR	Wykoff	0.61***	−0.26***	−0.14***	180.35	0.00	1.00	0.76	1.00
KR	Lorimer	0.41***	−0.46***	−0.17***	183.45	3.10	0.21	0.16	4.71
KR	CI-6	0.47**	−0.40***	−0.16***	185.04	4.69	0.10	0.07	10.43
KR	Null	–	–	–	368.12	187.77	0.00	0.00	5.94E+40
LW	DBH	0.80***	–	–	369.40	0.00	1.00	0.63	1.00
LW	Lorimer	0.98***	0.13	0.12**	371.03	1.63	0.44	0.28	2.26
LW	Wykoff	0.95***	0.11	0.11*	373.24	3.84	0.15	0.09	6.82
LW	Null	–	–	–	556.14	186.74	0.00	0.00	3.55E+40
RL	CI-6	0.55**	−0.41*	−0.28***	169.45	0.00	1.00	0.63	1.00
RL	Lorimer	0.72***	−0.24	−0.28***	170.65	1.20	0.55	0.44	1.82
RL	Null	–	–	–	285.86	116.41	0.00	0.00	1.07E+23
TC	Wykoff	0.75***	0.28	−0.36***	365.60	0.00	1.00	0.47	1.00
TC	Lorimer	0.30	−0.26	−0.31***	366.00	0.40	0.82	0.39	1.22
TC	CI-6	1.12***	0.52*	−0.28***	368.34	2.74	0.25	0.12	3.94
TC	CI-5	0.43***	−0.18	−0.23***	372.30	6.70	0.04	0.02	28.50
TC	Null	–	–	–	425.16	59.56	0.00	0.00	8.58E+12
WT	Wykoff	–	−0.67***	–	223.70	0.00	1.00	1.00	1.00

Table 3 (continued)

Site	Model	DBH	CI	DBH × CI	AIC	ΔAIC	Relative likelihood	Weights	Evidence ratio
WT	Null	–	–	–	287.91	64.21	0.00	0.00	6.70E+13
All	CI-6	0.47***	−0.23*	−0.13***	1327.60	0.00	1.00	0.54	1.00
All	Lorimer	0.52***	−0.21*	−0.12***	1328.66	1.06	0.59	0.47	1.70
All	Wykoff	0.54***	−0.19***	−0.07**	1330.28	2.68	0.26	0.16	3.82
All	Null	–	–	–	1840.15	512.55	0.00	0.00	3.42E+221

Note: Model refers to the formula of CI used; see Table 2 for details. DBH (diameter at breast height), CI, and DBH × CI columns display standardized partial regression coefficients (beta weights) of model terms, when present. Also provided are Akaike's information criterion (AIC) model comparisons (Burnham and Anderson, 2003) within sites and models comparing CI across sites. Symbols are as follows: AIC, difference compared to best-fitting model (ΔAIC); relative likehood; Akaike weights (weights); evidence ratio. Akaike weights calculated for models within the confidence sets also incorporate null intercept models. See Fig. 1 for site abbreviations.

(Table 3). The distance-independent Wykoff (1990) and Lorimer (1983) indices had substantial support at all sites. Wykoff's (1990) index was the best performing of the indices tested at Toimi Creek, Kupcho Run, and Waskish Trail, where support for the best-performing alternative indices ranged from strong to negligible (ΔAIC = 3.1, 0.4, and >8, respectively). Lorimer's (1983) index was the best performing at Lake Williams, and second-best performing CI at Kupcho Run, Round Lake, and Toimi Creek (ΔAIC = 3.1, 0.0, and 0.4, respectively). Finally, the distance-independent index, CI-6, was the best-performing at Round Lake, and third-best performing at Kupcho Run (ΔAIC = 4.69). Of the distance-dependent indices, the most size asymmetric, CI-5, was the best supported but only included in the confidence set of Waskish Trail (ΔAIC = 6.70). A bivariate model including Wykoff's (1990) index was the most parsimonious model at Lake Williams, with competing regression models lacking substantial AIC support (ΔAIC > 8). The slope of the CI main effect was positive but insignificant in models at Lake Williams.

With the exception of Waskish Trail, CI influenced growth both as a main effect and through interaction with DBH (Table 3). Within the range of the data, growth effects of CI varied from almost neutral in small trees to negative with increasing size in larger trees (Fig. 2). At Kupcho Run, Round Lake, and Waskish Trail, CI had a negative main effect, while also interacting negatively with increasing DBH, which suggests CI had negative growth impacts that became more severe with increasing target tree size. At Lake Williams, the confidence set included a weak, positive interaction effect in two less-supported models, suggesting growth increased with CI, but at a faster rate when target tree size was larger. Models for Round Lake and Toimi Creek included the largest interaction effects.

The best-performing model by CI based on pooled data included CI, DBH, and the CI × DBH interaction (Table 3). Index 6 had the highest performance based on AIC, with Lorimer's and Wykoff's indices also having substantial support (ΔAIC = 1.06 and 2.68, respectively). In all cases, the main effect of DBH had the largest standardized
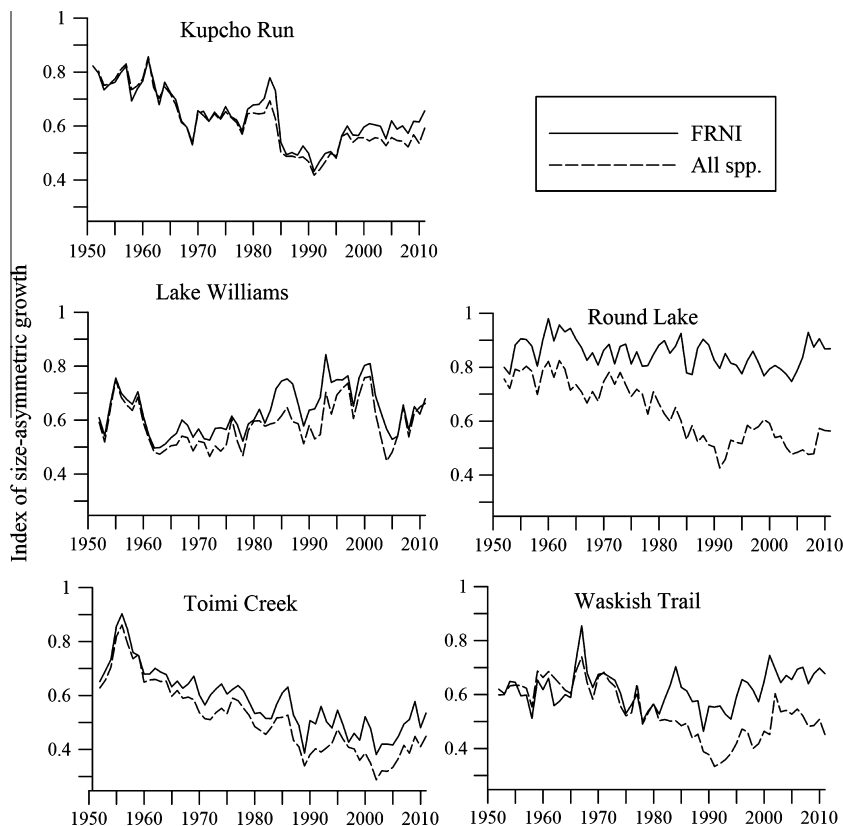
Fig. 3. Trends in Metsaranta and Lieffers (2010) size-growth relationship (SGR) index for 5 multiaged *Fraxinus nigra* stands, 1952–2011. The SGR is provided separately for each site based on all-species data and calculated separately for *Fraxinus nigra*. SGR values <1 indicate inverse size-asymmetric growth, values >1 indicate size-asymmetric growth, and values = 0 indicate size-symmetric growth.

partial regression coefficient, followed distantly by CI and the CI × DBH interaction, and had greater significance for models with high AIC support. The DBH × CI coefficient also declined but remained significant in the model using Wykoff's index.

3.2. Size-growth relationships

For the 1952–2011 period, SGR averaged 0.58 ± 0.001 for all species combined (Fig. 3). Round Lake showed the highest all-species SGR at 0.64 ± 0.01, followed by Lake Williams (0.62 ± 0.01), Kupcho Run (0.61 ± 0.01), Waskish Trail (0.54 ± 0.01), and Toimi Creek (0.51 ± 0.02). SGR calculated for *F. nigra*-only was highest at Round Lake at 0.85 ± 0.01, followed by Kupcho Run (0.63 ± 0.02), Lake Williams (0.63 ± 0.01), Waskish Trail (0.62 ± 0.01), and Toimi Creek (0.58 ± 0.01). At Waskish Trail, a plausible model including SGR type (*F. nigra*-only vs. all species combined) suggested SGR was marginally higher for the *F. nigra* component (F = 14.7, p < 0.001; Table 4), although this model had less AIC support than the Round Lake intercept-only model (F = 3.17, p = 0.078, ΔAIC = 4.1). At Round Lake, there was evidence of a difference in type of SGR, but this model had equivalent AIC support to the null model for the site.

Although not as well supported as intercept-only models, there was model support for a decline in SGR over time at Toimi Creek (F = 20.4, p < 0.001, ΔAIC = 6.32, Fig. 3) and Kupcho Run (F = 14.65, p < 0.001, ΔAIC = 5.98). There was minimal evidence for an SGR type × year interaction (ΔAIC > 8) at any site.
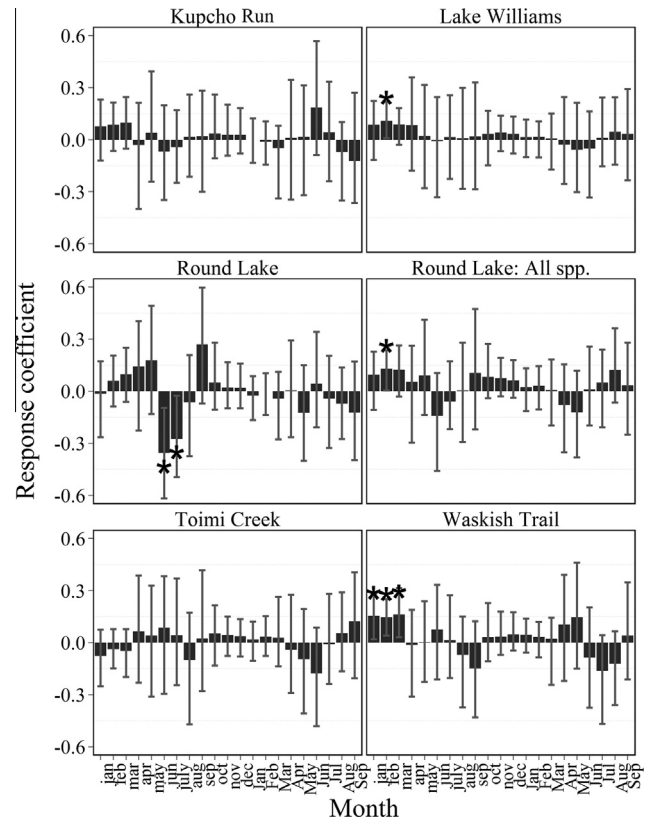
3.3. Climate

Due to inconsistent and generally insignificant relationships between SGR, temperature, and precipitation across sites, as well as the lack of consistent trends in adjacent months, we omitted these variables in favor of PDSI. We found significant (p < 0.05) but tenuous relationships between *F. nigra* SGR and PDSI for certain months at three of the five sites (Fig. 4). *Fraxinus nigra* SGR increased in years in which there was greater moisture availability in the winter of the previous year, as evidenced by the positive response functions for previous February PDSI at Lake Williams, and previous January-February-March PDSI at Waskish Trail. SGR for all species increased at Round Lake in response to previous February PDSI. The PDSI response of all-species-SGR was equivalent to that of *F. nigra* SGR at all other sites. At Round Lake, *F. nigra* SGR was lower in years with greater moisture availability during the preceding June and July, but was not responsive to preceding June-July PDSI. We did not find any significant SGR/PDSI relation-

Fig. 4. Relationships between spline-standardized Metsaranta and Lieffers (2010) size-growth relationship (SGR) index and Palmer's (1965) drought severity index (PDSI) based on bootstrapped response function analysis. Analysis based on annual SGR values and monthly PDSI, 1952–2011. Response functions were calculated separately for all-species and for *F. nigra*-only SGR. Positive coefficients indicate increased size-asymmetry of growth in wet years; negative relationships indicate reduced tree growth in wet years. Response functions for all-species SGR are omitted for brevity due to showing responses equivalent to *F. nigra*-only SGR except at Round Lake, where responses differed. Months shown in lower case are from previous year. ∗ significant at p < 0.05; ∗∗ significant at p < 0.01; ∗∗∗ significant at p < 0.001.

ships at Kupcho Run or Toimi Creek, and SGR did not vary significantly with current year PDSI at any site.

4. Discussion

4.1. Individual-tree growth and competition

At the individual tree level, we found support for the continued importance of competition in the late-successional *F. nigra* stands we sampled. While the importance of competition varied substantially by site, competition was universally best described in terms of the relationship between target tree size and the size of neighboring trees, independent of neighbor tree distance. Given that spatial point pattern analysis showed irregular tree spacing on three of our five late-successional *F. nigra* study sites (D'Amato, *unpublished data*), this result contradicts the theory that distance-dependent CIs can better predict growth in complex, uneven-aged, irregularly spaced stands (Inoue et al., 2008). Our finding confirms the observation of previous researchers that distance-dependent CIs do not consistently improve growth predictions compared to distance-independent CIs (Busing and Mailly, 2004). The inconsistent performance of distance-dependent CIs suggests that the benefits of distance information in growth modeling may vary substantially between systems (Aakala et al., 2013; Busing and Mailly, 2004).

Table 4
Summary of confidence set SGR models for individual sites (ΔAIC ≤ 8).

Site	Model	Year	SGR type	AIC	ΔAIC
KR	Null	–	–	−372.84	0
KR	Year	−0.004[***]	–	−366.86	5.98
RL	Null	–	–	−374.46	0
RL	Type	–	0.201[***]	−374.37	0.09
TC	Null	–	–	−386.40	0
TC	Year	−0.004[***]	–	−380.08	0
TC	Type	–	0.060	−382.30	2.22
WT	Type	–	0.083	−341.20	0
WT	Null	–	–	−344.60	3.40

Note: Potential model included SGR type (*F. nigra*-only or all species) and year (1952–2011). Columns display unstandardized regression coefficients, when present. Models are ranked within sites in terms of AIC support, with models presented in order of declining support. See Table 3 for explanation of symbols related to AIC. See Fig. 1 for site abbreviations. Lake Williams is not included as there was no AIC support for either a time or species effect on SGR.
[*] Significant at p < 0.05.
[**] Significant at p < 0.01.
[***] Significant at p < 0.001.

As expected in our mature, predominantly closed-canopy stands (Schwinning and Weiner, 1998), we found greater support for size-asymmetric indices (i.e., large trees disproportionately suppressing the growth of smaller trees), especially the distance-independent Lorimer's (1983), Wykoff's (1990), and CI-6 indices, than for size-symmetric indices. Of the size-asymmetric, distance independent indices, CI-6, which assumes competition is more highly asymmetric by squaring the ratio between competitor and target DBH, had better support than Lorimer's index in pooled data models. The low performance of the size-symmetric, distance-independent CI-1 across all sites suggests belowground competition is of secondary importance in these stands, as size-asymmetric competition in plants is frequently interpreted as reflecting light limitation (Weiner, 1990). Unfortunately, the lack of young, even-aged stands in the dataset prevented us from testing whether the degree of size-asymmetrical competition (Schwinning and Weiner, 1998) decreases with stand age, as suggested by Masaki et al. (2006).

In contrast to several previous upland forest studies (Canham et al., 2006, 2004; Gómez-Aparicio et al., 2011), we found individual tree response to competition increased with tree size at most sites. Biondi (1996) inferred a similar process in multi-aged *Pinus ponderosa* Laws. (ponderosa pine), where old-growth trees show evidence of decline in response to historical increases in young cohort density. We propose several non-exclusive hypotheses to account for this finding. Higher responsiveness to competition as expressed in slowed growth rates in larger trees may reflect ontogenetic declines in shade tolerance (Valladares and Niinemets, 2008) or rising respiration costs with size (King, 1990). In addition, taller trees are subject to greater wind stress; thus crown abrasion, resulting in reduced leaf area, could increase with canopy position (Oliver and Larson, 1996). Nevertheless, if large trees are indeed more responsive to size-asymmetric competition, the effect is offset by the fact that relatively larger neighbors were uncommon compared to smaller trees (Coomes and Allen, 2007).

Individual-tree growth models indicated competition was likely an important process at all sites but Lake Williams, but tree size for the most part appeared to be a stronger indicator of growth, with DBH frequently having the highest standardized partial regression coefficient. Our finding of a positive relationship between BAI and DBH is corroborated by earlier work by Benedict and Frelich (2008). The strong positive relationship between tree size and growth is also consistent with general patterns typical of upland forest types, where individual tree BAI continues to increase with size (Long et al., 2004; Stephenson et al., 2014). Despite taking measures to assure limited multicollinearity in our models, target tree size was both an indicator of short-term periodic growth and an outcome of long-term tree-tree interactions that confounds analyses through correlation with CI (Biging and Dobbertin, 1995; Larocque, 2002).

We note that microsite variation may have reduced the importance of competition in this study. The increased response of large trees to competition at some sites may be spurious if *F. nigra* preferentially establishes on more suitable microsites, where small trees could display rapid growth despite locally high tree densities. Additionally, a lack of significant evidence of competition at Lake Williams and low partial regression coefficients at other sites could suggest trees are unable to fully occupy available growing space. Similarly, low-quality microsites may also have confounded our results, as trees on poor microsites face high abiotic stress despite having few neighbors (Greenwood and Weisberg, 2008).

4.2. Size-growth relationship

At the stand level, SGR was consistently less than 1:1 at all sites and showed evidence of inverse-size asymmetry (i.e., smaller trees growing faster), as expected given the advanced stand age. Furthermore, SGR appeared to be either stable or declining over the preceding 60 years. Our results support Binkley's (2004) prediction that smaller trees grow disproportionately faster than larger trees in mature stands, based on a model developed for dryer forest types. In addition, the inverse-size asymmetric SGRs found in this study are consistent with Castagneri et al. (2012), who found SGR < 1 in an older stand of *Picea abies*, as well as with the results of studies that found faster growth of smaller relative to larger trees in mature, multilayered stands of other species (Binkley et al., 2006; Ex and Smith, 2014). A caveat of retrospectively reconstructing SGR is that long-term patterns may be obscured by past tree mortality, which we could not account for due to rapid decay of dead trees. A modeling study suggests unaccounted mortality may obscure stand-level growth trends (Foster et al., 2014), but to our knowledge mortality has not been investigated in the context of SGR.

Our results suggest that multi-aged *F. nigra* stands may exhibit inverse-size asymmetric SGR, even as individual trees compete asymmetrically for light late into stand development. However, in terms of the hypothesis that inverse size-asymmetric-SGR in mature stands reflects declining importance of light competition (Doi et al., 2010; Metsaranta and Lieffers, 2010; Pretzsch and Biber, 2010), we found contradictory evidence in individual-tree growth models. In agreement with this hypothesis, we found a lack of strong evidence of competition at Lake Williams, where the most parsimonious model suggested growth was directly proportional to tree size. Yet overall, we found greater support for size asymmetric indices both within and among sites. While we would have expected higher performance of size-symmetric CI-2, given the prevalence of inverse size-asymmetric SGR, CIs based on above-ground tree attributes may be poor indicators of diffuse below-ground processes (Larocque, 2002). In addition, Pretzsch and Biber (2010) note that large, inefficient trees in mature stands may depress SGR, even as small trees face intense competition. Inverse size-symmetric SGR in this study more likely reflects declining overstory efficiency, as opposed to competitive interactions between canopy layers. Our use of biomass in estimating SGR may also exaggerate declining efficiency compared with SGR based on leaf area index (Ex and Smith, 2014). However, while the individual-tree and SGR analyses differ in terms of growth metric (BAI vs. biomass increment, respectively), the strong relationship between biomass increment and BAI suggests this discrepancy was not responsible for the sometimes contradictory results of these analyses.

At Round Lake and Waskish Trail, we found evidence that SGR for *F. nigra* alone was higher than for all species combined. With the exception of *T. americana*, *A. balsamea*, *P. glauca*, and *Populus tremuloides* at the Kupcho Run site, non-*F. nigra* species were relegated to lower crown classes. The possible decline in SGR when including these species further suggests large *F. nigra* are growing relatively inefficiently. At Round Lake and Waskish Trail, which showed the greatest contrast between all-species and *F. nigra* SGR, the more shade-tolerant *A. balsamea* and *U. americana* were present in lower strata. Binkley et al. (2006) report similar patterns in their analysis of growth dominance in Rocky Mountain *P. tremuloides* stands with and without conifer understories. Light partitioning between an intolerant upper strata and tolerant lower strata may increase stand productivity as well as depress SGR (Binkley et al., 2006; Pretzsch, 2005).

The patterns observed in our competition models and analyses of SGR could also reflect recent periods of canopy disturbance in these ecosystems. In particular, many of the sites contained a minor *U. americana* component in the canopy prior to the arrival of Dutch elm disease (*Ophiostoma novo-ulmi* Brasier) in northern Minnesota in the early 1980s. Analyses of growth releases and tree

recruitment in these stands indicate significant periods of canopy disturbance in the 1980s in response to the loss of the *U. americana* component (D'Amato et al. *unpublished data*). As a result, smaller trees occupying gaps may have affected size-related patterns in tree growth response to competition. In addition, following periods of drought in the early 2000s, declines in crown condition and vigor have been recently observed in Minnesota *F. nigra* stands (Palik et al., 2011). Crown dieback is particularly pronounced in large, old *F. nigra* on wet sites and may account in part for inverse asymmetric SGR. While the etiology of this phenomenon is not entirely understood, competition among large trees could contribute to lower vigor and SGR. We found evidence of increasing growth responsiveness to CI with size at Toimi Creek and Round Lake. Loss of upper canopy cover also reduces SGR by promoting growth in lower canopy layers. However, given that sapling *F. nigra* appear also to be affected by canopy dieback in stands showing overstory decline, albeit to a lesser degree than mature trees (Palik et al., 2012), *F. nigra* decline may be more likely to promote increased growth of other species.

4.3. Climate

Studies of climate-SGR relationships in upland forests have found that short-term variations in SGR reflect changes in abiotic stressors, such as climate and pollution (Pretzsch and Dieler, 2010); while others have been inconclusive (Metsaranta and Lieffers, 2010). Our results suggest that, when significant, moisture deficits as indicated by PDSI appear to influence the following year's SGR in some *F. nigra* stands. While the correlation between lagged SGR and precipitation was weakly significant for only three of the five sites that we studied, our finding is consistent with a previous study that assessed *F. nigra* growth, but not SGR, in a harsher floodplain setting in Quebec (Tardif and Bergeron, 1993). There, researchers found growth was negatively correlated with precipitation in the preceding spring and positively correlated with precipitation in the preceding July (Tardif and Bergeron, 1993). The authors suggested lagged *F. nigra* growth–climate relationships could reflect the effects of moisture availability on bud formation (Tardif and Bergeron, 1993). Finally, we note that the inability to account for trees that died before the start of measurement likely had an unknown impact on the results of the climate analyses.

5. Conclusions

We found evidence of competition within the five late-successional multi-aged *F. nigra* stands we studied. The mode of competition appeared to be size-asymmetric, and distance-dependent indices were less accurate predictors of growth than distance-independent ones. Competition was useful for predicting growth at all sites, although much less important at the wettest site. On sites where competition was important to explaining patterns in growth, trees appeared increasingly responsive to competition with size, and size was a more accurate predictor of growth than competition on all sites. The multi-aged *F. nigra* stands showed consistent patterns of inverse size-asymmetric SGR (i.e., competition disproportionately impacting larger individuals) that were generally consistent with previous observations of mature upland forests. The simultaneous presence of size-asymmetric competition suggests declines in large tree production efficiency are responsible for inverse asymmetric SGR in these stands. Recruitment of vigorous, shade-tolerant species, especially following Dutch elm disease in the 1980s, as well as a disease-decline complex may have accentuated declining SGR in recent decades. Moisture-deficit effects on SGR were sometimes evident but weak on both more mesic and extremely wet sites.

Our results are consistent with past silvicultural experience with *F. nigra*, which suggests multiaged management is preferable for promoting ecosystem resilience in these forests (Erdmann et al., 1987). In particular, stands with mixtures of shade-tolerant species, such as *U. americana* or *A. balsamea*, are potentially more productive than pure stands, and the combination of productivity and diversity may promote resilience following EAB invasion. The development of inverse asymmetric SGR in multi-aged *F. nigra* stands indicates that lower cohorts can grow efficiently under partial shade, a general requirement for efficient management under selection systems. Unfortunately, EAB invasion may render long-term silvicultural experiments involving mature *F. nigra* infeasible in coming decades. However, managers may expect shade-tolerant, non-*F. nigra* species to respond positively to overstory loss, providing decreased evapotranspiration from *F. nigra* tree loss does not prohibitively increase site moisture. Based on our results, it appears large tree growth in some *F. nigra* stands benefits from winter precipitation, while other stands may experience deleterious effects from heavy summer rains. As a result, managers may expect declines in large tree growth in some post-EAB stands should summer moisture availability increase as a result of reduced evapotranspiration following the loss of *F. nigra*.

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