



Succession, climate and neighbourhood dynamics influence tree growth over time: an 87-year record of change in a *Pinus resinosa*-dominated forest, Minnesota, USA

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Nomenclature

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Introduction

Increasingly, forests are characterized as complex adaptive systems rather than products of easily predicted, deterministic processes (Puettmann et al. 2009; Messier & Puettmann 2011). In this context, forest structure, species composition and associated tree-to-tree interactions in

Abstract

Question: Resource availability and its influence on tree-to-tree interactions are expected to change over the course of forest stand development, but the rarity of long-term data sets has limited examinations of neighbourhood crowding over extended time periods. How do a history of neighbourhood interactions and population-level dynamics, including demographic transition, impact long-term tree growth?

Location: Natural mature *Pinus resinosa*-dominated forest in northern Minnesota, USA.

Methods: Using a spatially explicit data set of repeated diameter measurements recorded over an 87-yr period, we modelled the influence of tree-to-tree interactions on growth as it varied over time. We also applied maximum likelihood estimation and simulated annealing to examine how inter- and intraspecific competition and the relative importance of neighbour size and distance varied over time and with different climatic conditions.

Results: Crowding had a consistent negative influence on growth, but crowding intensity and importance were dynamic over time and differed between trees that survived the entire study period compared to those that ultimately died. The scaling of neighbour diameter, neighbour distance, and neighbour species (inter- vs intraspecific competition) also varied as demographic transition occurred and longer-lived species assumed greater dominance.

Conclusions: Given observed relationships with moisture stress (based on precipitation: potential evapotranspiration) and maximum temperature, crowding intensity and importance may increase if temperatures rise in the future and water become more limiting. Long-term data sets, such as the record examined in this study, have immense value for testing assumptions about stand dynamics, particularly as forests respond to projected shifts in climate and disturbance regimes.

combination affect how forests respond to stress and disturbance (Brooker 2006; Weber et al. 2008; Linares et al. 2010; Castagneri et al. 2012; D'Amato et al. 2013; Coomes et al. 2014), which has long-term consequences for ecosystem functions and the provision of ecosystem services. Refining our understanding of individual and stand-level tree growth patterns over time is essential to

predicting future productivity and function as well as developing effective management strategies, particularly as forests respond to unprecedented global environmental change (Long et al. 2004; Brooker 2006; Puettmann 2011; Coomes et al. 2014).

Interactions between trees influence individual tree growth and often differ as a function of environmental conditions and the particular species present in a given community (Canham et al. 2004; Coates et al. 2009, 2013; van Mantgem & Das 2014; Bosela et al. 2015). Similarly, size–growth relationships and size asymmetry of competition (i.e. the degree to which competitive effects of small and large individuals are proportionate to size; Weiner 1990) also vary across populations and are affected by site quality (Schwinning & Weiner 1998; Pretzsch & Biber 2010). Size asymmetry may indicate whether tree-to-tree interactions occur predominantly above- or below-ground (Schwinning & Weiner 1998). For instance, when light most limits tree growth, size asymmetric competition occurs as larger individuals have both greater capacity for capturing light and a shading effect on smaller individuals (Schwinning & Weiner 1998). On the other hand, competition for soil nutrients below the ground is generally size-symmetric (Casper & Jackson 1997; Schwinning & Weiner 1998).

Changes in forest structure and composition over time influence resource availability (Gower et al. 1996), and thus have potential to change tree-to-tree interactions (Binkley 2004; D'Amato & Puettmann 2004). Forest canopy closure limits light availability for smaller trees, and reductions in plant-available N generally, but not always, occur with later stages of secondary succession (Vitousek et al. 1989) as trees store nutrients in above-ground biomass and decreasing litter quality increases N immobilization (Gower et al. 1996). Disturbance processes (Bradford et al. 2010; Hartmann & Messier 2011; Castagneri et al. 2012) and external stressors (Metsaranta & Liefers 2010) introduce additional variability by causing fluctuations in resources that also influence interactions over time. The complicated and dynamic nature of tree-to-tree interactions may explain why no single index for estimating the influence of tree-to-tree interactions on growth works effectively across all forest types and developmental stages (Burton 1993; Biging & Dobbertin 1995; D'Amato & Puettmann 2004).

Previous work has distinguished the intensity (direct effect) and importance (effect relative to other factors) of neighbourhood interactions on growth (Welden & Slauson 1986; Burton 1993; Brooker et al. 2005; Kunstler et al. 2011), demonstrating the utility of this distinction for assessing the relative importance of plant-to-plant interactions given stress (Grace 1991; Brooker et al. 2005; Brooker & Kikvidze 2008). Measures of importance allow

testing of the hypothesis that the role of competition on plant processes is larger in more resource-rich environments and diminishes with increasing stress (Grime 1979; Grace 1991; Brooker et al. 2005; Baribault & Kobe 2011). The stress gradient hypothesis (SGH) contends that plant competition is higher in more resource-rich and benign environments whereas facilitative interactions are more likely when resources are limited or conditions are physically stressful (Bertness & Callaway 1994). The ideas underlying a refined SGH (Maestre et al. 2009) most closely align with the intensity of interactions (Brooker & Kikvidze 2008). For example, in a forest where water availability limits growth, increased intensity of competition (negative interactions) might be expected during particularly wet years if some individuals are disproportionately more capable of taking advantage of the increased water resource. Importance and intensity are often (Kunstler et al. 2011), but not always, correlated (Welden & Slauson 1986; Burton 1993; Brooker et al. 2005). Crowding intensity and, to a lesser extent, importance have been examined for various plant communities arrayed along stress gradients (Canham et al. 2006; Coomes & Allen 2007; Kunstler et al. 2011); however, far less is known about how these metrics vary over time, particularly considering that climate patterns may alter stress levels due to associated resource limitations.

Few studies to date have examined how neighbourhood crowding changes over extended time periods in forests, and how the legacy of those historical patterns ultimately influences forest stand dynamics. Instead, data constraints have restricted most studies to examining young forests (Wagner & Radosevich 1991; Stoll et al. 1994) or periods less than 40 yrs in length (Martin & Ek 1984; D'Amato & Puettmann 2004; Das 2012), which restricts predictions of long-term growth (Burton 1993). Chronosequences (Getzin et al. 2006; Gray & He 2009) have value for examining many of the processes described here. However, some limitations exist (Walker et al. 2010), particularly when trends might diverge as a result of climatic fluctuations or stochastic events (He & Mladenoff 1999; Walker et al. 2010). Dendrochronological techniques allow reconstruction of past competitive environments and effects on growth (Canham et al. 2004; Weber et al. 2008; Hartmann & Messier 2011; Castagneri et al. 2012; Aakala et al. 2013); however, the influence of neighbouring trees that died and are absent at the time of sampling cannot be included empirically (but see Fraver et al. 2014). This inability to fully reconstruct past forest structure constrains the appropriate length of study despite long tree ring records (Weber et al. 2008). Thus, long-term data sets with direct field observations have immense value for increasing understanding of processes that influence stand dynamics and

tree growth to complement data gleaned from other approaches (Pickett 1989; Harmon & Pabst 2015).

The 87-yr study period examined here conveniently captures the demographic transition occurring between the stem exclusion stage of forest stand development and understorey re-initiation (Oliver & Larson 1990) as *Pinus banksiana*, a shorter-lived early successional species, declines and dies. Our research makes use of a novel data set that includes mapped tree locations and repeated measurements to examine temporal changes in competitive neighbourhoods and growth of the *Pinus resinosa* that persist. We address the following question: how do neighbourhood crowding intensity and importance, species effects and the influence of different neighbourhood characteristics vary over the course of stand development and with climate? Our findings provide insights into long-term changes in tree growth and forest stand development that may not have emerged from a more temporally restricted data set, and they shed light on forest growth responses that may be expected under a changing climate.

Methods

Study area

Data for this study were collected from a *P. resinosa*-dominated forest located in Itasca State Park, Minnesota, USA (47°13'N, 95°14'W) that regenerated naturally after an 1803 fire (Silver et al. 2013a). When first inventoried in 1923, *P. resinosa* (red pine) and *P. banksiana* (jack pine) dominated the stand. The importance value (IV), calculated as the average of relative density and relative basal area (adapted from Curtis 1951), for these two species was 68.8% and 19.9%, respectively. Other important species included *Pinus strobus* L. (white pine, IV = 8.2%) and *Picea glauca* (Moench) Voss (white spruce, IV = 3.1%). Of the dominant canopy species, *P. banksiana* is least tolerant of shade (very intolerant), followed by *P. resinosa* (intolerant) and *P. strobus* (intermediate; Burns & Honkala 1990). Although *P. banksiana* trees can survive to 250 yrs (Heinzelman 1973), the average lifespan is much shorter, with death commonly occurring between 105 yrs (Cayford & McRae 1983) and 160 yrs (Bergeron & Dubuc 1989). *P. resinosa* trees live much longer, with the oldest individuals known to persist up to 400 yrs (Burns & Honkala 1990; Fraver & Palik 2012). It is generally accepted that N is the most limiting nutrient for forests in this region, but both N and P content (but not cations) in the upper 25 cm of soil correlate strongly with the site index for red pine, suggesting both nutrients could be limiting to growth (Alban 1974). The site index (16 m at 50 yrs for *P. resinosa*), a measure of potential productivity based on the relationship between tree height and site quality, indicates this site is average for this species (Spurr & Allison 1956; Burns &

Honkala 1990). The stand lies at about 450 m a.s.l., with undulating slopes ranging from 0% to 20% and the dominant aspect WSW. Soils consist of sandy loams and loamy sands derived from glacial outwash. Comparison with other old-growth red pine stands in the region suggests that the stand is representative of this forest type and development stage (Fraver & Palik 2012; Silver et al. 2013b).

Field sampling

In 1923, J.H. Allison established a 2-ha plot in the stand for the purpose of studying growth and development in naturally regenerated *P. resinosa* forests (Spurr & Allison 1956). At that time, species, diameter at breast height (DBH) and a unique tag number were recorded for all live and dead trees >3 in (7.98 cm) in DBH. The entire stand was mapped and all tree locations recorded in 1952 and again in 2010 such that coordinates within the plot were assigned to each tree to 0.1 m (Silver et al. 2013a). For the purposes of our study, we applied a 20-m buffer to the historic plot and present analyses of data from 1923, 1928, 1933, 1938, 1943, 1948, 1952, 1957 and 2010. The population of *P. resinosa* within the buffered plot declined from 590 live trees in 1923 (DBH 8.6–49.9 cm) to 256 in 2010 (DBH 17.2–61.1 cm; Fig. 1). In-growth (shade-tolerant tree species established under the pine canopy) was not meaningfully recorded until 2010.

Crowding indices

We assessed the effectiveness of six crowding indices based on previous research in a variety of forest types, including old-growth *P. resinosa* (Hegyí 1974; Lorimer 1983; Canham et al. 2004; Aakala et al. 2013). The chosen indices each differ slightly in the way they characterize tree-to-tree interactions, which enables interpretation of the mechanisms underlying those interactions. For each focal *P. resinosa* tree alive in each sampling period and located >20 m from the plot border, we calculated relative dominance (RD_S; Glover & Hool 1979) to characterize stand-scale crowding, relative dominance within a defined neighbourhood (RD_N; adapted from Wykoff et al. 1982), which considers influences only from larger neighbours (emphasizing above-ground competition), a distance-dependent neighbourhood crowding index that includes all neighbours (NCI_{H1}; Hegyí 1974), a distance-independent neighbourhood crowding index that includes all neighbours (NCI_{L1}; Lorimer 1983), and modified versions of NCI_{H1} and NCI_{L1} with empirically estimated exponential modifiers that scale neighbour distance, neighbour size and the relative contribution of different species (NCI_{H2}, and NCI_{L2}; Table 1; Canham et al. 2004). Neighbourhoods used for estimation of NCI_{H1}, NCI_{H2}, NCI_{L1}, NCI_{L2} and RD_N

were circular, with a radius of 20 m. Rooting zones for *P. strobus* and *P. resinosa* are believed to achieve lengths equal to tree height, with observed rooting zones for 100-yr-old *P. strobus* and *P. resinosa* extending up to 18.3 m and 12.2 m, respectively (Brown & Lacate 1971). Heights of 'free' *P. resinosa* in 1923 were estimated at 22 m (Spurr

& Allison 1956), increasing to an average height of 29.3 m observed in 2012. Neighbourhood radius for calculation of crowding indices was informed based on these observations, while also maintaining an adequate sample size, as larger neighbourhoods require a larger buffer around the plot. Equations used for the calculation of each index are given in Table 1.

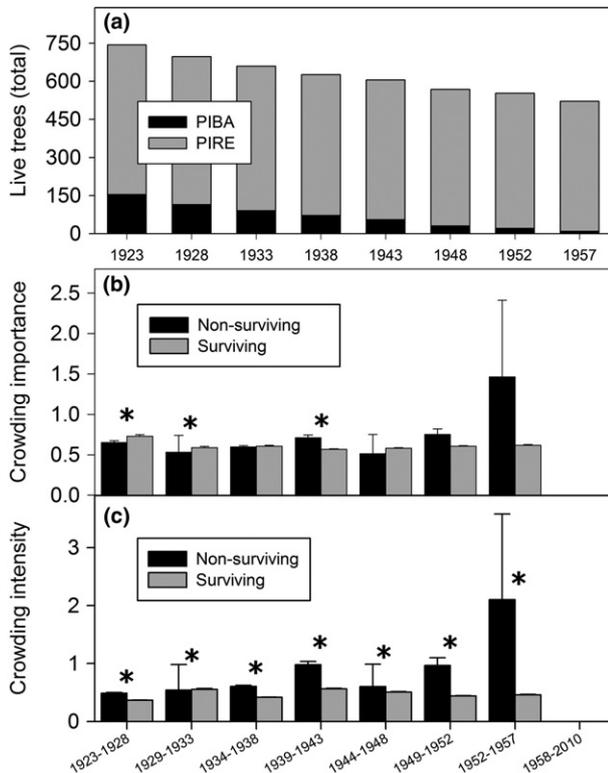


Fig. 1. Live trees within plot (a), crowding importance (b), and crowding intensity (c) for each sampling period 1923–1957. Asterisks indicate significant differences in crowding intensity and importance between groups for each period based on Wilcoxon rank-sum tests (Bonferonni-corrected, $P < 0.05$). Abbreviations: *Pinus resinosa*, PIRE; *Pinus banksiana*, PIBA).

Estimation of α , β and λ

For the indices NCI_{H2} and NCI_{L2} , we estimated parameters α , β and λ that scale the diameter of neighbouring trees, the distance of neighbouring trees and the relative influence of different species, respectively, during each sampling period using maximum likelihood estimation and simulated annealing (Table 1; Goffe et al. 1994; Canham et al. 2004). The λ parameter was only estimated for tree species with a minimum of 100 pair-wise interactions (Coates et al. 2009; van Mantgem & Das 2014), which allowed us to quantify λ for *P. resinosa* and *P. banksiana*, individually. To accommodate the smaller number of individuals present, we grouped *P. strobus* and *P. glauca* (van Mantgem & Das 2014). Analyses were performed using the likelihood package (<http://cran.r-project.org/web/packages/likelihood/index.html>) in R v. 3.0.2 (R Foundation for Statistical Computing, Vienna, AT).

Intensity and importance of crowding

To estimate the intensity of crowding (C_{int}), we used the following equation:

$$C_{int} = \frac{G_p - G_c}{G_p} \tag{1}$$

where G_p represents the potential growth expected in the absence of neighbours and G_c represents the growth expected given crowding at the time of sampling (Brooker & Kikvidze 2008; Kunstler et al. 2011). G_p and G_c were

Table 1. Indices used for estimating neighbourhood tree-to-tree interactions (crowding).

Index	Equation	Source
NCI_{H1}	$\sum_j^n (1/DBH_t) \times (DBH_{Ni}/distance)$	Hegy (1974)
NCI_{H2}	$\sum_j^n \lambda(1/DBH_t) \times (DBH_{Ni}^\alpha/distance^\beta)$	Hegy (1974), Canham et al. (2004)
NCI_{L1}	$\sum_j^n DBH_{Ni}/DBH_t$	Lorimer (1983)
NCI_{L2}	$\sum_j^n \lambda(DBH_{Ni}^\alpha/DBH_t)$	Lorimer (1983), Canham et al. (2004)
RD_N	$\sum_{DBH_{Ni} > DBH_t}^n BA_{Ni}$	Adapted from Wykoff et al. (1982)
RD_S	BA_t/BA_{stand}	Glover & Hool (1979)

DBH_t , DBH of the focal tree; DBH_{Ni} , DBH of neighbour i ; distance, distance between focal tree and neighbour i ; BA_t , basal area of the focal tree; BA_{stand} , basal area of a tree with the mean diameter of the stand; $BA_{neighbor}$, basal area of neighbour i ; α , β and λ are parameters defined using maximum likelihood estimation that modify neighbour distance, neighbour diameter and species influence, respectively. t first year of a given sampling period.

calculated for each focal tree using predictions from the best performing growth model. To estimate G_p the value for crowding was set at 0. These values were then used to calculate crowding importance (C_{imp}), which was defined as:

$$C_{imp} = C_{int} \times \frac{G_p}{G_{max} - G_c} \quad (2)$$

where G_{max} represents the maximum growth possible under optimal resource conditions (Brooker & Kikvidze 2008). In studies examining intensity and competition along resource gradients, the estimation of competition importance includes the value of growth achieved under optimal resource availability (Kunstler et al. 2011). We examined these metrics over time, given that stand development, stochastic events and changing climatic conditions likely alter resource availability and growth allocation, thereby influencing the importance of competition. Thus, we defined G_{max} as the maximum growth achieved over the entire sampling period for any tree within the same 5-cm diameter class as the focal tree. Our final growth model distinguished growth between trees that survived to 2010 ($n = 256$) and those that ultimately died between 1957 and 2010 ($n = 178$), allowing us to compare intensity and importance between the two groups. We used basal area increment (BAI, $\text{cm}^2 \cdot \text{yr}^{-1}$), calculated from repeated field measurements, as our growth metric.

Model selection and hypothesis testing

Those models with an index of crowding (fixed effect) also included a random slope for tree size and for crowding by year as well as a random intercept for year. Repeated measurements were accounted for using an autoregressive covariance structure for residuals.

Model selection was based on Akaike's information criterion for small sample sizes (AICc; Hurvich & Tsai 1989; Burhnam & Anderson 2002). Each model i with $\Delta_i < 2$, where $\Delta_i = \text{AICc}_i - \text{AICc}_{\text{min}}$, were considered as having substantial support (Burhnam & Anderson 2002). Each alternate model was fitted using mixed linear regression in PROC MIXED in SAS v. 9.4 (SAS Institute, Cary, NC, US). Model bias was assessed by examining whether the slope of observed growth regressed against predicted growth (intercept of zero) differed from 1. Goodness of fit for the top-ranked models was estimated using R^2 of the regression of observed growth on predicted growth for each model (Canham et al. 2004). All models with neighbourhood crowding indices included focal tree basal area at the beginning of the sampling period as a predictor to account for the potential relationship between tree size and growth (Lorimer 1983; MacFarlane & Kobe 2006). The response

variable, BAI, and predictor variables (crowding, size) were natural log-transformed to meet assumptions for linearity. Residuals were examined visually for homogeneity of variance.

Climate data

We used monthly temperature and precipitation data from the nearest weather station (<5 km from the study site) to estimate mean seasonal climate for each 4–6-yr sampling period (National Climate Data Center, www.ncdc.noaa.gov). Seasons were defined as follows: previous autumn (September, October, November), previous winter (December, January, February); spring (March, April, May) and summer (June, July, August). Calculations included the minimum seasonal ratio between precipitation and potential evaporation (P/PET), taken as an inverse measure of water stress (Hargreaves & Samani 1982; Martinez-Vilalta et al. 2012), mean maximum seasonal temperature and mean seasonal precipitation because these variables were expected to have the largest influence on growth in this mildly water-limited system (Dymond et al. 2015). Pearson's correlation coefficient was used to assess relationships between climate variables and C_{imp} , C_{int} , α and β . None of the climate variables included correlated with time.

Results

Crowding and growth

A strong negative relationship existed between growth and crowding during all sampling periods, with all crowding indices significantly improving prediction of *P. resinosa* BAI compared with the null model and initial size alone (Appendix S1, Fig. 2). Variance in residuals increased with

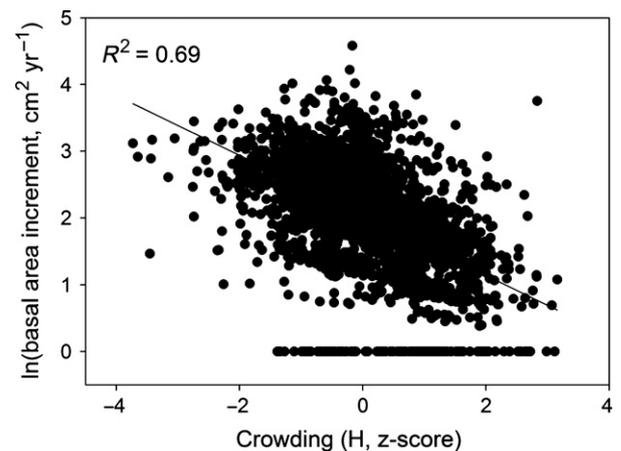


Fig. 2. Relationship between annual growth (basal area increment) and crowding. The value given for R^2 indicates fit of the best-performing model (Appendix S1).

increasing growth rates, as has been reported in other studies (Canham et al. 2004; Das 2012). Models provided unbiased estimates of BAI (the slope of the regression of observed BAI on predicted BAI did not differ from 1). The model including NCI_{H1} had the strongest support, with $\Delta_i > 30$ for all other models (Appendix S1). Accordingly, analysis of crowding intensity and crowding importance (presented below) are based on NCI_{H1} .

Scaling of neighbour distance, size and species

The scaling of neighbour DBH (α) followed similar trends over time between the distance-independent (NCI_{L2}) and distance-dependent (NCI_{H2}) crowding indices. Considering the *P. resinosa* alive in each sampling period, the range of α for NCI_{L2} (1.03–1.18) indicates that the crowding influence from neighbouring trees was size-asymmetrical and disproportionately higher for larger trees early and late in the study period. It became more symmetrical (closer to 1) in 1929–1933 and 1939–1943, the latter years corresponding with demographic transition as mortality rates in *P. banksiana* increased. Mean winter precipitation showed a weak positive correlation with α (NCI_{H2} and NCI_{L2}). This, coupled with a negative correlation with minimum autumn *P/PET*, suggests that larger neighbours had greater influence when water stress immediately prior to the current growing season was higher (*P/PET* lower).

Estimates of the scaling parameter for neighbour distance (β) were low over the course of the study, indicating relatively little decline in neighbour influence with longer distance from focal trees (Table 2). A weak negative relationship existed between mean maximum temperature during the previous autumn and β , indicating that the contribution of further neighbours to crowding was stronger and diminished less by their distance when autumn temperatures were higher. (A decrease in β also generally increased the value of the crowding index.)

Overall, values of λ for both NCI_{H2} and NCI_{L2} suggest that *P. banksiana* exerted less competitive influence on *P. resinosa* growth than did other species, but only prior to 1939 and when crowding indices included neighbour distance (Table 2). From 1939 to 1957, inter- and intraspecific competition were equivalent, as indicated by λ equal to 1 for all species present, and between 1958 and 2010 inter-specific competition for *P. resinosa* was less than intraspecific competition (Table 2).

Crowding importance and intensity

Both the intensity and importance of crowding to growth varied over time, but not always in concert (Fig. 2). During the periods 1923–1928, 1938–1942 and 1949–1952, there was no relationship between the two values for *P. resinosa*

Table 2. Maximum likelihood parameter estimates with support intervals. All *Pinus resinosa* Alive in Each Period ($n = 512-255$)

Growth Period	NCI_{L2}					NCI_{H2}				
	α	λ_{PIRE}	λ_{PIBA}	λ_{OTHER}	β	α	λ_{PIRE}	λ_{PIBA}	λ_{OTHER}	
1923–1928	1.14 (1.14–1.14)	1 (1.0–1.0)	0.98 (0.98–0.98)	1 (1.0–1.0)	0.28 (0.28–0.28)	0.78 (0.78–0.78)	1 (1.0–1.0)	0.95 (0.95–0.95)	1 (1.0–1.0)	
1929–1933	1.04 (1.04–1.04)	1 (1.0–1.0)	0.99 (0.98–1.0)	1 (1.0–1.0)	0.25 (0.25–0.25)	0.72 (0.72–0.72)	1 (1.0–1.0)	0.97 (0.96–0.98)	1 (1.0–1.0)	
1934–1938	1.11 (1.11–1.11)	1 (1.0–1.0)	0.99 (0.99–1.0)	1 (1.0–1.0)	0.25 (0.23–0.23)	0.78 (0.78–0.78)	1 (1.0–1.0)	0.97 (0.96–0.98)	1 (1.0–1.0)	
1939–1943	1.03 (1.03–1.03)	1 (1.0–1.0)	1 (1.0–1.0)	1 (1.0–1.0)	0.23 (0.22–0.23)	0.73 (0.73–0.73)	1 (1.0–1.0)	1.0 (0.99–1.0)	1 (1.0–1.0)	
1944–1948	1.07 (1.07–1.07)	1 (1.0–1.0)	1 (1.0–1.0)	1 (1.0–1.0)	0.23 (0.24–0.24)	0.77 (0.77–0.77)	1 (1.0–1.0)	1 (1.0–1.0)	1 (1.0–1.0)	
1949–1952	1.09 (1.09–1.09)	1 (1.0–1.0)	1 (1.0–1.0)	1 (1.0–1.0)	0.24 (0.24–0.24)	0.79 (0.79–0.79)	1 (1.0–1.0)	1 (1.0–1.0)	1 (1.0–1.0)	
1953–1957	1.09 (1.09–1.09)	1 (1.0–1.0)	1 (1.0–1.0)	1 (1.0–1.0)	0.22 (0.29–0.29)	0.81 (0.81–0.81)	1 (1.0–1.0)	1 (1.0–1.0)	1 (1.0–1.0)	
1958–2010	1.18 (1.18–1.18)	1 (1.0–1.0)	n/a	1 (1.0–1.0)	0.26 (0.23–0.23)	0.86 (0.86–0.86)	0.91 (0.91–0.91)	n/a	1 (1.0–1.0)	

trees that survived to 2010, whereas there was a strong positive correlation between importance and intensity for surviving trees for 1929–1933 and 1939–1947 ($P < 0.0001$; Appendix S2) and throughout the study for trees that died between 1957 and 2010 (Appendix S2). As expected, crowding intensity was generally higher for trees that ultimately died compared to those that survived to 2010 (Fig. 2). Crowding importance was only higher for non-surviving tree growth occurring in 1943–1947, but was higher for surviving trees in 1923–1933.

Correlations with seasonal temperature and seasonal precipitation suggest climate influences importance and intensity of crowding, but those relationships differ between surviving and non-surviving trees. Higher maximum temperature during the previous autumn correlated positively with both crowding intensity and importance for non-surviving trees (Table 3). For surviving trees, lower competition intensity corresponded with higher winter precipitation. There was also a negative relationship between summer maximum temperatures and the importance of crowding to growth in surviving trees. Mean growth (BAI) for all trees strongly correlated with the intensity (negative relationship) and the importance (positive relationship) of crowding for surviving trees, but no correlations were observed for trees that died prior to 2010 (Table 3).

Discussion

This long-term, spatially explicit data set provided an unparalleled opportunity to examine the influence of stand development, including demographic transition, on tree growth over the course of 87 yrs. Throughout

the period and regardless of conditions, tree-to-tree interactions had a consistent negative impact on growth; however, neighbourhood interactions were dynamic. The importance and intensity of crowding as it related to growth varied both with successional changes and with climate, highlighting the importance of accounting for the dynamic nature of neighbourhood interactions when predicting forest growth and development over extended time periods and climate conditions.

Crowding and growth

A strong negative relationship existed between growth and crowding during all sampling periods, indicating that crowding indices generally approximated competitive relationships. Our comparison of crowding indices demonstrates that tree-to-tree interactions occurring within local neighbourhoods relate more strongly to individual tree growth than relative tree dominance (i.e. focal tree size relative to the entire population) throughout the period of development studied. That is, the stand-wide measure of relative dominance (RD_s) consistently had lower levels of support than neighbourhood indices in model comparisons (Appendix S1). Given that this is a natural origin stand, these findings may not be surprising (Martin & Ek 1984), although relative dominance at the stand scale has performed better than neighbourhood crowding indices in younger developmental stages in stratified mixed-species stands (D'Amato & Puettmann 2004) and in other naturally regenerated, old-growth forests, particularly in single cohort stands (Aakala et al. 2013).

Table 3. Pearson's R correlations between crowding importance (C_{imp}), crowding intensity (C_{int}), α (neighbour size modifier for NCI_{H2}), β (neighbour distance modifier for NCI_{H2}) and mean basal area increment (BAI) with mean maximum temperature, mean precipitation (P)/potential evapotranspiration (PET) by season (defined using 3-month windows) and mean BAI.

	C_{int}		C_{imp}		α (NCI_{H2})	β (NCI_{H2})	α (NCI_{L2})	Mean BAI
	Surviving	Non-Surviving	Surviving	Non-Surviving				
Mean max T								
Autumn (prev.)	0.34 (0.460)	0.88 (0.010)	-0.21 (0.657)	0.82 (0.024)	0.17 (0.708)	-0.70 (0.077)	-0.38 (0.395)	-0.30 (0.506)
Spring	0.61 (0.145)	-0.03 (0.944)	-0.15 (0.743)	-0.08 (0.869)	-0.69 (0.084)	-0.03 (0.941)	-0.56 (0.196)	-0.53 (0.221)
Summer	0.57 (0.181)	0.25 (0.594)	-0.76 (0.05)	0.13 (0.786)	-0.20 (0.661)	-0.53 (0.22)	-0.55 (0.198)	-0.58 (0.174)
Mean P								
Winter (prev.)	-0.84 (0.017)	0.20 (0.669)	0.61 (0.144)	0.32 (0.486)	0.72 (0.070)	0.23 (0.560)	0.75 (0.052)	0.80 (0.032)
Spring	0.14 (0.763)	0.24 (0.608)	-0.54 (0.214)	0.09 (0.852)	0.31 (0.497)	-0.62 (0.135)	-0.24 (0.602)	-0.27 (0.553)
Summer	0.08 (0.862)	0.37 (0.413)	-0.44 (0.318)	0.24 (0.607)	0.39 (0.383)	-0.67 (0.098)	-0.21 (0.640)	-0.207 (0.656)
Min P/PET								
Autumn (prev.)	0.66 (0.106)	-0.29 (0.527)	-0.33 (0.473)	-0.37 (0.419)	-0.79 (0.035)	-0.04 (0.9397)	-0.64 (0.120)	-0.62 (0.138)
Summer	-0.19 (0.673)	0.07 (0.889)	-0.01 (0.979)	0.00 (0.992)	0.38 (0.396)	-0.25 (0.575)	0.09 (0.853)	0.09 (0.851)
Mean BAI	-0.99 (<0.001)	-0.03 (0.945)	0.88 (0.0096)	0.17 (0.722)	0.77 (0.097)	0.62 (0.138)	0.99 (<0.001)	1 (1.0)

C_{int} and C_{imp} are calculated for two populations of trees, those that survived to 2010 ('surviving') and those that died between 1957 and 2010 ('non-surviving'). Exact P -values are given in parentheses.

Neighbourhoods and climate

Disentangling the effects of above- vs below-ground competition has long presented a challenge (e.g. Coomes & Allen 2007). Above-ground competition, generally accepted to be driven by light availability, is likely most influenced by the structure of the neighbourhood immediately surrounding a tree (Stiell 1970), hence the benefit of incorporating crown structure into competition indices observed in some cases (Biging & Dobbertin 1995; Canham et al. 2004; Fraver et al. 2014), whereas accounting for below-ground competition may require a larger neighbourhood (Stiell 1970). Studies of *P. resinosa* rooting zones have demonstrated that roots can extend up to a distance equal to tree height, with lengths of up to 18.3 m and 12.2 m for 100-yr-old *P. strobus* and *P. resinosa*, respectively (Brown & Lacate 1971). The expected general increase in neighbourhood (zone of influence) over time corresponds with a reduction in tree density, increase in tree height and assumed expansion of root systems, yet in our study the weight given to neighbour distance (within 20-m neighbourhoods) fluctuated. We observed a negative correlation between β and maximum temperatures during the previous autumn. This means that the contribution of more distant neighbours had a larger influence on *P. resinosa* growth following a warm autumn than in other years, suggesting that the conditions created by higher previous autumn temperatures may increase below-ground competition for resources. It is possible that warm autumn temperatures influenced decay rates and nutrient availability. The evidence for increased below-ground competition is also consistent with other work that suggests high autumn temperatures may induce water stress and reduce stand-scale *P. resinosa* growth (D'Amato et al. 2013).

Inter- vs Intraspecific competition

Our results (interpretation of the λ parameter) suggest a lesser contribution to crowding from *P. banksiana* when compared to other species. However, we note that less variability among species was observed here than has been reported in previous studies (Canham et al. 2004, 2006; van Mantgem & Das 2014). The competitive influence of *P. resinosa*, *P. strobus* and *P. glauca* on *P. resinosa* growth was similar over time (Table 2), and models with crowding indices that treated all neighbour species as equivalent (i.e. NCI_{H1} , NCI_{L1}) consistently outperformed those adapted with the species-specific modifier, λ (NCI_{H2} , NCI_{L2} ; Appendix S1). Given the increased mortality and ultimate loss of *P. banksiana* from the stand during the study period (Silver et al. 2013a), *P. banksiana* neighbours may have been less competitive (indicated by smaller λ) because they were already declining. Without

characterizing crowding during the period prior to 1923, when *P. banksiana* likely dominated in terms of average growth rates, it is not possible to fully characterize those competitive relationships. Nevertheless, this study underscores the importance of accounting for temporal dynamics in the strength of interspecific effects due to differences in species life-history traits.

Crowding importance and intensity

As a forest stand develops and previously dominant early successional trees decrease in abundance, as observed here, the availability of resources often increases, at least temporarily. Based on previous observations and established hypotheses (Grime 1979; Grace 1991; Brooker et al. 2008; Kunstler et al. 2011), we expected the direct effect of crowding (intensity) on *P. resinosa* growth to increase with increased resource availability, as *P. banksiana*, which had an importance value of nearly 20% at the beginning of the study, was lost from the stand. While crowding intensity did not increase substantially with the loss of *P. banksiana*, it did remain consistently high for those *P. resinosa* trees that died prior to 2010, particularly compared to those trees that survived regardless of fluctuations in climate and other conditions. This suggests that increased crowding may increase mortality risk, and is supported by analyses of mortality patterns for this stand (M.T. Curzon, A.W. D'Amato, S. Fraver, E.S. Huff & B.J. Palik, unpubl data).

Independent of stand development processes, we expected crowding intensity and crowding importance to be relatively higher during periods with higher water availability in accordance with dominant theories about plant interactions, but no significant relationships with P/PET , an inverse approximation of water limitation, were observed for either measure. Instead, both intensity and importance increased during what are normally considered more stressful climate conditions. Intensity for surviving trees was negatively correlated with winter precipitation (an indication of higher water availability in spring), and both intensity and importance exhibited significant positive relationships with maximum temperature, which is known to induce stress and reduce stand-scale growth in *P. resinosa* forest either directly or through water limitation (D'Amato et al. 2013). However, the strong positive correlation between mean tree growth and crowding importance for surviving trees conformed to hypotheses suggesting that crowding (or competition) importance increases when productivity is higher (Grime 1979), at least for those trees that survive. Also, even though the positive correlation between crowding importance and winter precipitation is not significant, there is a significant positive correlation between mean tree growth

and winter precipitation, another indication that importance can increase when growing conditions are favorable (Table 3). It is possible that factors driving stand growth (such as climate) influence tree-to-tree interactions differently than expected based on total stand response (D'Amato et al. 2013), particularly those trees at a competitive disadvantage, such as individuals that did not survive the study period. Regardless, if the decrease in soil moisture observed in response to increasing temperatures over the last century continues (Dymond et al. 2014), our results suggest the importance and intensity of crowding to individual tree growth may increase in the future, which has implications for forest management.

Conclusions

The influence of ever-changing tree-to-tree interactions on growth over extended time periods, particularly spanning demographic transition, has not been extensively examined in forest ecosystems. Long-term data sets such as the record examined in this study are rare and have exceptional value for testing assumptions about stand dynamics and tree growth. Our findings demonstrate that the nature of tree-to-tree interactions changes during demographic transition, responds to changing climate conditions and has implications for long-term patterns of survival. Further study with finer temporal resolution may be able to more clearly distinguish and define these effects. These results also suggest potential for increased importance and intensity of competitive interactions should climatic changes increase water stress in the future.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Model comparisons.

Appendix S2. Correlations between crowding importance and crowding intensity over time.