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Size-growth relationship, tree spatial patterns, and tree-tree competition influence tree growth and stand complexity in a 160-year red pine chronosequence

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ABSTRACT

Extended rotations have been suggested as a strategy for balancing timber production and ecological objectives. By lengthening the period of stand development, extended rotations may increase tree size inequality and other elements of structural complexity, thus reducing the disparity between managed and old-growth stands. A potential limitation of extended rotations is the tradeoff between reduced stand-level productivity and greater large-tree growth that typically occurs with stand age. The mechanisms driving this tradeoff have not been fully explored. To fill this knowledge gap, we investigated the size-growth relationship (SGR), tree spatial patterns, and tree-tree competition along an established 160-yr chronosequence of 19 single-cohort, unthinned red pine (*Pinus resinosa*) stands in northern Minnesota, USA. We analyzed SGR, a stand-level metric used to estimate the relative efficiency with which different sized trees utilize available resources, to assess how the relationship between tree size and growth changed over an extended period of stand development. We performed spatial analysis to examine whether tree spatial clustering, a criterion of structural complexity, increased with stand age. We modeled individual-tree biomass increment to test whether competition along the chronosequence was size-symmetric (access of individual trees to resources is directly proportional to size) or size-asymmetric (larger trees suppress the growth of smaller individuals by preempting resources), and how SGR, tree spatial patterns, and competition together influenced individual-tree growth. We found low SGR (i.e., disproportionately slow growth of larger trees compared to smaller trees) across the chronosequence, a finding that contrasts with hypothesized models of SGR during stand development but is consistent with previous research on pine-dominated systems. Tree spatial patterns trended towards clustering with stand age, indicating higher structural complexity over time. In agreement with our SGR findings, competition across the chronosequence was size-symmetric, suggesting that competition reduced individual-tree growth while maintaining relative size equality. Individual-tree biomass increment was strongly dependent on tree size, with the growth of small trees appearing relatively less affected by competition. Differences in SGR did not translate into individual-tree growth, and tree spatial clustering was associated with reduced growth, especially in larger trees. Our results indicate that disproportionately slow large-tree growth and size-symmetric competition throughout stand development may delay the emergence of stand structural complexity in extended rotation red pine stands. Silvicultural treatments may be required to promote stand structural complexity and increase large crop-tree growth.

1. Introduction

Forest managers are increasingly focused on balancing timber production with ecological objectives such as biodiversity conservation, carbon sequestration, and maintaining wildlife habitat (Bauhus et al., 2009; Curtis, 1997; Puettmann et al., 2012). One potential silvicultural strategy for achieving these goals is extending stand rotation ages as a means of reducing the disparity between managed stands and old

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growth forests in terms of structure, composition, and function (Bauhus et al., 2009; Curtis, 1997; D'Amato et al., 2010). By lengthening the period of stand development, extended rotations may enhance multiple criteria of stand complexity, including larger maximum tree size, greater size inequality, increased spatial clustering, and higher carbon storage (Bradford and Kastendick, 2010; McElhinny et al., 2005; Silver et al., 2013).

A potential limitation of extended rotations is the tradeoff between reduced annual-scale stand-level productivity, which reaches a maximum relatively early in stand development prior to canopy closure (Curtis, 1997; Long et al., 2004), and individual large-tree growth, which typically increases with age (Stephenson et al., 2014). Declining stand-level productivity can adversely affect non-timber management objectives, particularly carbon sequestration (Bradford and Kastendick, 2010). However, declining stand productivity is also associated with greater tree size inequality in intensively managed stands (Luu et al., 2013; Soares et al., 2016). It is unclear whether a similar relationship exists between productivity and size inequality in less intensively managed, extended rotation stands (Ex and Smith, 2014; Long and Shaw, 2010).

Size-growth relationship (SGR), a stand-level metric that indicates the relative efficiency with which different-sized trees utilize available resources, can provide insights into factors that influence growth efficiency, productivity, and size inequality over stand development (Binkley, 2004; Metsaranta and Lieffers, 2010; Pretzsch and Biber, 2010). Binkley (2004) proposed a stand development model in which trees within newly established stands display size-symmetric SGR, meaning that large and small trees grow at proportionately similar rates. With canopy closure, SGR will become size-asymmetric, with large trees growing disproportionately faster than smaller trees, thus promoting size inequality (Binkley, 2004). Late in stand development as large trees decline in production efficiency, SGR is hypothesized to become inverse size-asymmetric, with smaller trees growing disproportionately faster than larger trees (Binkley, 2004). Subsequent research has found inverse size-asymmetric SGR in some older stands (Baret et al., 2017; Binkley et al., 2006; Biondi, 1996; Pothier, 2017), although it may not emerge in many systems (Binkley et al., 2006; Castagneri et al., 2012).

A limitation of SGR and other size-inequality-based stand summary metrics is that they do not explicitly consider the influence of tree spatial patterns on tree size inequality (Cordonnier and Kunstler, 2015; Weiner et al., 2001). Studies of intensely managed gum (*Eucalyptus* L'Her. spp.) plantations suggest spatial variation in size inequality influences productivity independent of competition (Luu et al., 2013; Ryan et al., 2010), with greater size inequality disproportionately reducing larger tree growth (Luu et al., 2013). Although competition-induced mortality during early stand development is expected to promote increasing spatial uniformity over time (Kenkel, 1988; Larson et al., 2015; Metsaranta and Lieffers, 2008), greater maximum tree size and age may increase susceptibility to windthrow and pathogens in extended rotation stands (Bauhus et al., 2009), resulting in patchy mortality and subsequent tree recruitment. These dynamics could potentially promote clustered (non-uniform) spatial patterns in extended rotation forests (Getzin et al., 2006), with higher stand densities within tree clusters influencing both tree productivity and size inequality by locally intensifying competition (Fraver et al., 2014; Luu et al., 2013).

In addition to interacting with tree spatial patterns during stand development, SGR is predicted to reflect shifts between size-symmetric competition, which tends to maintain relative tree sizes, and size-asymmetric competition, which tends to increase size inequality (Binkley et al., 2006; Cordonnier and Kunstler, 2015; Metsaranta and Lieffers, 2010; Pothier, 2017). When competition is size-symmetric, access of individual trees to resources is directly proportional to size, as with competition for soil resources (Schwinning and Weiner, 1998). When competition is size-asymmetric, larger trees disproportionately suppress the growth of smaller individuals by preempting access to resources, as with competition for light (Schwinning and Weiner, 1998). During stand development, competition is theorized to shift from size-symmetric (as for soil resources) during the symmetric SGR phase when tree growth is proportional to size, to size-asymmetric (as for light) during the size-asymmetric SGR phase when larger trees grow disproportionately faster, and finally back to size-symmetric (as for soil resources) during the inverse-asymmetric SGR phase when growth of aging, larger trees becomes disproportionately slower (Binkley et al., 2006; Metsaranta and Lieffers, 2010). Pothier (2017) found that competition size-symmetry at the individual-tree level was correlated as predicted with stand-level SGR (Binkley et al., 2006; Metsaranta and Lieffers, 2010). In contrast, a study of old-growth black ash (*Fraxinus nigra* Marsh.) wetland stands found that tree-tree competition was best characterized as size-asymmetric (as for light), despite inverse-asymmetric stand-level SGR, suggesting that competition for light may remain influential even in later developmental stages in some systems (Looney et al., 2016). To date, the broader interactions among SGR, tree spatial patterns, and competition, together with their implications for individual tree growth, have not been investigated.

Red pine (*Pinus resinosa* Aiton) forests are an ideal system in which to examine these interactions. With typical rotation ages ranging from 50 to 90 years when managed for timber (Gilmore and Palik, 2006), contemporary red pine stands are generally younger and less species-diverse than the fire-influenced stands that existed prior to European settlement (Silver et al., 2013), and extended rotations have been proposed to increase their structural complexity (D'Amato et al., 2010; Gilmore and Palik, 2006). In particular, extended rotations have been found to increase tree size inequality in red pine stands (Bradford and Kastendick, 2010). Repeated thinning may maintain stand-level productivity in extended-rotation red pine stands (D'Amato et al., 2010), and knowledge of individual-tree contributions to stand-level growth and responses to stand structure is needed to guide the design of more effective thinning regimes (Bradford et al., 2010).

We investigated the potential of extended rotations to enhance red pine stand structural complexity, which for the purposes of this paper is defined as increased tree size inequality and non-uniform spatial distribution (McElhinny et al., 2005). To accomplish this, we retrospectively examined SGR, tree spatial patterns, individual-tree competition, and growth over an established 160-yr chronosequence (space-for-time substitution; Pickett, 1989) of single-cohort, unthinned red pine stands in northern Minnesota, USA (Bradford and Kastendick, 2010). Our purpose was to determine a) how SGR and tree spatial patterns change over an extended period of stand development, and b) how these stand-level factors may interact with tree competition and size to influence individual-tree productivity. The overarching goal of our research was to use the red pine chronosequence to elucidate the mechanisms driving trade-offs between stand-level productivity and individual large-tree growth in order to aid the development of management strategies using extended rotations to meet multiple objectives.

2. Methods

2.1. Site description

Our study was conducted in 19 red pine stands that were part of a red pine/aspen-birch chronosequence established in 2007 by Bradford and Kastendick (2010) to evaluate temporal patterns in carbon storage. All stands were located near the Cutfoot Experimental Forest, Itasca County, Minnesota, USA (centered at 47.549 N, 94.092 W). In keeping with the chronosequence approach, which seeks to minimize biotic and edaphic variation to facilitate comparisons across ages (Pickett, 1989), the 19 stands shared similar topography, soils, and climate. Soils in the study area are classified as Menahga loamy sand derived from glacial outwash deposits and having high permeability (Tarpey et al., 2008). Climate is continental, with mean 1981–2010 January and July

Table 1
Stand summary statistics for live trees (> 2.5 cm DBH) at 19 red-pine dominated chronosequence sites.

Stand age 2007	Trees ha-1 (TPH)	TPH% PIRE	Basal area (BA) (m2 ha-1)	BA% PIRE	QMD (cm)	SDI*	Stand origin
19	2175.1 ± 1720.3	57.8 ± 40.6	27.7 ± 2.1	80.8 ± 27.5	13.3 ± 1.5	692.2 ± 123.9	P
29	2047.8 ± 684.4	87 ± 18.3	39.8 ± 3.4	98 ± 4.5	15.9 ± 1.0	915 ± 59.5	P
36	1729.5 ± 752.1	81.6 ± 17.3	51.2 ± 4.9	97.2 ± 4.4	19.7 ± 1.3	1110.5 ± 130.3	P
38	1347.5 ± 637.3	86.7 ± 21.5	50.3 ± 17.5	93.1 ± 20.8	21.9 ± 0.4	1049.5 ± 427	P
56	1655.2 ± 124.8	74.3 ± 40.3	62.8 ± 5	93.8 ± 10.6	22.0 ± 0.4	1278.4 ± 137.5	N
62	870 ± 728.5	42.2 ± 25.4	31.3 ± 18.6	75.2 ± 56.9	22.3 ± 3.2	594.5 ± 293.5	P
69	1570.3 ± 519.5	85.2 ± 13.7	43.8 ± 18.2	76.1 ± 44.4	19.0 ± 2.2	941.7 ± 256.8	P
72	1379.3 ± 500.4	68.4 ± 35.8	55.8 ± 25	97.3 ± 6.6	22.7 ± 1.4	1082.4 ± 409.1	N
84	1549.1 ± 1187.6	45.6 ± 19	46.8 ± 18.9	93.8 ± 3.6	20.3 ± 2.3	905.3 ± 445.3	N
92	477.5 ± 187.2	70.2 ± 44.2	35.1 ± 7.5	96 ± 9.8	30.9 ± 2.1	600.4 ± 151.5	N
97	1061 ± 971.2	55.9 ± 42	52.6 ± 16.6	92.6 ± 11	26.5 ± 3.0	948.2 ± 341.3	N
115	891.3 ± 436.7	75.5 ± 6	42.5 ± 13.5	89.4 ± 11	24.8 ± 0.6	810.2 ± 301.3	N
129	785.2 ± 530.6	53.7 ± 31	37.9 ± 23.2	90.1 ± 5.4	25.0 ± 0.9	699.8 ± 459	N
130	1082.3 ± 543.9	26.9 ± 37	50.5 ± 2.1	69.7 ± 43.5	24.7 ± 1.6	894.5 ± 97.6	N
132	785.2 ± 376.1	39.9 ± 25	46.1 ± 10.6	77 ± 23.9	27.6 ± 1.3	819.4 ± 233.2	N
147	976.2 ± 424.7	28.4 ± 7.1	37.8 ± 12.8	79.2 ± 9.5	22.4 ± 1.6	663.8 ± 154.9	N
149	615.4 ± 219.1	38.2 ± 47.7	49.8 ± 28.5	72.6 ± 52.2	32.1 ± 3.5	826 ± 436.2	N
154	923.1 ± 595.2	57.7 ± 44.1	41.7 ± 21.1	88.6 ± 25.8	25.0 ± 4.7	729.7 ± 287.4	N
160	1305.1 ± 389.6	29.9 ± 34.5	50.1 ± 25.4	80.5 ± 10.1	22.0 ± 0.8	893.1 ± 484.8	N

Note: Statistics represent mean ± 95% confidence interval (CI) for the 3 plots that make up each chronosequence site. Stand ages as of 2007 are used to facilitate comparison with Bradford and Kastendick (2010). All other data are based on measurements collected in 2009. In the Stand origin column, P = planted post-harvest; N = natural origin after fire or unknown disturbance. Abbreviations: QMD = quadratic mean diameter; SDI = stand density index.

* SDI was calculated using the summation method, as for CI-1, rather than with QMD.

temperatures averaging − 19.6 °C and 13.5 °C degrees, respectively (PRISM Climate Group, 2015). During the same period, total precipitation averaged 692 mm yr^{-1}, with precipitation concentrated in summer.

The 19 stands shared similar species composition, with red pine accounting for 70–98% of individual stand basal area (BA; Table 1). Other tree species included paper birch (*Betula papyrifera* Marsh.), jack pine (*Pinus banksiana* Lamb.), balsam fir (*Abies balsamea* (L.) Mill.), eastern white pine (*Pinus strobus* L.), and northern red oak (*Quercus rubra* L.). Shrub species included beaked hazel (*Corylus cornuta* Marshall), juneberry (*Amelanchier spp*. Medik.), chokecherry (*Prunus virginiana* L.), red raspberry (*Rubus idaeus* L.), northern bush honeysuckle (*Diervilla lonicera* Mill.) and lowbush blueberry (*Vaccinium angustifolium* Aiton).

When first surveyed in 2007, the stands ranged in age from 19 to 160 years (Table 1). We refer to the stands by the 2007 ages throughout to facilitate comparisons with the original Bradford and Kastendick (2010) study. Stand histories indicated that the 56-yr and 72-yr through 160-yr stands were natural origin following fire or unknown disturbance, whereas all other stands were planted post-harvest (Table 1). All stands developed from a single cohort, although older stands showed development of younger age classes. No known thinning or catastrophic disturbances had occurred in the stands since initiation (Bradford and Kastendick, 2010). Lack of thinning over the relatively long chronosequence represents a passive form of extended rotation management (Curtis, 1997; Silver et al., 2013), which for our purposes was ideal because it avoided the confounding influence of management effects on the processes of interest.

2.2. Data collection

The 19 red pine stands were resampled in 2009. Each stand was buffered 20 m from its boundaries to minimize edge bias, and GIS was used to randomly divide the unbuffered stand area into three equal polygons. Within each polygon, one 10-m-radius (0.031 ha) plot location was randomly selected. In each plot, stems of all woody species ≥2.5 cm diameter at breast height (DBH; 1.37 m) were inventoried. Trees were surveyed for DBH, status (live vs. dead), and Cartesian (X, Y) coordinates. A single increment core was collected at breast height from all live trees > 5.0 cm DBH. Flat terrain and large sample sizes safeguarded against biases that may have arisen from sampling a single increment core per tree. Smaller-diameter stems were sampled for DBH but not for growth.

2.3. Sample preparation

We used standard dendrochronological techniques to prepare increment cores for analysis (Speer, 2010). Following core mounting and sanding, we measured annual ring widths (to 0.01 mm resolution) on finished cores using a Velmex sliding-stage measuring system. Cores were visually cross-dated, and cross-dating was validated using the COFECHA program (Holmes, 1983). We converted raw ring widths to annual aboveground biomass increment (i.e., combined biomass of wood, bark, branches, and foliage) using species-specific, diameter-based equations published in Lambert et al. (2005). We used total aboveground tree biomass in our analyses of tree SGR and individual-tree productivity to account for age-related shifts in aboveground productivity not reflected in stem wood volume alone (Looney et al., 2016).

2.4. Statistical analysis

2.4.1. Size-growth relationships

From the SGR indices proposed in the literature (Binkley, 2004; Metsaranta and Lieffers, 2010; Pretzsch and Biber, 2010), we selected Metsaranta and Lieffer's (2010) approach for ease of calculation and interpretation. This index of SGR is the slope of annual linear regression between current-year proportional biomass increment (individual-tree biomass increment relative to total stand increment) and previous-year proportional tree size (previous-year individual-tree biomass relative to total stand biomass). Values greater than 1 indicate size-asymmetric SGR (larger trees grow disproportionately faster than smaller trees), a value of 1 indicates size-symmetry (large and small trees grow at proportionately similar rates), and values less than 1 indicate inverse size-asymmetry (larger trees grow disproportionately slower than smaller trees). Both proportional biomass increment and previous-year biomass are center log-ratio transformed (Aitchison, 1986) to standardize the variables and linearize the relationship between them. We confirmed that these transformations met the analysis assumption of a linear relationship between rescaled variables.

To calculate SGR, we began by pooling data for all live trees ≥ 5.0 cm DBH from the three plots in each stand because preliminary analysis showed that low numbers of trees in older plots created spurious non-linear relationships when analyzed at the plot-level. Next, we followed Metsaranta and Lieffers (2010) in calculating each stand's annual SGR values for 1999–2008. We restricted our calculations of SGR to the last 10 years of data because longer-term reconstructions were constrained by the short time-series of the youngest stand. Finally, to control for inter-annual climatic variation, which may cause fluctuations in SGR unrelated to long-term stand dynamics (Castagneri et al., 2012; Metsaranta and Lieffers, 2010), we added the additional step of averaging the annual SGR values for each stand to obtain the 10-year mean ± 95% confidence interval, which serves as an indicator of inter-annual variability.

2.4.2. Tree spatial patterns

We calculated the Clark-Evans (Clark and Evans, 1954) index, a commonly used indicator of spatial clustering in forests, as a summary statistic of tree spatial patterns. The Clark-Evans index is based on the difference between the expected Poisson and observed distributions of nearest-neighbor distances (Baddeley et al., 2015) and provides a convenient single summary statistic of stand-level spatial clustering for use in forest modeling. Values < 1 suggest clustering, while values > 1 suggest uniformity. We calculated the Clark-Evans index for live trees > 2.5 cm DBH based on stem maps of living trees as of 2009, using the spatstat package (Baddeley and Turner, 2013) for R (R Core Team, 2016). For each stand, we calculated the mean and 95% confidence ratio of the index based on individual-plot estimates. We used the cumulative distribution function for edge correction given the circular plot design (Baddeley et al., 2015).

2.4.3. Individual-tree red pine growth models

To construct the red pine growth models, we began by using competition indices (CIs) to assess the effects of tree-tree competition on individual-tree growth. Given the relatively small 10 m radii of the plots, we selected three distance-independent CIs, rather than more elaborate distance-dependent indices, in which competitor trees are weighted by distance from the target tree (Larocque et al., 2012). Because we were also interested in whether competition size-symmetry varied with stand age, we used CIs that modeled competition as either size-asymmetric (as for light) or size-symmetric (as for soil resources). Size-asymmetric competition indices discount the influence of competitors smaller than the target tree, while size-symmetric indices treat competitor influences as directly proportional to size (Larocque et al., 2012). Only measurements for trees living at the end of the 1999–2008 observation period were included in the indices.

The first index, CI-1, was a variation of the SDIL index developed by del Río et al. (2014), which models competition as size-asymmetric (i.e., larger trees disproportionately influence the growth of smaller trees by preempting access to resources, as with competition for light). To accommodate the irregular diameter distributions of older stands, we modified the original index by employing the summation method of Long and Daniel (1990), modified to use individual tree diameters as opposed to coarser diameter classes. Thus, CI-1 was computationally different, but conceptually equivalent, to the original SDIL index (del Río et al., 2014). CI-1 was calculated as:

$$CI = \sum_{\substack{j=1 \\ D_j > D_i}}^{n} \left(\frac{D_j}{25}\right)^{1.605} \tag{1}$$

where D_i is the diameter of target tree i, D_j is the diameter of plot neighbor tree j, and n is the total number of plot neighbors.

The second index, CI-2, is Wykoff's (1990) index, which is commonly used in forest growth and yield applications. CI-2, which models competition as more highly size-asymmetric (as for light) than CI-1, was calculated as:

$$CI = \sum_{\substack{j=1 \\ D_J > D_i}}^{n} (D_j)2^{*}0.00007854 \tag{2}$$

where symbols are as per Eq. (1).

CI-3 is Glover and Hool's (1979) index, which models competition as size-symmetric (individual-tree access to resources is proportional to size, as for soil resources). We calculated CI-3 as:

$$CI = (D_i^2/\overline{D}^2) \tag{3}$$

where $\overline{D}$ is the mean diameter of all sampled trees in the plot and other symbols are as per Eq. (1).

Next, we used multilevel mixed-effects modeling to examine how stand-level variables (SGR and Clark-Evans index) might affect individual tree biomass increment, both directly and through interaction with the individual-tree variables (CI and current tree biomass). This approach allowed us to investigate the linear additive and non-additive effects of each variable on individual-tree growth, while indirectly inferring how the strength of these relationships might shift over stand age. To match the growth metric and observation window used for SGR, we used 10-yr (1999–2008) mean aboveground biomass increment as the response variable. Because tree size strongly influences growth (Canham et al., 2006), we included end-year (2008) above-ground tree biomass as a predictor to account for variation in tree size. In addition to CI, we included a tree biomass x CI interaction term to account for the possibility that the size of individual red pines determines their responsiveness to competition (Biondi, 1996; Canham et al., 2006).

We examined four two-way interactions between stand level (SGR and Clark-Evans index) and individual-tree variables (biomass and CI). Stand-level SGR may reflect differences in the importance of competition (Binkley et al., 2006; Pretzsch and Biber, 2010); therefore, we included the SGR x CI interaction in modeling to examine this possibility. Because SGR appears to reflect the efficiency of large tree growth (Baret et al., 2017), we included an SGR x biomass interaction term. Because tree spatial variability may interact with both CI and tree size to influence growth (Fraver et al., 2014; Luu et al., 2013), we included Clark-Evans index x CI and Clark-Evans index x biomass terms accordingly. We excluded higher-order interactions as these were difficult to interpret on ecological grounds and to avoid overfitting. Interactions were only included in models if constituent main effects were as well.

We performed multimodel inference using the information-theoretic approach based on corrected Akaike's information criterion (AICc; Burnham and Anderson, 2003). We began model construction based upon a null biomass-only model, which modeled red pine growth as a simple function of current tree biomass. In addition to including other main effects, progressively more complex alternative models included the individual-tree biomass x CI interaction, as well as interactions of tree CI and biomass with stand-level SGR or Clark-Evans index (as above). We compared AICc only on the finished set of candidate models rather than using stepwise selection approaches. For both simplicity and to avoid overfitting, candidate models did not include more than a single interaction between stand-level and tree-level variables. We considered models within $\Delta AICc \leq 7$ of the best supported model to be plausible (Burnham and Anderson, 2003). To account for the influence of spatial autocorrelation on growth, we modeled spatial autocorrelation by fitting an exponential spatial variogram to model residuals (Fraver et al., 2014). We confirmed that the exponential autocorrelation structure was appropriate for the data based on AICc comparisons of models with other autocorrelation structures, as well as plots of variogram fits. Random effects included a stand term to properly constrain the degrees of freedom for SGR and the Clark-Evans index, while also helping control for age-related changes to individual-tree growth. We added a nested random effect of plot within stand to stratify tree coordinates for autocorrelation estimates.

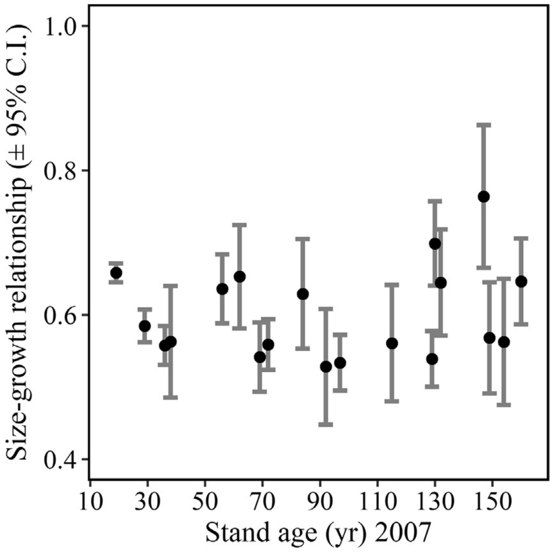

Fig. 1. Plot of the 10-year mean size-growth relationship (SGR) for 19 red pine chronosequence sites for the period 1999–2008. Shown are mean ± 95% confidence interval for all trees pooled across the 3 plots that make up each chronosequence site. Sites are labeled using 2007 stand ages to facilitate comparison with Bradford and Kastendick (2010).

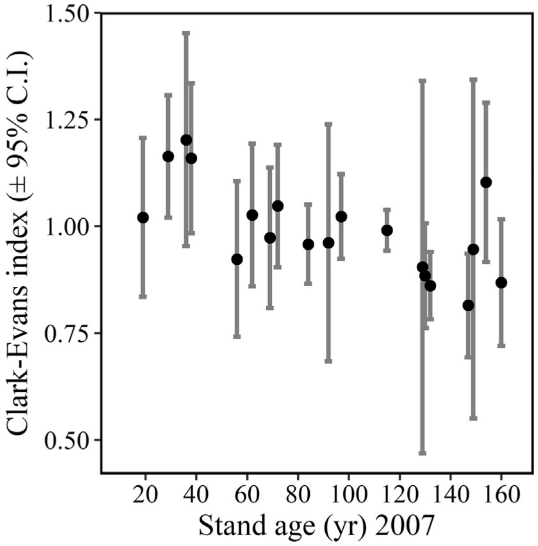

Fig. 2. Mean values of the Clark-Evans index of spatial clustering ± 95% confidence interval for 19 red pine chronosequence sites. The Clark-Evans index was calculated for all live trees ≥2.5 cm DBH. Values > 1 indicate spatial uniformity; values < 1 indicate spatial clustering. Sites are labeled using 2007, rather than 2009, stand ages to facilitate comparison with Bradford and Kastendick (2010).

We confirmed model assumptions of residual normality and homogeneity of variance by examining residuals plots. To meet these assumptions, the highly right-skewed biomass increment and right-skewed current tree biomass were fourth-root and log-transformed, respectively. We also log-transformed CI-3 to meet model assumptions, while the first two CI were left untransformed. Prior to analysis, we converted both predictors and biomass increment to Z-scores to compare the relative influences of model terms on a common scale (Quinn and Keough, 2003). Although we considered variance inflation factors (VIFs) < 10 to indicate a permissible level of multicollinearity (Quinn and Keough, 2003), VIFs did not exceed 5 for any model. Growth modeling was performed using the nlme package (Pinheiro et al., 2016) for R (R Core Team, 2016). We used the lsmeans package (Lenth, 2016) to help interpret interactions where present.

3. Results

3.1. Size-growth relationship

Over the 1999–2008 period, SGR (mean ± 95% confidence interval) averaged 0.60 ± 0.04 across the chronosequence (Fig. 1), where values greater than 1 indicate size-asymmetric SGR (large tree growth is disproportionately faster), a value of 1 indicates size-symmetric SGR (tree growth is proportional to size), and values less than 1 indicate inverse size-asymmetric SGR (large trees growth is disproportionately slower). In all stands, values of SGR were less than 1, indicating inverse-asymmetric SGR. Size-growth relationship of all species combined showed evidence of a broad decline between stand ages of 19 (0.66 ± 0.02) and 92 (0.53 ± 0.08) years. Between stand ages of 92 and 160 years, SGR slightly increased, achieving a study-wide maximum of 0.76 ± 0.08 in the 147-yr stand.

3.2. Tree spatial patterns

The mean ± 95% confidence interval of the Clark-Evans index was 0.99 ± 0.22. The index ranged from a low of 0.81 ± 0.12 in the 147-yr stand to a high of 1.2 ± 0.25 in the 36-yr stand age (Fig. 2). The Clark-Evans index declined linearly with stand age, although within-stand variability appeared to increase at older ages. A simple linear regression of the Clark-Evans index against stand age confirmed that this relationship was significant ($F = 12.74$, $p = 0.002$, $r^2 = 0.43$). The change from higher to lower values of the Clark-Evans index with increasing stand age suggested a shift from more uniform tree patterns towards greater clustering over time.

3.3. Individual-tree red pine growth models

We found substantial AICc support for two candidate red pine growth models (Table 2). The best-supported model included the main effects of CI-3 ($F = 407.6$, $p < 0.001$), individual-treebiomass ($F = 3451.25$, $p < 0.001$), and the Clark-Evans Index ($F = 8.11$, $p = 0.004$). This model alsoincluded the Clark-Evans x biomass ($F = 19.23$, $p < 0.001$) and CI-3 x biomass ($F = 72.6$, $p < 0.001$) interactions. The second model with substantial support was equivalent to the first, except that it included an SGR term. For the second model, the main effects of CI-3 ($F = 404.1$, $p < 0.001$), individual-tree biomass ($F = 3451.9$, $p < 0.001$), and the Clark-Evans index ($F = 8.1$, $p = 0.004$) were all significant at the 5% significance level for this second model. Although AIC comparisons supported the inclusion of a non-significant SGR effect ($F = 0.53$, $p = 0.47$), the standardized partial regression coefficient of this term was minor and not significant (Fig. 3). The Clark-Evans x biomass ($F = 19.11$, $p < 0.001$) and CI-3 x biomass ($F = 72.53$, $p < 0.001$) interactions were both significant. All other models, including those with only main effects and the biomass-only null model, had low AICc support ($\Delta\text{AICc} \geq 10.5$). In particular, there was negligible support for models that did not use CI-3 ($\Delta\text{AICc} \geq 112.4$).

The two best-supported models showed similar relationships among red pine biomass increment and model terms (Fig. 3). Individual-tree biomass had the single largest (and positive) main effect of any predictor on growth. The CI-3 index of size-symmetric competition had a comparatively smaller, but positive relationship with growth, indicating that trees in superior competitive positions grew faster. The main effects of the stand-level factors, SGR and the Clark-Evans index (both positive), showed comparatively high variation, reflecting smaller sample sizes relative to individual-tree variables. Size-growth relationship was positively correlated with individual red pine growth in the second best-supported model, such that higher SGR was associated with higher mean individual-tree biomass increment. However, the

Table 2
Summary of supported (ΔAICc < 7) models of individual-tree red pine biomass increment.

Model	Predictors	AICc	ΔAICc	Relative likelihood	Weights	Evidence ratio
1	C.E., CI-3, Bio, CI-3 x Bio, CE x Bio	896.16	0.00	1.00	0.68	1.00
2	SGR, C.E., CI-3, Bio, CI-3 x Bio, C.E. x Bio	897.69	1.52	0.47	0.32	2.13
Null	Bio	1286.8	390.64	0.00	0.00	3.81235E + 68

Note: Abbreviations are as follows: SGR = size-growth relationship, C.E. = Clark-Evans index, CI-3 = Glover-Hool symmetric competition index, Bio = individual-tree biomass, AICc = corrected Akaike's information criterion, ΔAICc = difference compared to best-fitting model. See text for supporting ANOVA results for the two plausible models. The null, biomass-only model is provided for the purposes of comparison.

effect size was both minor and variable. The stand-level Clark-Evans index was also positively associated with individual-tree biomass increment, with an effect size approximately 77–90% of CI-3 (albeit more variable). The increase in biomass increment with the Clark-Evans index suggested that more uniform tree spatial patterns enhanced the growth of individual red pines.

Interaction effects were generally weaker than main effects in the two models with substantial AICc support. The biomass x CI-3 interaction positively related to individual-tree growth in both models (Fig. 3). Because higher CI-3 values indicate higher relative dominance, this interaction indicated that the growth of large trees was more responsive to relative dominance than that of smaller trees (Fig. 4). The Clark-Evans index interacted with biomass to positively influence biomass increment in both models, suggesting growth of larger trees was relatively faster than growth of smaller trees in stands with more uniform tree spatial patterns (Fig. 4).

4. Discussion

4.1. Developmental trends in SGR

We found inverse-asymmetric SGR (less than 1) throughout the 19 to 160-yr red pine chronosequence, suggesting that larger trees exhibited disproportionately slow growth during all phases of stand development. This finding is broadly consistent with the prediction of disproportionately slow large-tree growth in older, mature stands (Baret et al., 2017; Binkley et al., 2006; Metsaranta and Lieffers, 2010). Inverse-asymmetric SGR late in stand development has been previously documented in several pine-dominated forests (Binkley and Kashian, 2015; Ex and Smith, 2014; Pothier, 2017), but is not a universal trait of these systems (Metsaranta and Lieffers, 2010).

In contrast, our finding of inverse-asymmetric SGR runs contrary to hypothesized patterns of size-asymmetric SGR at younger stand ages, when the competitive advantages of large trees should theoretically translate into disproportionately faster large tree growth and size-asymmetric SGR (Binkley, 2004; Binkley et al., 2006; Metsaranta and Lieffers, 2010). Studies have reported similarly early development and persistence of inverse-asymmetric SGR in lodgepole pine (*Pinus contorta* Douglas ex Loudon; Binkley and Kashian, 2015), as well as in a variety of boreal and mixed-wood species in eastern Canada (Pothier, 2017). Some hypothesized mechanisms driving disproportionately slow growth in large trees include declining photosynthetic efficiency with tree size (Baret et al., 2017) or shifts to below-ground biomass allocation not captured by above-ground stem measurements (Binkley and Kashian, 2015). The only other study of red pine SGR to date found that, while generally size-symmetric in unthinned 50- to 90-yr stands, SGR was still low in comparison to many forest types (Bradford et al., 2010). Bradford et al. (2010) calculated SGR using Binkley's (2004) growth dominance method, suggesting that different SGR metrics, such as Binkley's (2004) growth dominance and the Metsaranta and Lieffer's, 2010 index used in our study, may not necessarily yield equivalent results, a topic that merits of future research.

The consequences of persistent inverse-asymmetric SGR for the development of structural complexity in red pine stands are unclear. Disproportionately high growth of smaller trees is expected to reduce size inequality in stands (Castagneri et al., 2012). However, tree size inequality, as indicated by the Gini coefficient, increased with age across the red pine chronosequence (Bradford and Kastendick, 2010).

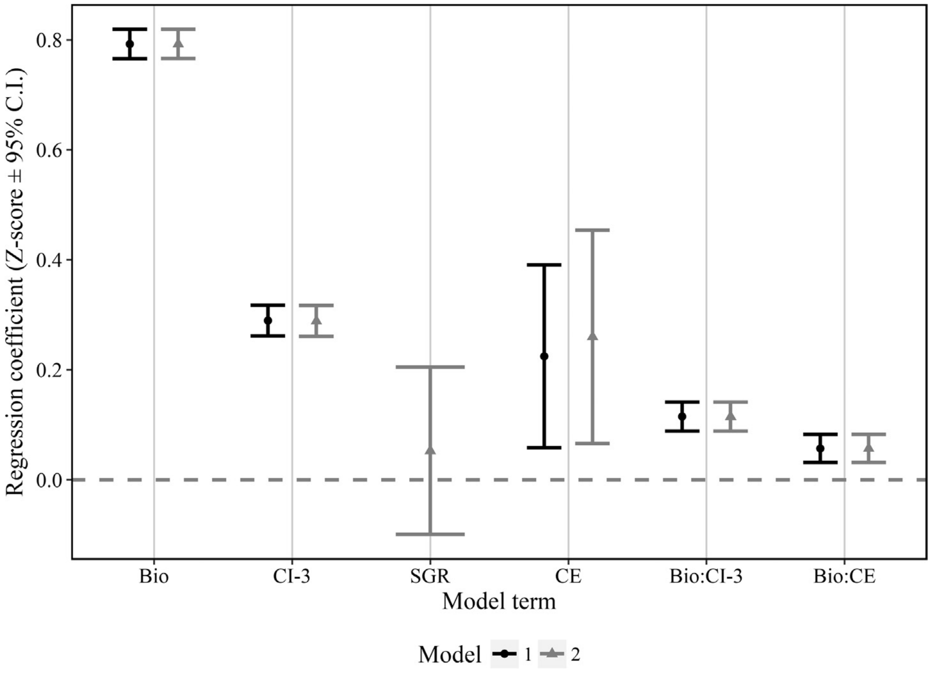

Fig. 3. Graphical summary of terms of two plausible models of individual-tree red pine biomass increment. The Y-axis displays the standardized partial regression coefficient (Z-scores; mean ± 95% confidence interval). The X-axis denotes the main effects and interaction terms examined. See Table 2 note for abbreviations. Note that the difference between the two models is whether the main effect of SGR is included.

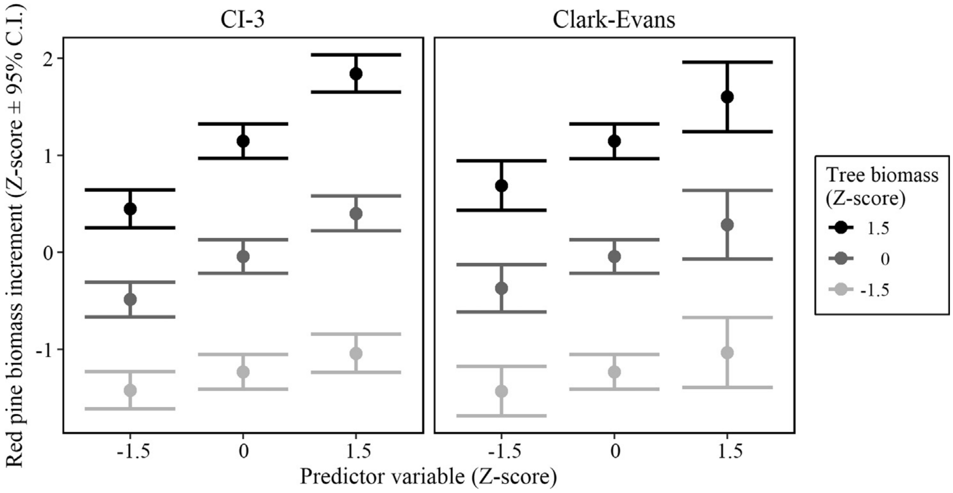

Fig. 4. Interaction plot illustrating the effects of interactions between stand-level variables and individual-tree biomass on red pine biomass increment, based on the best-supported red pine growth model. All variables have been converted to Z-scores). The left panel shows the biomass x CI-3 interaction; the right panel shows the biomass x Clark-Evans index interaction. Points illustrate estimated least-squares mean ± 95% confidence interval of red pine biomass increment at discrete minimum (−1.5), average (0), and maximum (1.5) values of the predictor variables in Z-scores. These minimum and maximum values were selected based on data range constraints of the least-variable factor (the Clark-Evans index). Shading denotes minimum, average, and maximum values of tree biomass.

The early emergence of inverse-asymmetric SGR during stand development may be an artifact of self-thinning mortality. We noted a steady decline in trees ha^{-1} with stand age, and self-thinning could conceivably have depressed SGR estimates in younger stands by removing small, low-vigor trees from the sample. Fully accounting for tree mortality may be important not only in interpreting stand-level declines in productivity (Foster et al., 2014), but individual-tree-driven patterns of SGR.

4.2. Developmental trends in tree spatial patterns

We found that tree spatial relationships shifted from uniformity to clustering with stand age. This finding of increased spatial heterogeneity over time is consistent with previous work in red pine systems, which found that spatially random tree mortality contributes to clustered patterns of surviving trees (Aakala et al., 2013). Competition between trees is expected to result in increasing tree spatial uniformity in early stand development (Kenkel, 1988; Larson et al., 2015), as closely spaced neighbors experience self-thinning mortality (Gray and He, 2009), a pattern that has been found in several forest types (Gray and He, 2009; Kenkel, 1988; Larson et al., 2015). However, mortality processes such as self-thinning do not always predictably alter the spatial patterns of surviving trees (Aakala et al., 2013; Larson et al., 2015). Examination of stand age structures indicated that recruitment of new age classes continued throughout the timespan of the chronosequence (Appendix, Fig. A1), and newly established trees may increase spatial clustering within stands, offsetting the tendency of adult tree mortality to promote spatial uniformity (Lutz et al., 2014).

All but one of the chronosequence stands 69-years and younger originated from post-harvest plantings, which tend toward uniform spacing. In contrast, stands 72-years and older were natural origin following fire or unknown disturbance. Variation in the severity and behavior of stand-initiating fires may increase tree spatial heterogeneity in older stands by locally sparing advance regeneration and creating variable microsite conditions for new seedlings (Sánchez Meador et al., 2009). Gap-forming disturbances could also potentially explain clustered tree spatial patterns (Franklin and Van Pelt, 2004; Larson et al., 2015), given that an anticipated consequence of larger tree size under extended rotations is heightened tree susceptibility to windthrow, insects, and pathogens (Bauhus et al., 2009). Although stand histories indicated that the chronosequence stands experienced no catastrophic disturbances since initiation, detailed surveys of minor damaging agents, canopy gaps, and regeneration, as well as dendrochronological records of tree release, would be needed to fully elucidate mechanisms driving the development of spatial clustering in these red pine stands.

4.3. Individual-tree red pine growth models

In agreement with earlier research, both red pine biomass and local competitive environment strongly influenced individual-tree growth (Canham et al., 2006; Fraver et al., 2014), with red pine biomass most influential. Red pine biomass and competition appeared to interact to reduce growth, suggesting that competition disproportionately limited the growth of large trees. Greater responsiveness of larger trees to competition in terms of reduced growth has previously been reported in ponderosa pine (*Pinus ponderosa* C. Lawson, Biondi, 1996) and black ash (Looney et al., 2016), but the reverse pattern appears more common among other temperate forest species (Canham et al., 2006).

Reduced large-tree growth allocations to foliage production and declining photosynthetic efficiency may drive declines in large tree growth in many forests (Baret et al., 2017; Binkley and Kashian, 2015; Pretzsch and Biber, 2010). However, we did not find substantial model support for an interaction between SGR and red pine biomass. We found only limited evidence of marginally more rapid growth of both large and small individual-trees in stands with less pronounced inverse-asymmetric SGR. This weak main effect of SGR on individual-tree growth may reflect differences in site quality (Castagneri et al., 2012; Pretzsch and Dieler, 2010), although such differences would have been minimized by consistency of soils, topography, and climate across the chronosequence (Bradford and Kastendick, 2010). Alternatively, our use of DBH-only biomass equations may have masked some age-related changes in SGR or individual-tree growth, as the DBH-growth response is generally more variable than the height-growth response to competition (Lanner, 1985). It would be useful to compare the results of DBH-only and DBH-height biomass equations to assess differences in predicting biomass production throughout stand development for studies such as ours, where direct biomass sampling via harvesting is infeasible.

In addition to large-tree growth efficiency, stand-level SGR is thought to reflect the relative influence of size-asymmetric competition on growth (Binkley et al., 2006; Metsaranta and Lieffers, 2010). As the canopy closes early in stand development and high leaf area renders light a scarce resource, size-asymmetric competition (i.e., larger trees disproportionately suppressing the growth of smaller individuals) is expected to correlate with stand-level size-asymmetric SGR (large trees growing disproportionately faster than smaller trees (Binkley et al., 2006). Instead, we found inverse-asymmetric SGR (large trees growing disproportionately slower than small trees) with size-symmetric competition (i.e., individual-tree growth is proportional to size, as for soil resources) for all stands in our red pine chronosequence. Pothier (2017) similarly found inverse-asymmetric SGR with size-symmetric competition in a variety of forest types; whereas a study of black ash found size-asymmetric competition, with large trees suppressing the growth of smaller trees, in stands where SGR varied from inverse-asymmetric to size-asymmetric (Looney et al., 2016). The different levels of inference involved when using stand-level versus individual-tree competition metrics may account for occasional discrepancies between these approaches (Sheil et al., 2017), suggesting a potential topic for additional research.

In accordance with earlier studies (Fraver et al., 2014; Luu et al., 2013), we found evidence that stands with more uniform tree spatial patterns, as indicated by higher values of the Clark-Evans index, supported greater individual-tree growth. In particular, more uniform spatial patterns were associated with the faster growth of larger trees relative to smaller trees. A study of multiage Scots pine stands (*Pinus sylvestris* L.) similarly found that individual-tree size was greater and displayed less variability under more uniform tree spatial patterns (Adams et al., 2013; Stiell, 1982). Reduced heterogeneity has also been linked to increased growth in gum plantations, with the effect separate from competition (Luu et al., 2013; Stape et al., 2010). We hypothesize that more clustered spatial distributions may be associated with a relative increase in inverse-asymmetric SGR, as clustering appeared to depress large tree growth. Because inverse-asymmetric SGR is anticipated to reduce tree size inequality (Metsaranta and Lieffers, 2010; Pretzsch and Dieler, 2010), the spatial complexity of clustered tree distributions could paradoxically simplify forest structure. Long-term repeated measurements, as opposed to the more static chronosequence approach, would aid in testing this hypothesis.

Competition is theorized to intensify under clustered tree spatial patterns, promoting the development of tree size inequality (Weiner et al., 2001), and localized increases in clustering have been associated with reduced tree growth (Fraver et al., 2014). However, we found no evidence that the stand-level Clark-Evans index interacted with competition to substantially influence tree growth, suggesting the influence of competition changed little under spatial clustering. Trees may exhibit asymmetric crown growth to exploit light at the edges of dense clusters (Stiell, 1982), potentially reducing the intensity of size-asymmetric competition below what would be expected from the spatial patterns of stems alone (Adams et al., 2013).

Given that tree competition does not appear to drive the relationship between red pine spatial patterns and individual-tree growth, we cannot definitively resolve the casual mechanisms behind this relationship based on our data. Instead, we propose several non-exclusive possibilities. First, the partitioning of light or soil resources may be less efficient under more spatially clustered patterns, particularly between trees of different species (De Boeck et al., 2006; Luu et al., 2013). Second, clustering may reflect microsite variation, which can in turn exert a strong influence on tree growth (Fajardo and McIntire, 2007). However, microsite effects on growth appear more pronounced earlier in stand development (Fajardo and McIntire, 2007), and we have no reason to suspect that older stands had more microsite variation. Third, pathogens such as root diseases may result in canopy gaps and clustered patterns of surviving trees (Franklin and Van Pelt, 2004; Larson et al., 2015), and the reduced growth of trees in stands with more clustering may reflect disease-related declines. Regardless of the mechanisms involved, the increased prevalence of clustering at older stand ages in our study suggests associated declines in tree growth may become more pronounced over time.

5. Conclusions

Our findings have implications for the use of extended rotations as a strategy for managing red pine, and potentially other forest types, to balance timber production with ecological services. The presence of inverse-asymmetric SGR throughout stand development may slow the development of tree size inequality, a criterion of stand structural complexity (Cordonnier and Kunstler, 2015). Previous research suggests thinning from below may maintain the productivity of extended rotation red pine stands (D'Amato et al., 2010). However, the disproportionately slow growth of larger trees in this study suggests that thinning from above to retain smaller trees that do not interfere with crop-tree growth may be more effective in increasing the yield of larger crop-trees while simultaneously promoting total stand biomass production and stand structural diversity (Puettmann et al., 2012).

In the absence of intermediate silvicultural treatments, red pine stands showed evidence of increasing tree spatial clustering over time. Non-uniform tree spatial patterns are often cited as a criterion of forest complexity (Franklin and Van Pelt, 2004) and thus provide support for the use of extended rotation management to achieve structural complexity. Evidence of spatial clustering increased with stand age up to 160 years, well in excess of the typical 50 to 90-yr rotation age of regional red pine stands (Gilmore and Palik, 2006). Extended rotation management, therefore, appears effective in increasing red pine spatial complexity. However, our modeling of individual-tree red pine growth suggested that increased stand-level spatial complexity is associated with decreased growth of individual trees, creating a tradeoff that may present an added cost when attempting to balance multiple ecological objectives with productivity in extended rotation red pine stands.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.04.044.

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