Growth, yield, and structure of extended rotation *Pinus resinosa* stands in Minnesota, USA

Anthony W. D'Amato, Brian J. Palik, and Christel C. Kern

Abstract: Extended rotations are increasingly used to meet ecological objectives on forestland; however, information about long-term growth and yield of these systems is lacking for most forests in North America. Additionally, long-term growth responses to repeated thinnings in older stands have received little attention. We addressed these needs by examining the growth and yield of red pine (*Pinus resinosa* Ait.) in a growing stock experiment in northern Minnesota. Stands were 85 years old at the onset of this experiment and were repeatedly thinned to five levels of basal area (13.8, 18.4, 23.0, 27.5, and 32.1 $m^2 \cdot ha^{-1}$) over 58 years. Cumulative volume production and volume growth were lowest within the lowest stocking treatment and similar across other stocking levels. Late-successional structural attributes, such as the density of trees with ≥40 cm diameter at breast height, was similar across stocking levels. The mean annual volume growth culminated between 130 and 140 years. Additionally, positive growth responses were observed within the highest stocking-level treatments after thinning at 138 years, demonstrating the ability of older red pine to respond to reductions in competition. These results illustrate that extended rotations with repeated thinnings in red pine help achieve ecological goals, including the restoration of old-forest structure, while also maintaining high levels of stand productivity.

Résumé : On utilise de plus en plus des rotations allongées pour atteindre des objectifs écologiques en forêt. Cependant, on manque d'information sur la croissance et la production à long terme de ces systèmes pour la plupart des forêts d'Amérique du Nord. De plus, la réaction en croissance à long terme à des éclaircies répétées dans les vieux peuplements est peu documentée. Pour combler ces besoins, nous avons étudié la croissance et la production associées à une expérience de densité variable de pin rouge (*Pinus resinosa* Ait.) établie au nord du Minnesota. Les peuplements étaient âgés de 85 ans au début de cette expérience et ont été éclaircis de façon répétée selon cinq niveaux de surface terrière (13,8, 18,4, 23,0, 27,5 et 32,1 $m^2 \cdot ha^{-1}$) pendant une période de 58 ans. Les plus petites valeurs de production cumulative et de croissance en volume ont été obtenues dans le cas du traitement qui maintenait la plus faible surface terrière, mais il n'y avait pas de différence entre les autres traitements. Les attributs de la structure en fin de succession, comme la densité des arbres ≥40 cm, étaient semblables peu importe la densité. L'accroissement annuel moyen en volume était maximal entre 130 et 140 ans. De plus, une réaction positive en croissance a été observée à la suite d'une éclaircie réalisée à l'âge de 138 ans dans le traitement qui maintenait la plus forte densité, ce qui démontre la capacité des vieux pins rouges à réagir à une diminution de la compétition. Ces résultats indiquent que des rotations allongées accompagnées d'éclaircies répétées dans des peuplements de pin rouge permettent d'atteindre des objectifs écologiques, notamment la restauration de la structure des vieilles forêts, tout en maintenant de hauts niveaux de productivité à l'échelle du peuplement.

[Traduit par la Rédaction]

Introduction

Over the past several decades, many traditional silvicultural systems and approaches have been modified to address a greater range of objectives, including maintenance of native biodiversity, restoration of late-successional forest communities, and enhanced stand structural complexity (Seymour and Hunter 1999; Lindenmayer and Franklin 2002; Bauhus et al. 2009). In general, these modifications have involved an increased emphasis on the forest structures created and maintained through treatment applications, as well as the patterns and frequency with which harvest entries are made (Swanson and Franklin 1992; Harvey et al. 2002; Seymour et al. 2002). One example of such modifications has been the use of extended rotations, or recovery periods (sensu Franklin et al. 2007), in which final harvests in even-aged stands are delayed well beyond the rotation ages traditionally recommended for maximizing timber production or economic returns (Curtis 1997). This approach has been suggested as a means for restoring stand-level and landscape-level complexity through the retention of older age classes and structures (Seymour and Hunter 1999), as well as for increasing overall carbon storage within forested landscapes (Harmon and Marks 2002).

Traditionally, stand rotation lengths in North America have been based on either financial criteria related to maximizing discounted present net value (Davis et al. 2001) or biological standards related to annual timber production

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A.W. D'Amato.[1] Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, USA.
B.J. Palik. USDA, Forest Service, Northern Research Station, 1831 Highway 169 E, Grand Rapids, MN 55744, USA.
C.C. Kern. Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, USA; USDA, Forest Service, Northern Research Station, 1831 Highway 169 E, Grand Rapids, MN 55744, USA.

[1]Corresponding author (e-mail: damato@umn.edu).

(Newman 1988) based on culmination of mean annual growth increment. Overall, the rotation ages suggested for extended rotation systems tend to be well beyond those developed based on financial criteria (Curtis 1997) largely because the interest rates used in economic optimization tend to favor short-term financial returns (Bettinger et al. 2009). In addition, a short-coming of basing rotation age on culmination of mean annual increment is that in unthinned stands, time to growth culmination can be quite short, relative to tree life-spans. For instance, volume growth of site index 170 Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirbel) Franco) culminates at around 65 years in unthinned stands (McArdle et al. 1949), despite the life-span of this species regularly exceeding 300 years (e.g., Tappeiner et al. 1997).

Because of the long history of forest management and forestry research within Europe, there have been numerous examinations of the growth of forest stands repeatedly thinned well beyond ages that would be considered commercial rotation ages based on the abovementioned criteria (e.g., Assman 1970; Sterba 1987; Pretzsch 2005). This work has been invaluable in our understanding of density–growth relationships (Assman 1970; Smith et al. 1997), as well as in demonstrating the importance of site factors, species, and stand age on the long-term responsiveness of forest stands to repeated thinning treatments (Pretzsch 2005). Until recently, similar examinations of replicated experiments with commercially important North American tree species were rare; however, recent analyses of several long-term studies within coastal systems of Douglas-fir in the Pacific Northwest suggest that less incongruity may exist between traditional objectives for maximizing annual volume production and the use of extended rotations for ecological objectives (Curtis and Marshall 1993; Curtis 1995). In particular, studies examining patterns of volume growth in long-term thinning and growing stock trials have demonstrated that with repeated thinnings mean annual volume growth culminates at much greater ages than previously reported (Curtis 1995; Stinson 1999). These findings suggest that the use of repeated thinning treatments within extended rotation systems in Douglas-fir may provide a means to maintain greater levels of volume production while also providing the ecological benefits of older forest conditions (Curtis and Carey 1996; O'Hara 2001). Nonetheless, little information exists on the application of this approach to commercially important species in other regions of North America, making economic predictions and ecological expectations challenging to assess.

Within the Great Lakes region, the use of extended rotations for red pine (*Pinus resinosa* Ait.) forests has been suggested as a means to meet ecological objectives and restore later successional structural elements lacking in younger stands (Duvall and Grigal 1999; Gilmore and Palik 2006). Despite the potential longevity of this species (>300 years, Benzie 1977), red pine has typically been managed in even-aged plantations or relatively pure natural stands with rotation ages ranging from 60 to 100 years (Buckman 2006; Gilmore and Palik 2006). Although numerous studies have demonstrated the positive impacts that repeated thinning treatments have on the growth and development of red pine stands, this work has been limited to stand ages within traditional rotation lengths (e.g., Bradford and Palik 2009) or has been based on simulation models (Benzie 1977; Buckman 2006). As such, our ability to predict the response of older red pine stands to repeated thinning treatments within the context of extended rotation systems is greatly limited. Moreover, there have been no formal evaluations of how effective extended rotation systems are at restoring late-successional structural elements to managed red pine stands.

We sought to address these limitations by examining the patterns of growth and yield within a replicated long-term red pine growing stock study established in 85-year-old red pine stands and repeatedly thinned through age 143. Specifically, our objectives were (1) to determine the influence of repeated thinning treatments on the development of late-successional forest stand structure and composition, (2) to quantify the long-term patterns of growth and yield within repeatedly thinned red pine stands grown on extended rotations, and (3) to examine how these patterns differ across various levels of growing stock.

Methods

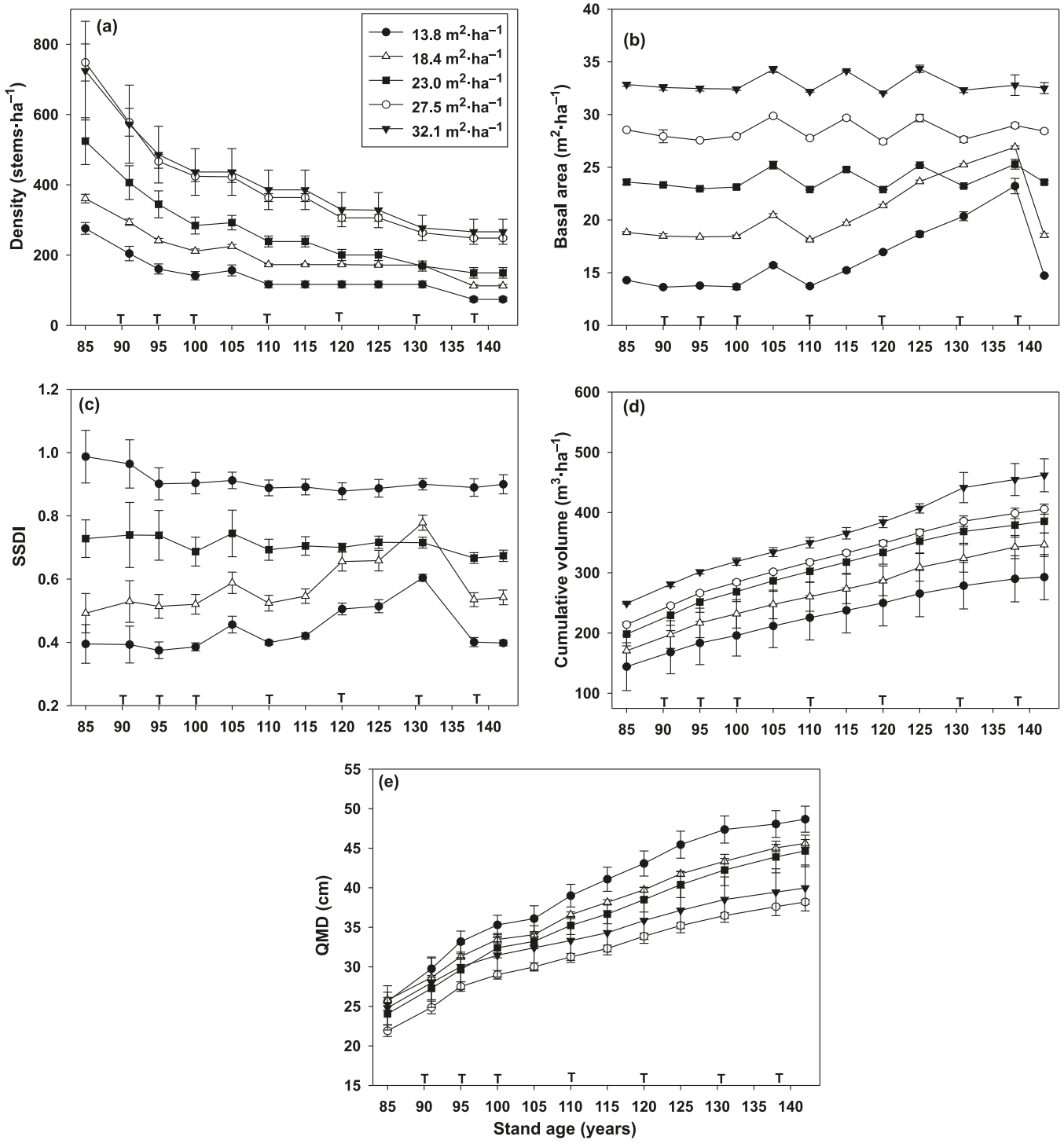
Study area

The study site is located on the Cutfoot Sioux Experimental Forest within the Chippewa National Forest in north-central Minnesota, USA (47°40′N, 94°5′W). This area has a continental climate with mean temperatures ranging from –14.2 °C in January to 19.7 °C in July, and annual precipitation averaging 73.1 cm (Midwestern Regional Climate Center 2006). Soils are deep well-drained sands derived from glacial outwash, and the site index for red pine for the stands examined is 15.2 m at 50 years (Buckman 1962). Stands in this study originated naturally following a fire in 1864 and were 85 years old at the time of treatment establishment in 1949, at which time, the stands were well stocked and very uniform in structure, with volumes averaging 128.2 $m^3 \cdot ha^{-1}$. Red pine was the dominant tree in these systems with lesser amounts of white pine (*Pinus strobus* L.) and jack pine (*Pinus banksiana* Lamb.). Prior to the establishment of treatments, the stands were entered twice: in 1940 to salvage trees damaged by a spring glaze storm, and again in 1945, to further salvage trees that died from damage incurred by the 1940 storm.

Long-term growing-stock-levels experiment

From 1949 to 1951, a replicated growing-stock-level experiment was installed within these stands that consisted of five levels of residual red pine growing stock (13.8, 18.4, 23.0, 27.5, and 32.1 $m^2 \cdot ha^{-1}$ basal area). Each treatment was assigned to experimental units ranging in size from 1.0 to 2.0 ha and was replicated three times. After treatment assignment, thinning treatments were initially applied every 5 years to maintain growing stock levels; however, the length between thinning entries was extended to 10 years in 1964 because of the small growth increment on some of the treatments. Thinnings occurred at 10-year intervals thereafter until 2004 for all stands with the exception of the 13.8 and 18.4 $m^2 \cdot ha^{-1}$ stocking-level treatments, which did not receive thinning treatments from 1975 to 2003. Correspondingly, these lower stocking-level treatments received five thinning treatments over the duration of this study (i.e.,

Fig. 1. (*a*) Stand density, (*b*) basal area, (*c*) standardized stand density index (SSDI), (*d*) net cumulative volume, and (*e*) quadratic mean diameter (QMD) over time for each red pine growing stock level on the Cutfoot Sioux Experimental Forest, Chippewa National Forest, Minnesota. Error bars represent one standard error. T along *x* axis indicates the time of thinning treatment application. Only the higher stocking levels (23.0, 27.5, and 32.1 $m^2 \cdot ha^{-1}$) were thinned at stand ages 120 and 130 years. SSDI was calculated following Pretzsch (2005) and represents the ratio between the stand density index (SDI) of a given stocking level and the SDI of the highest stocking-level treatment (i.e., 32.1 $m^2 \cdot ha^{-1}$) at a given point in time.



1949–2007), whereas the other stocking-level treatments were thinned seven times. With the exception of the lowest stocking-level treatments, thinning treatments effectively maintained consistent stocking levels within each treatment over the entire course of the study (Fig. 1). In general, treatments were thinned from below; however, high density areas were marked to leave residual trees evenly spaced to meet the target basal area. In addition, jack pine was initially fa-

vored for removal over red pine because of its poor condition. In 1975, timber stand improvement crews removed the small red pine, jack pine, white pine, balsam fir (*Abies balsamea* (L.) P. Mill.), white spruce (*Picea glauca* (Moench) Voss), and paper birch (*Betula papyrifera* Marsh.) that had recruited into the treatment plots. Overall, stand-level *d*/*D* (quadratic mean diameter of trees removed (*d*) divided by quadratic mean diameter of trees before harvesting (*D*)) for the thinning treatments ranged from 0.29 to 0.99 throughout the study period. Thinnings generally removed between 4.9% and 21% of the stand basal area depending on stocking-level treatment; however, the final thinnings in the 13.8 and 18.4 $m^2 \cdot ha^{-1}$ stocking levels removed 39.2% and 32.1% of the stand basal area, respectively (Table 1).

Three 0.08 ha permanent measurement plots were established in each treatment unit and were measured at roughly 5-year intervals coinciding with thinning treatments beginning in 1949. Within each plot, diameter was measured on all trees >8.9 cm diameter at breast height (DBH). Individual whole-tree stem volume (*V*, in cubic feet, outside bark) was calculated from DBH (in inches) for each tree within a plot using the following formula derived for red pine in north-central Minnesota (Gilmore et al. 2005):

$$V = 0.1202(\mathrm{DBH})^{2.0565}$$

This equation was chosen because of its superior performance in a previous study evaluating the predictive ability of several existing volume equations within red pine stands located in close proximity to our study area (Gilmore et al. 2005).

Individual tree-level measurements were used for determining standing volume, thinned volumes, mortality volumes, ingrowth, and quadratic mean diameter (QMD) at each measurement period. In addition, the density of large trees (≥40 cm; cf. Zenner and Peck 2009), diameter distributions, and tree species and size-class diversity (based on the Shannon–Weaver index) were determined using tree-level measurements from the final measurement period. Gross periodic annual increment (PAI) was calculated as the difference in standing volumes between measurement periods, including thinned volumes and mortality during the period. Similarly, gross mean annual increment (MAI) was calculated for each measurement year by dividing stand cumulative volume (stand volume + cumulative thinning volume + mortality) by stand age. Although most replicates contained minor components of white pine at the onset of this study (<20% of total basal area), we chose to focus exclusively on red pine in our analyses of stand growth and yield. Moreover, species other than red pine made up 0.2%–6.1% of the total stand basal area by the end of the study and therefore contributed little to the overall growth and production within these systems.

Data analysis

The influence of growing stock level on PAI and MAI was examined using a mixed-model repeated-measures analysis of variance (ANOVA) in which treatment unit was treated as a random effect and growing stock level and time were treated as fixed effects, following the SAS MIXED procedure (SAS Institute Inc. 2010). The statistical model used was

Table 1. Mean basal area removed at each thinning entry for the red pine growing-stock-levels experiment at the Cutfoot Sioux Experimental Forest, Chippewa National Forest, Minnesota.

Stocking-level treatment	Basal area removed ($m^2 \cdot ha^{-1}$) at stand age of:									
	90 years	95 years	100 years	105 years	110 years	115 years	120 years	125 years	130 years	135 years
13.8 $m^2 \cdot ha^{-1}$	3.2 (18.7)	2.1 (13.3)	1.5 (10.1)	0 (0)	3.7 (21.0)	0 (0)	0 (0)	0 (0)	0 (0)	8.5 (39.2)
18.4 $m^2 \cdot ha^{-1}$	3.3 (14.9)	2.8 (13.2)	1.7 (8.7)	0 (0)	3.9 (17.8)	0 (0)	0 (0)	0 (0)	0 (0)	8.4 (32.1)
23.0 $m^2 \cdot ha^{-1}$	3.2 (12.1)	2.8 (10.7)	2.1 (8.5)	0 (0)	4.1 (15.4)	0 (0)	3.9 (14.6)	0 (0)	4 (14.8)	2.4 (9.9)
27.5 $m^2 \cdot ha^{-1}$	4.1 (12.7)	2.9 (9.4)	1.8 (6.1)	0 (0)	4 (12.5)	0 (0)	4.3 (13.4)	0 (0)	4.1 (13.1)	1.6 (5.4)
32.1 $m^2 \cdot ha^{-1}$	3.8 (10.5)	2.4 (6.9)	2.2 (6.4)	0 (0)	4.1 (11.2)	0 (0)	4.2 (11.7)	0 (0)	4.1 (11.5)	1.6 (4.9)

Note: Numbers in parentheses represent the percentage of the total basal area removed at each entry.

$$Y_{ijk} = \mathrm{GSL}_i + \mathrm{Period}_j + (\mathrm{GSL} \times \mathrm{Period}_{ij}) + \mathrm{Unit}_k + e_{ijk}$$

where GSL_i is the effect of the ith growing stock level, Period_j is the effect of the jth measurement period, GSL × Period_{ij} is the interaction between treatments and time, Unit_k is the random effect of the kth experimental unit, and e_{ijk} is the residual error. In cases in which significant growing-stock-level effects were detected, orthogonal polynomial contrasts were used to evaluate linear, quadratic, and cubic trends between PAI, MAI, and growing stock level. A single-factor mixed-model ANOVA that treated stocking level as a fixed effect and treatment unit as a random effect was used to test the effects of growing stock level on final stand structure (QMD and density of large trees); species diversity; and cumulative volume production, ingrowth, and mortality rates of red pine. For all analyses, data distributions were checked for normality and homogeneity of variances and were transformed using natural logarithmic transformations as necessary. A P value of 0.05 or less was defined as statistically significant.

Results

At the final measurement period, all treatments were strongly red pine dominated; however, other species, including *A. balsamea*, *Acer rubrum* L., *B. papyrifera*, and *Quercus rubra* L. were represented to varying degrees within the smaller diameter classes (Fig. 2). The abundance of these other tree species was greatest within the lowest stocking-level treatment in which *Q. rubra*, *B. papyrifera*, and *A. balsamea* constituted 22.1%, 15.6%, and 11.5% of the total stems, respectively (Fig. 2). Correspondingly, this treatment had the greatest diversity of tree species at the final measurement period (Table 2). Within each treatment, the distribution of red pine diameters was strongly unimodal with diameters ranging primarily from 35 to 50 cm (Fig. 2). There were no significant differences in the density of large trees (≥40 cm DBH) across treatments, with mean densities ranging from 66 to 115 trees·ha^{-1} (Table 2). Likewise, there were no differences in the diversity of diameters found across stocking-level treatments (Table 2).

After a 52-year period of repeated thinning treatments, mean red pine QMD was greatest in the lowest stocking-level treatment, with no significant differences in QMD among the other stocking levels, although mean QMD generally decreased with increased stocking level (Fig. 1*e*, Table 2). In contrast, net cumulative volume production was lowest for the 13.8 m^2·ha^{-1} stocking level and similar across the higher stocking-level treatments (Table 2, Fig. 1*d*). Importantly, these cumulative volumes are likely an underestimate of the total production on these sites, as they do not include volumes removed by salvage logging prior to the establishment of this experiment, previous mortality, or other species harvested during timber stand improvement operations in 1975. Red pine ingrowth volumes were considerably higher in the lowest stocking-level treatment, with the 52-year mean totals being 2.7 to 34.7 times greater than those found in the other stocking-level treatments (Table 2). Overall, mortality (expressed as percentage of gross volume yield) was quite low over the duration of this study, and there were no significant differences in mortality rates

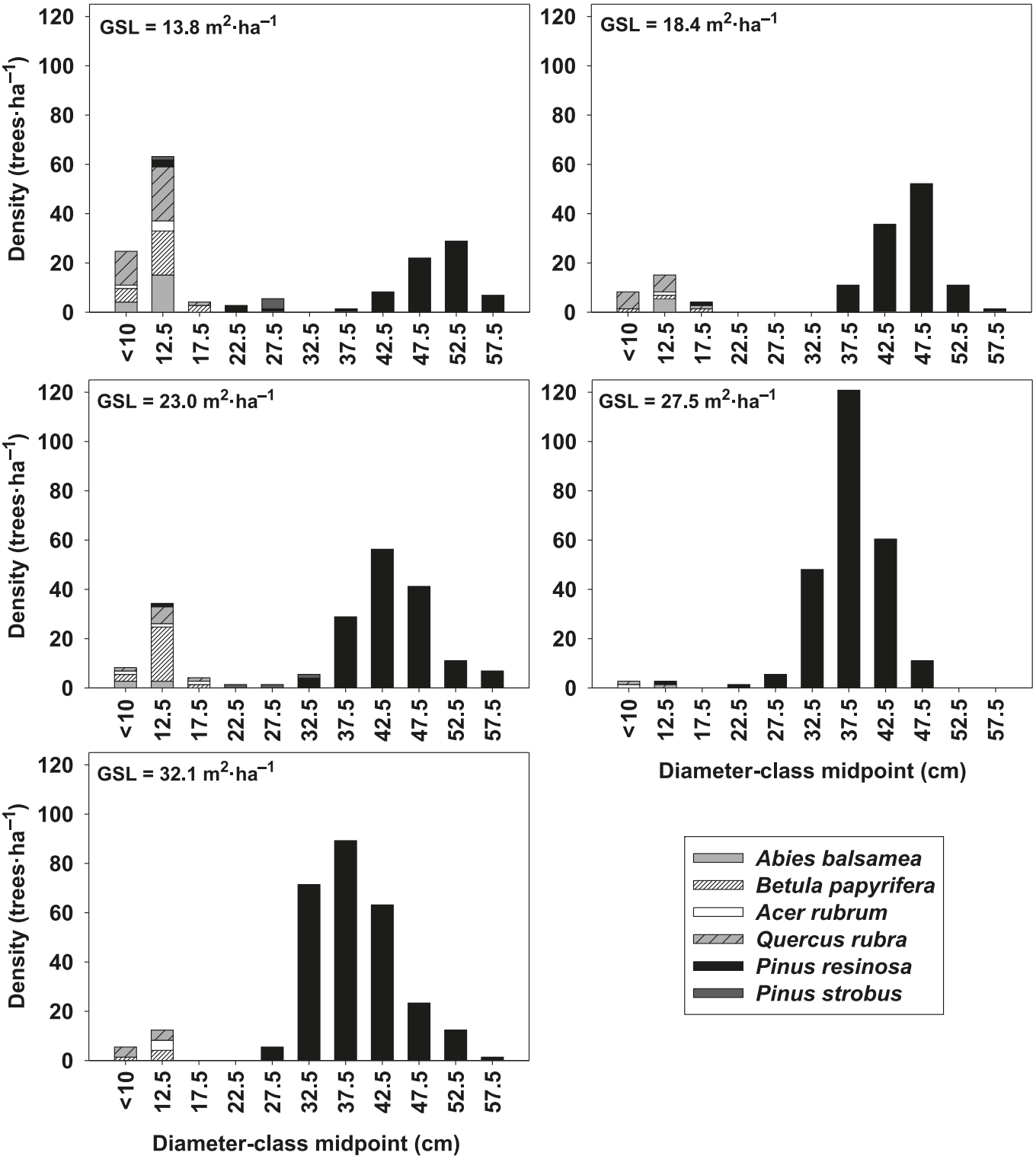
Table 2. Mean (standard error) stand attributes within repeatedly thinned red pine stands on the Cutfoot Sioux Experimental Forest, Chippewa National Forest, Minnesota, at age 142 years.

Stocking level	QMD (cm)	Cumulative volume (m^3·ha^{-1})	Mortality (% of gross volume yield)	Ingrowth volume (m^3·ha^{-1})	Density of large* trees (no./ha)	Tree species diversity (Shannon's index)	Diameter-class diversity (Shannon's index)
13.8 m^2·ha^{-1}	49.22 (1.17)a	292.76 (37.62)a	1.20 (0.75)a	15.20 (2.65)a	66 (4)a	1.34 (0.05)a	1.67 (0.08)a
18.4 m^2·ha^{-1}	45.77 (0.66)ab	346.53 (19.53)ab	4.84 (2.95)a	5.72 (0.55)b	100 (5)a	0.62 (0.05)b	1.59 (0.09)a
23.0 m^2·ha^{-1}	44.24 (1.64)ab	385.49 (19.58)ab	1.99 (1.79)a	3.50 (0.32)b	115 (11)a	0.67 (0.18)b	1.70 (0.17)a
27.5 m^2·ha^{-1}	38.32 (0.38)b	405.62 (8.36)ab	2.11 (0.87)a	2.05 (0.56)b	71 (12)a	0.07 (0.07)b	1.31 (0.03)a
32.1 m^2·ha^{-1}	39.89 (2.88)b	461.86 (27.36)b	8.00 (4.69)a	0.44 (0.22)b	100 (32)a	0.25 (0.24)b	1.42 (0.19)a

Note: Annual mortality rates and ingrowth are based on measurements from ages 90 to 142 years. Values for QMD (quadratic mean diameter), cumulative volume, mortality, and ingrowth are only for red pine, whereas all other variables include all species. Different letters indicate significant differences among growing stock levels for a given attribute (Tukey–Kramer's test, $P < 0.05$).

*Large trees have diameter at breast height of ≥40 cm.

Fig. 2. Diameter distribution of each red pine growing-stock-level (GSL) treatment at age 142 years.



across growing stock levels (Table 2). In addition, there were no differences among treatments in the mean DBH of trees that died over the course of the study (data not shown). In most cases, trees that died had a lower QMD than the QMD for a given treatment, suggesting they died from resource competition; however, mortality of larger trees did occur and was due to an isolated incidence of *Diplodia* shootblight (see below).

PAI increased linearly with increased stocking level and decreased with age within a treatment (Figs. 3 and 4, Table 3). The PAI for the two lowest stocking-level treatments (13.8 and 18.4 $m^2 \cdot ha^{-1}$) was significantly lower than that for

Table 3. Summary of type 3 tests of fixed effects for periodic annual increment (PAI) and mean annual increment (MAI) for repeatedly thinned red pine stands on the Cutfoot Sioux Experimental Forest, Chippewa National Forest, Minnesota, from 1955–2007 (age 90–142 years).

		PAI volume ($m^3 \cdot ha^{-1} \cdot year^{-1}$)		MAI volume ($m^3 \cdot ha^{-1} \cdot year^{-1}$)	
Source of variation	df	*F*	*P*	*F*	*P*
Stocking level	4	4.99	**0.0179**	5.64	**0.0122**
Age	10	33.69	**<0.0001**	16.48	**<0.0001**
Stocking × age	40	1.04	0.4254	0.46	0.9964
Contrast					
Linear		18.91	**0.0014**	22.24	**0.0008**
Quadratic		0.44	0. 5221	0.07	0.7909
Cubic		0.53	0.4852	0.11	0.7490

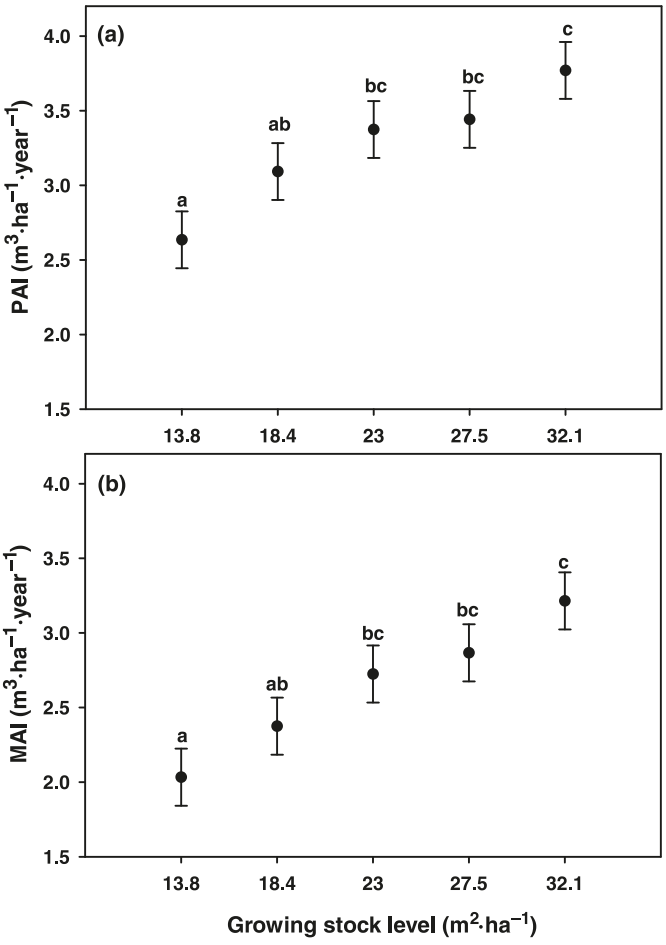


Fig. 3. Mean (*a*) gross periodic annual increment (PAI) and (*b*) gross mean annual increment (MAI) across stocking-level treatments. Values represent least square means and error bars represent one standard error. Values with different letters are significantly different at $P = 0.05$.

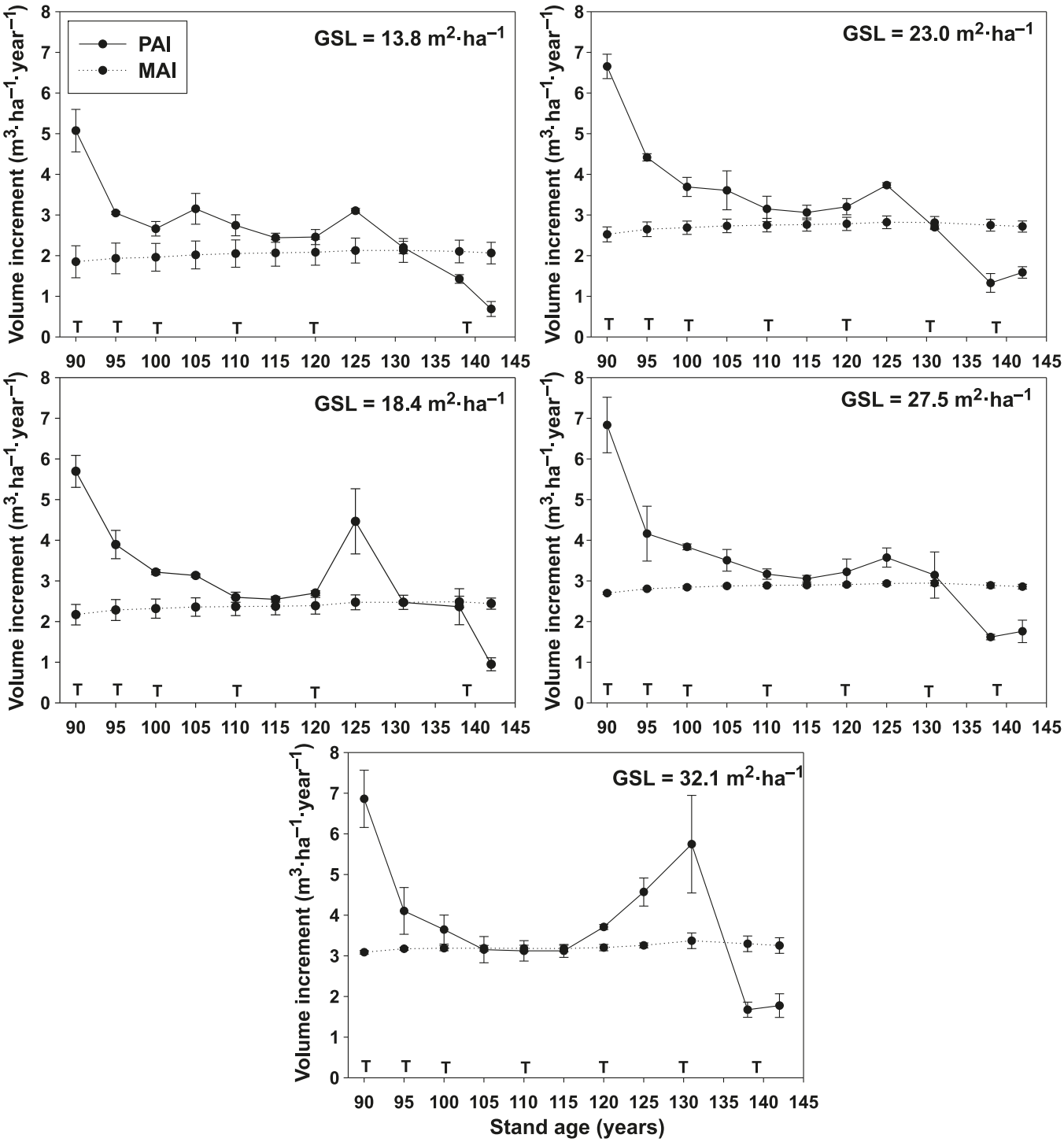
the highest stocking-level treatment (32.1 $m^2 \cdot ha^{-1}$). In addition, the PAI for the 13.8 $m^2 \cdot ha^{-1}$ stocking level was also significantly lower than that for the 23.0 and 27.5 $m^2 \cdot ha^{-1}$ treatments, whereas there were no differences in PAI among the higher stocking-level treatments (Fig. 3, Table 3). PAI increased for the three highest stocking levels during the last measurement interval, likely in response to thinning treatments applied at age 138 years (Fig. 4). A similar increase in PAI was not observed in the lowest stocking levels (Fig. 4). Note, the pronounced increase in PAI observed for the highest stocking-level treatment between ages 125 and 130 years is likely partially related to the mortality of several large trees during a *Diplodia* tip blight (*Diplodia pinea* Grove) outbreak on one of the plots within a treatment unit of this stocking level during this period (J. Elioff, USDA Forest Service, personal communication, 2009). This is reflected in the greater level of variation in PAI during this period (Fig. 4), as well as the higher mean mortality rates within this treatment (Table 2).

Similar to PAI, MAI increased linearly with increased stocking level and was broadly similar across the range of stand ages examined in this study (Figs. 3 and 4, Table 3). As with PAI, the primary differences in MAI existed between the lowest and highest stocking-level treatments. In particular, the MAI for the lowest stocking-level treatment was significantly less than all other stocking levels, with the exception of the 18.4 $m^2 \cdot ha^{-1}$ treatment (Fig. 3). Culmination age for MAI was fairly consistent across stocking levels, with MAI culminating between 130 and 140 years across all treatment levels (Fig. 4).

Discussion

Achievement of more ecologically oriented management objectives, such as the restoration of late-successional forest structure in managed forests, has required the application of silvicultural treatments and approaches often outside of traditional frames of reference (e.g., Lilja et al. 2005; Roberts and Harrington 2008; Bauhus et al. 2009). As such, opportunities to evaluate the long-term impacts of management approaches like extended rotation systems are invaluable for filling in key information gaps on the impacts of these emerging management strategies on stand growth and yield. Notably, the findings of our study for extended rotation red pine systems lend further support to the notion that the use of repeated thinning treatments can maintain greater levels of volume production beyond traditional rotation ages (i.e., 60–100 years; Buckman 2006; Gilmore and Palik 2006). To our knowledge, this is a phenomenon previously demonstrated in only one other North American tree species (coast Douglas-fir; Curtis 1995), yet widely highlighted within European forest systems (Assman 1970; Pretzsch 2005). In

Fig. 4. Gross mean annual increment (MAI) and gross periodic annual increment (PAI) for each red pine growing stock level (GSL) on the Cutfoot Sioux Experimental Forest, Chippewa National Forest, Minnesota. T along the *x* axis indicates the time of thinning treatment application. Error bars represent one standard error.



addition, the positive post-thinning growth responses (based on PAI) we observed for red pine within higher stocking-levels treatments after thinnings applied at age 138 years are consistent with a growing body of literature that has demonstrated the responsiveness of several North American conifer species to density reductions at advanced ages (Youngblood 1991; Latham and Tappeiner 2002; Fajardo et al. 2007). Collectively, these findings highlight the potential for using repeated thinning treatments and extended rotations beyond stand ages of 120 years to simultaneously meet ecological and economic goals within red pine forests.

A primary justification for using extended rotations is the restoration of older forest structural conditions, such as large living and dead trees and well-developed understory layers,

in forests managed for wood production (Curtis 1997; Lindenmayer and Franklin 2002). In our study, the tree size structure and species composition of several of the stands we examined are similar to those documented for old-growth red pine stands within the Great Lakes region (Day and Carter 1990; Zenner and Peck 2009; S. Fraver and B.J. Palik, unpublished data, 2009). In particular, studies in old-growth red pine forests in Minnesota and Ontario have documented large-tree (≥40 cm DBH) densities ranging from 84 to 164 trees·ha^{-1} (Day and Carter 1990; Zenner and Peck 2009; S. Fraver and B.J. Palik, unpublished data) — a range that three of the growing stock levels (18.4, 23.0, and 32.1 m^2·ha^{-1}) fell within in the current study (Table 2). Nonetheless, the managed stands examined in the current study lacked trees in the largest size classes (>60 cm DBH) typically found in old-growth red pine stands (Day and Carter 1990), suggesting that longer rotation lengths may be needed to restore these elements on sites similar to those we examined.

In addition to high large-tree densities, the development of lower canopy strata dominated by a mixture of early to late-successional species, including *B. papyrifera*, *A. rubrum*, *Q. rubra*, and *A. balsamea*, has been documented as a characteristic of old-growth red pine systems in which ground fires are fairly infrequent (Day and Carter 1990; Frelich and Reich 1995; Zenner and Peck 2009). Although treatments were applied at stand age 110 years within the current study to remove ingrowth of these species, the lack of subsequent vegetation control treatments over the past three decades likely led to the development of a lower canopy stratum, particularly within the lowest stocking-level treatments (Fig. 2). If the restoration of these lower strata represents a management objective for red pine systems, the achievement of these conditions may represent a trade-off in terms of stand yield. In particular, the stocking level with conditions best approximating those described for old-growth red pine stands (i.e., large-tree densities and well-developed lower canopy strata; cf. Zenner and Peck 2009) also had the lowest overall yield and volume production rates among stocking levels (Table 2, Fig. 3). In contrast, the stand structures and volume yields observed within the 18.4 and 23.0 m^2·ha^{-1} stocking levels suggest these treatments may represent a potential compromise for simultaneously achieving ecological and traditional production goals in extended rotation systems with red pine. Importantly, the diameters of all red pine remaining within each treatment, especially within the lowest stocking level, were above minimum sawlog specifications for this species, highlighting that all treatments resulted in the concentration of volume on larger and more valuable trees (cf. Burgess and Robinson 1998; Stinson 1999), even if total volume yields were lower within the lowest stocking-level treatments.

Long-term comparisons of growth between thinned and unthinned stands have largely demonstrated that thinning treatments serve to prolong culmination age for MAI (Assman 1970; Curtis 1995; Stinson 1999). Within the context of the current study, we did not have an unthinned control for comparison; however, comparisons with volume increments reported for red pine normal yield tables suggest that the culmination ages observed for the thinned stands in this study (130–140 years) were 40–70 years greater than those for fully stocked stands on similar sites (65–85 years; Brown and Gevorkiantz 1934; Payandeh 1973; Plonski 1974). Correspondingly, it is possible that growth within the stands we examined already culminated prior to the installation of the study at age 85 years. Nonetheless, the culmination ages we observed were similar to those reported for long-term simulations of growth and yield for repeatedly thinned red pine stands (Benzie 1977), highlighting the potential for growing this species on longer rotations while also maintaining high levels of volume production. Moreover, the relatively flat MAI curves displayed for each growing stock level close to and beyond culmination age suggest that rotations could be extended or truncated with little overall impact on stand production in these systems (Curtis and Marshall 1993). Importantly, because the stands examined within this study were largely unmanaged prior to treatment establishment, future evaluations of long-term thinning studies initiated earlier in stand development (<60 years) will be needed to further examine the influence of extended rotation systems on volume production in red pine.

The influence of stocking level on total stand production has been the focus of several long-term silvicultural trials in North America over the last 50 years (Buckman 1962; Curtis et al. 1997; Oliver 2005) and over a century within Europe (Pretzsch 2005). In particular, this work has focused on testing if similar levels of volume production are observed over a wide range of stocking levels ("the Langsaeter hypothesis;" Smith et al. 1997), with recent results from coast Douglas-fir studies suggesting volume production continues to increase with increasing levels of stocking (Curtis et al. 1997). We found some support for a similar linear trend between stand growth (expressed as PAI) and stocking level within the red pine stands examined in this study (Fig. 3); however, the primary differences in PAI were between the lowest and highest stocking-level treatments, with little difference among other stocking levels. As such, the observed relationships between growth and growing stock level observed in this study are likely more consistent with those suggested by the Langsaeter hypothesis in that volume growth appeared relatively constant across the higher stocking-level treatments, with the lowest stocking-level treatment not fully occupying the site (Smith et al. 1997). This finding is consistent with those found by Gilmore et al. (2005) within a younger red pine plantation in which there was little difference in volume production across similar stocking levels to those examined in this study. In contrast, Pretzsch (2005) found in his examination of over 120 years of data from *Picea abies* thinning experiments that older stands tend to have greater PAI values at higher stocking levels. The largely asymptotic density–growth relationships observed in this study are important in the context of restoring late-successional structural attributes to red pine systems, as a greater range of flexibility may exist for choosing stocking levels that promote structural development (see Discussion above) and maintain a high level of stand productivity.

Thinning treatments are increasingly being applied to older forest stands in attempts to increase residual tree vigor, reduce fuel loads, and promote and maintain structural characteristics of old-growth stands in forests managed for wood

(e.g., Latham and Tappeiner 2002; Fajardo et al. 2007; Kolb et al. 2007). A surprising result of recent studies examining the response of older trees to various density manipulations has been the positive growth response of older trees to these treatments (Latham and Tappeiner 2002; Bebber et al. 2004; Powers et al. 2009). The stand-level growth increases observed within the higher stocking-level treatments over the final measurement interval of our study lend further support to the notion that older forest stands are responsive to thinning treatments, despite peaks in stand- and tree-level productivity occurring at younger ages (Ryan et al. 1997; Smith and Long 2001). These findings suggest that the application of thinning treatments after culmination of MAI can be used to maintain relatively high levels of stand production, particularly in cases in which the achievement of ecological objectives (e.g., development of tree diameters >60 cm) require rotation lengths beyond those suggested by peak MAI.

Conclusion

As forest management practices continue to adapt to diversifying objectives, long-term silvicultural experiments, such as the red pine growing-stock-levels experiment we examined, are critical for filling information gaps on how emerging approaches like extended rotations or recovery periods (sensu Franklin et al. 2007) affect stand growth and yield and the achievement of ecological goals. This long-term study has demonstrated that extended rotation systems employing repeated thinning treatments can be effective at both maintaining high levels of stand productivity, as well as restoring late-successional structural elements to managed red pine forests. Nonetheless, our findings suggest that potential trade-offs exist in terms of volume production and restoration of late-successional structural conditions within given stocking levels. For the red pine systems we examined, the use of stocking levels between 18.4 and 23.0 $m^2 \cdot ha^{-1}$ may represent a potential compromise for simultaneously achieving these objectives. In addition, the high densities of large-diameter, high-value trees across treatments highlight the potential for using extended rotation systems to produce stands with higher economic values, particularly through the periodic application of thinning treatments that remove low-quality trees and concentrate volume increment on larger, more valuable trees.

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