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The vertical development of early successional forests in northern Michigan, USA

BRIAN J. PALIK* and KURT S. PREGITZER
Department of Forestry, Michigan State University, East Lansing, MI 48824-1222, USA

Summary

1. Studies have shown that differences in height growth rates are characteristic of tree species that differ in understory tolerance and relative successional status. Less-tolerant species have greater juvenile height growth rates than more-tolerant species and thus, in a mixed-species forest, the former gain an early competitive advantage after a stand-initiating disturbance. Species-level height stratification is the predicted outcome under this model.
2. Silvicultural evidence suggests that a species-level differential growth rate model is idealistic because height stratification among species differing in understory tolerance is not consistently expressed within an even-aged forest. Stratification may fail to develop if individuals of a relatively tolerant species are competitively uninhibited, establish earlier than less-tolerant species, or are of vegetative-origin.
3. The establishment and height growth histories of three species differing in understory tolerance were examined within two forests in northern Michigan, USA. Objectives of the study included: (i) determining if species height stratification paralleling understory tolerance was a characteristic of these forests; (ii) assessing the degree of height variation within species populations; and (iii) determining if species age distributions, changes in individual competitive environments, or regenerative origin influenced population height structures.
4. In both forests, *Populus grandidentata*, an intolerant, early successional species was typically taller than *Quercus rubra*, a mid-tolerant, later successional species, which in turn was taller than *Acer rubrum*, a tolerant, later successional species. However within *Quercus* and *Acer* populations, heights were often highly variable, with some individuals equalling the heights of *Populus*. Age differences had no influence on height patterns
5. Growth rate differences among surviving stems determined species stratification patterns and height variation within populations. *Populus* typically outgrew both *Quercus* and *Acer*, although some individuals of the latter two species had height growth rates equivalent to *Populus*. Most *Quercus* and *Acer* appeared to be of vegetative origin, as were all *Populus* ramets. For individuals of the former two species, potential juvenile height growth rates were likely greater than that of true seedlings, thus allowing some individuals to match growth rates of *Populus*.
6. *Populus* numerically dominated the forests because a large proportion of growing space was occupied by its root systems and ramets, relative to *Quercus* and *Acer*. Vertical domination by *Populus* was apparently the result of competitive inhibition of most, but not all, *Quercus* and *Acer*, not because of inherent, species-specific differences in juvenile height growth rates.

Key-words: even-aged forests, forest disturbance, stand development, tree growth

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* Correspondence author.
Present address: Joseph W. Jones Ecological Research Center, Route 2, Box 2324, Newton, GA 31770, USA.

Introduction

Physiologically or morphologically based differences in height growth rates, particularly juvenile growth rates, are characteristic of tree species that differ in understory tolerance and relative successional status (Loach 1970; Drury & Nesbitt 1973; Marks 1975; Bazzaz 1979; Bormann & Likens 1979, pp. 115–128; Canham & Marks 1985; Tilman 1985, 1988, 1990; Kozlowski, Kramer & Pallardy 1991, pp. 100–102). Species-specific growth rate differences are thought to be expressed even in environments with increased resource availability; for example, following a stand-initiating disturbance (Marks 1975; Bormann & Likens 1979, p. 125; Fig. 1 in Canham & Marks 1985). Under this view, less-tolerant species should have an initial advantage (*sensu* Harper 1977) over more-tolerant species early in even-aged forest development because of inherently faster juvenile height growth rates and should thus achieve competitive (vertical) superiority quickly following a stand initiating disturbance.

Indeed, species height stratification paralleling accepted rankings of understory tolerance and relative successional status is a common characteristic of many even-aged forests (Marquis 1967, 1981; Oliver 1978; Stubblefield & Oliver 1978; Bormann & Likens 1979; Wierman & Oliver 1979; Hibbs 1983; O'Hara 1986; Kelty 1986; Larson 1986; Clatterbuck & Hodges 1988; Foster 1988; Hix & Lorimer 1990; Oliver & Larson 1990; Palik & Pregitzer 1991, 1992b). However, silvicultural studies have shown a population-level, differential-growth-rate model to be idealistic because stratification is often inconsistently expressed within an even-aged stand. In fact, the height range within populations of more-tolerant species can be quite wide, with some individuals attaining heights and height growth rates that equal or exceed those of less-tolerant species (Cayford 1957; Stubblefield & Oliver 1978; Oliver 1980; Guldin & Lorimer 1985; Kelty 1986; Hix & Lorimer 1990).

Stratification may fail to develop when relative spacing between individuals differing in understory tolerance is large (Cayford 1957; Stubblefield & Oliver 1978; Wierman & Oliver 1979; Guldin & Lorimer 1985; Smith 1986; Oliver, Clatterbuck & Burkhardt 1990; Oliver & Larson 1990; Shainsky & Radosevich 1992) or when the competitive environment of an initially suppressed individual of a tolerant species improves during the course of stand development (e.g. see Deal, Oliver & Bormann 1991). Facing less resource-limitation, individuals of initially slower-growing species may be able to catch up with individuals of species with faster juvenile growth rates. Individuals of tolerant species may maintain early height growth rates comparable to less-tolerant species if relative heights of the former initially exceed that of the latter; for example, when the tolerant species is initially present as advanced regeneration (Marquis 1981; Guldin & Lorimer 1985; Kelty 1986; Foster 1988; Deal, Oliver & Bormann 1991), or when it establishes several years earlier than a less-tolerant species (Newton, El Hassan & Zavitkovski 1968; Stubblefield & Oliver 1978; Palik & Pregitzer 1991). By definition, such forests would still be considered even-aged (Smith 1986). Regenerative origin may also influence height relationships because sprouts of hardwood species often have an initial growth advantage over seedlings of the same species (Jensen 1943; Wilson 1968; Oliver 1978; Beck & Hooper 1986). Thus, stratification may be less likely to develop in a forest comprised predominantly of sprout-origin individuals. Given the potential for compensation of species-specific juvenile height growth rate differences, through the mechanisms outlined above, the expression of stratification within a particular forest may depend on stand structure, regenerative-origin, or population age distributions. Few studies have assessed the influence of these compensating mechanisms on the development of vertical structure in even-aged forests.

This study examined the height and age structures of three tree species differing in understory tolerance and relative successional status in two mature forests in northern Lower Michigan that are dominated by *Populus grandidentata* Michx. (bigtooth aspen). These forests are typically viewed as even-aged, having initiated following region-wide logging and repetitive slashed-fuelled wildfires at the turn of the twentieth century (Kilburn 1957, 1960; Graham, Harrison & Westell 1963; Roberts & Richardson 1985). The fires promoted vigorous vegetative regeneration of *Populus* from rapidly spreading clonal root systems (Barnes 1966). Initial observations indicated that *Quercus rubra* L. (red oak) and *Acer rubrum* L. (red maple) were the only additional tree species of consistent numerical importance in the overstories of the particular forests studied. Limited evidence suggests that many *Quercus* and *Acer* in mature *Populus*-dominated forests may also be of vegetative origin, having regenerated after fire from stumps remnant from the predisturbance forest (Graham, Harrison & Westell 1963; Roberts & Richardson 1985). The three species differ in understory tolerance and relative successional status; from very intolerant early-successional *Populus*, to mid-tolerant, relatively later-successional *Quercus*, to tolerant later-successional *Acer* (Spurr & Barnes 1980). Objectives for the study included:

1. determining if species height stratification paralleling understory tolerance occurred in these forests;

2. assessing the degree of variability in heights within species populations;

3. determining if age differences, regenerative mode, or changes in an individuals competitive environment had any influence on population height structures; and

4. assessing the degree to which vertical structure in the forests examined deviated from that expected under a model of species-level differential height growth rates.

Study locations

Research was conducted within the Huron National Forest in north-eastern Lower Michigan (44°15′–45°00′N, 83°15′–84°45′W) and the University of Michigan Biological Station in the extreme north-western portion of Lower Michigan (45°40′N, 84°40′W). The two study areas are separated by approximately 110 km. Superficial geology of both study areas consisted primarily of deep outwash sands overlaying till deposits (Cooper 1981; Padley 1989). Soils throughout the majority of both study areas were classified as Entic Haplorthods (Cooper 1981; Lapin 1990; Soil Conservation Service 1991; Michigan State University, Forestry Department data file). Detailed descriptions of the physiographic and climatic settings of the two study areas are found in Palik & Pregitzer (1992a).

Overstory composition of the two study areas was similar (Palik & Pregitzer 1992a). Mean relative density of *Populus* was approximately 60% at both locations. Mean relative densities of *Quercus* and *Acer* were 15% and 25%, respectively, in the Huron forest, and 8% and 10%, respectively, at UMBS. Additional overstory species that occurred infrequently in some of the UMBS plots included *Pinus resinosa* Ait., *Pinus strobus* L. and *Betula papyrifera* Marsh. Mean (±SE) total basal area and total density were both substantially higher in the Huron forest ($41{\cdot}6 \pm 2{\cdot}0\,\mathrm{m^2\,ha^{-1}}$ and 1117 ± 48 stems $\mathrm{ha^{-1}}$, respectively), than at UMBS ($28{\cdot}6 \pm 1{\cdot}5\,\mathrm{m^2\,ha^{-1}}$ and 890 ± 44 stems $\mathrm{ha^{-1}}$, respectively).

Methods

STAND AND PLOT SELECTION

Populus, *Quercus* and *Acer* population structures were examined within five stands at Huron and four stands at UMBS. Stands were selected from larger data pools at both locations (Lapin 1990; Michigan State University, Forestry Department data file). All stands within a study area belonged to similar ecological land classification units (following Barnes *et al.* 1982; Pregitzer & Barnes 1984). Selected stands met the following criteria: (i) minimum size of 1 ha; (ii) free from obvious disturbance since initiation; and (iii) 0–5% slopes. The distance between stands within each study area ranged from 1 to 14·5 km.

Four circular plots were randomly located within each stand. The plot sizes were $272\,\mathrm{m^2}$ at Huron and $475\,\mathrm{m^2}$ at UMBS. A larger plot size was used at UMBS so that a similar number of *Quercus* and *Acer* stems might be sampled as in the higher density Huron forest. The only criterion for plot selection was that, if possible, at least one overstory (d.b.h. >10 cm) *Quercus* and *Acer* genet occur in each plot. Given this criterion, plots were never rejected because of a lack of *Acer*. Initial locations for two of the 36 plots were rejected because of a lack of *Quercus*. The location of one of these plots was retained because an additional randomly selected plot did not contain any *Quercus*. Plots, rather than stands, were used as replicates in all subsequent statistical analyses. Replicating on plots was justified because sampling was conducted within forest landscapes characterized by relatively homogeneous composition, physical site characteristics, and disturbance history. Stands were simply subjective units defined by harvesting patterns or road locations within each landscape; they were not defined by any obvious criterion which may have influenced overstory development.

STEM SAMPLING

On each plot, selected *Populus* and all *Quercus* and *Acer* at least 1·5 m tall were destructively sampled as part of a related study of stand development. This paper reports on the development of the initial, post-disturbance cohorts of *Populus*, *Quercus* and *Acer* at each study location. The youngest *Quercus* and *Acer* in these cohorts established several decades prior to the next oldest individuals of the species (Palik & Pregitzer 1992b, and unpublished data).

For *Quercus* and *Acer*, only the tallest ramets were sampled from multi-stemmed genets. For *Populus*, one individual from the dominant crown class (all ramets were dominant or codominant) was randomly selected (rejecting decaying ramets) and destructively sampled on each plot. Sampling intensity for *Populus* was much lower than for other species because little height variation was observed within a plot and little age variation among ramets was expected. Both total heights of additional *Populus*, estimated with a clinometer, and ages of the sampled *Populus*, substantiated these expectations (see Results).

All sampled stems were felled at 0·5 m and total heights mere determined. Stumps and stems were marked at 25-cm intervals from the base to 2 m and at 1 m intervals thereafter. Marking continued to the 1-m multiple closest to the end of the dominant leader. Stem sections were cut at ground level and at each measurment interval up to a 3-cm-diameter top. The regenerative-mode of all genets (sprout or seedling) was assessed when possible.

STEM ANALYSIS

The terminal leader of each stem was aged in the field by counting the number of terminal bud scale scars preceding each height interval. Stem sections were removed to the lab where they were sanded to a smooth surface and wetted to aid ring examination.

Ages were determined by counting ring number on at last two radii (typically a long and short axis on oblique-shaped stems) of each section under a dissecting microscope. The oldest age of each section, if the counts differed, was recorded. Precision of ring counting was assessed by periodically recounting 20% of the stem sections from lots of 15–25 sections each. Recounts seldom differed by more than 1 year. Section ages were used to determine time of establishment and to reconstruct the height growth trajectories of each sampled individual. Stem heights at 10 year stand age intervals were derived from the growth trajectories (see Data analysis below). In some instances interpolation of stem height at a given stand age was required since the stem sampling method controlled stem height but not age. When this was required, the shapes of age–height plots for the individuals involved were examined to ensure accurate determination of height at the 10-year stand age of interest.

The age–height trajectories of each *Quercus* and *Acer* population were examined for evidence of suppression or release that might reflect changes in an individuals's competitive environment or ability. These episodes were defined following a procedure similar to one suggested for radial growth analysis (Lorimer 1984). Height trajectories were examined for obvious slope changes that persisted for at least 15 years and resulted in height growth rates that were minimally 50% above or below growth rates for the previous 15-year period. The 15-year minimum was used to filter out short periods of increased or reduced growth that might be related to factors other than a change in competitive status, such as climatic variation or insect defoliation. The 50% minimum growth rate change was used to filter out slower declines in height increment that occur as a stem matures (Oliver & Larson 1990; Zeide 1991).

DATA ANALYSIS

Total heights were compared among species over time using random-order cross-over, split-block repeated-measurement analysis of variance. For these analyses, plots were considered blocks, species were considered random-order 'mensurational treatments' within blocks, and time was the repeated measure. With this design, the overall effects of species can be analysed as a randomized block design, because no nuisance trends are associated with a random sequence of 'treatments' within a block (Gill 1978).

Variances in height over time were often heterogeneous within a species ($F_{\max}$-test $P < 0{\cdot}2$). Additionally, the correlation structure of most data sets was not homogeneous across time (sphericity assumption rejected at $P = 0{\cdot}25$; Gurevitch & Chester 1986). In most cases, variances were homogeneous among species at specific times. For some data sets, log or square-root transformations were used to homogenize variances over time (and within time when required). In some instances these transformations were effective at homogenizing variance over time but resulted in increased heterogeneity among variances within time and lessened the normality of residuals. When this was the case, untransformed data were analysed using conservative adjustments for heterogeneous variance–covariance structure as described in the next two paragraphs. All of the final data sets used met the assumption of normality of residuals (Shapiro–Wilke test, $P \geq 0{\cdot}1$).

When variance–covariance structure was heterogeneous over time, *F*-tests for the overall effects of time and time–species interactions were evaluated using the highly conservative Greenhouse–Giesser degrees of freedom (Gill 1978). This test reduces the degrees of freedom for time from $(b-1)$, $(b-1)(r-1)(t-1)$ to 1, $(r-1)(t-1)$, where b is the number of time periods, r is the number of blocks, and t is the number of treatments. For time–species interaction, degrees of freedom are reduced from $(b-1)(t-1)$, $(b-1)(r-1)(t-1)$ to $(t-1)$, $(r-1)(t-1)$. Box's adjusted degrees of freedom was used to evaluate overall *F*-tests for species effect when time–species interaction was not significant, but variances among species were heterogeneous (Gill 1978).

Individuals species means at specific time periods were separated using Bonferroni contrasts (two-sided) to test a-priori hypotheses regarding height patterns based on understory tolerance differences among species. We tested whether (i) *Populus* (intolerant) was taller than *Quercus* (mid-tolerant) at a specific time and (ii) *Quercus* was taller than *Acer* (tolerant) at the same time. These contrasts were designed to allow ranking of height patterns in *Quercus* and *Acer*, relative to *Populus*. We are not implying that *Quercus* may have been consistently influencing the growth of *Acer* throughout the forests. Variances of contrast means and degrees of freedome were adjusted, according to Gill (1978), when variances were heterogeneous within specific times (some cases) or variance–covariance matrices were not uniform across time (most cases). For all statistical tests, a type-one error probability of 0·05 was considered significant.

Results

REGENERATIVE MODES

The origin of *Quercus* and *Acer* stems was assessed by assigning genets to one of the following categories:

1. vegetative origin (multi-stemmed genets);

2. high probability of vegetative origin (single-stemmed genets with highly convoluted or crescent shaped stem bases, both of which may be indicative of development around remnant stumps);

3. seed origin (single-stemmed genets with uniform, approximately circular stem bases).

Ninety per cent of the *Acer* genets in both forests were apparently of vegetative origin and 90% of these were multi-stemmed (Table 1). Those genets apparently of seed origin were restricted to the smallest height classes. Apparent sprout-origin genets were found in a wide range of height classes. All of the tallest *Acer* sampled in this study appeared to be of vegetative origin, however not all of these were multi-stemmed. Eighty-four per cent of the *Quercus* genets in the Huron forest appeared to be of vegetative origin; two-thirds of these were multi-stemmed (Table 1). At UMBS, only 66% of the *Quercus* genets appeared to be of sprout origin and only one-third of these were multi-stemmed (Table 1). Both apparent sprout-origin and seed-origin *Quercus* occurred in a range of height classes, including some of the tallest individuals, but apparent sprout-origin genets were not found in the smallest height classes. Most *Quercus* did have high early radial growth rates, relative to later years, including those that appeared to be of seed origin (B.J. Palik & K.S. Pregitzer, unpublished data). Rapid early radial growth suggests that even apparent seed-origin *Quercus* may have been vegetative sprouts (Sander 1990).

POPULATION AGE AND HEIGHT STRUCTURES

All sampled stems in the Huron forest established, or resprouted, within a 10-year period following disturbance *c.* 70 years prior to sampling. The ages of the 20 sampled *Populus* differed by no more than 4 years. In the UMBS forest, stand ages ranged from 74 to 82 years. Within stands, *Populus* ages differed by 4–10 years. The age distributions for all species combined ranged from 4 to 15 years, with the exception of one plot containing a *Quercus* that was *c.* 20 years older than the oldest of its associates. In both study areas, the youngest individuals were always the slowest-growing *Acer*. These individuals may have been several years older than they appeared if they had dropped rings near their stem bases, as suppressed stems sometimes do (Larson 1956; Bormann 1965). Their influence on plot age distributions was probably minimal because mean ages among species were similar and not significantly different at either location (Table 2). For both forests power to detect a mean age difference of ±2 years was high (Table 2).

Mean heights of *Populus*, *Quercus* and *Acer* (all individuals pooled by species on a plot), at 10-year-age intervals stand are shown in Fig. 1. These comparisons were extended to 70 years, the maximum 10-year interval shared by all stands within both study locations. In the Huron forest, species–time interaction was significant ($P < 0{\cdot}0001$), indicating that temporal patterns of cumulative height increase differed among species. Within time periods, heights among species were significantly different at all stand ages ($P < 0{\cdot}05–0{\cdot}01$) except 10 years ($P > 0{\cdot}05$). The differences followed the predicted order based on shade tolerance; *Populus* was taller then *Quercus* which in turn was taller than *Acer*. At UMBS, species–time interaction was not significant ($P = 0{\cdot}096$), indicating that temporal patterns in height increase were similar among species. The overall species effect was significant ($P < 0{\cdot}0001$). Within time, *Populus* was taller than *Quercus* at almost all time periods (Fig. 1); however, the differences were significant only at stand ages of 60 and 70 years ($P < 0{\cdot}05$). *Quercus* was significantly taller than *Acer* at all 10-year intervals ($P < 0{\cdot}01$). The relative height relationships among species remained unchanged at the time of sampling in the older UMBS stands (data not shown).

POPULATION HEIGHT VARIATION

The examination of species mean heights over time (Fig. 1) suggests stratification of *Populus* over both *Quercus* and *Acer* in the Huron and UMBS forests. However, within plots, individual heights for the latter two species were often quite variable. This variability can be seen by examining time–height

Table 1. Percentage of *Quercus rubra* and *Acer rubrum* genets in the Huron and UMBS forests, northern Lower Michigan regenerating by the following modes: vegetative (multi-stemmed genets); ?vegetative (single-stemmed genets with highly convoluted stem bases); seedling (single-stemmed genets with uniform, circular stem bases)

		Regeneration method		
		Vegetative	?Vegetative	Seedling
Huron				
Querus	($n = 75$)	57	27	16
Acer	($n = 92$)	83	6	11
UMBS				
Quercus	($n = 35$)	22	44	33
Acer	($n = 69$)	78	11	11

Table 2. Mean (±SE) ages of *Populus grandidentata*, *Quercus rubra* and *Acer rubrum* in plots at the Huron and UMBS forests in northern Lower Michigan, USA. These were compared statistically using Friedman's randomized block method. The power to detect a mean age difference of ±2 years (at $\alpha = 0{\cdot}05$), P(±2 years), was also calculated

	Huron	UMBS
Mean age (years)		
Populus	65·9 ± 0·2	73·3 ± 1·1
Quercus	65·4 ± 0·2	73·8 ± 1·2
Acer	65·8 ± 0·2	71·0 ± 1·1
n	19	16
P	0·368	0·051
P(±2 years)	0·99	0·82

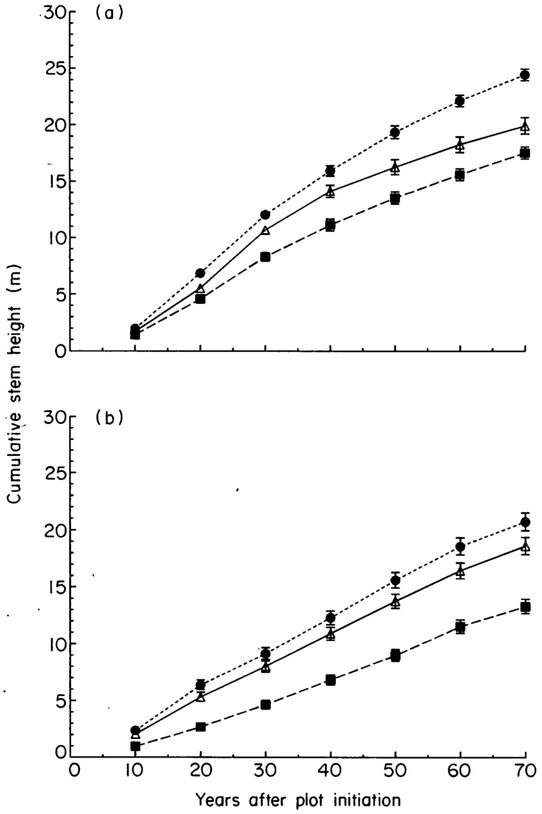

Fig. 1. Heights of *Populus grandidentata* (●), *Quercus rubra* (△) and *Acer rubrum* (■) at 10-year stand-age intervals in (a) the Huron forest and (b) the UMBS forest. Huron values are means (±SE) of 19 observations. UMBS values are back-transformed means (±95% confidence intervals) of 16 square-root-transformed observations. *Q. rubra* and *A. rubrum* values are the means of all individuals pooled by species on each plot.

reconstructions for several of the plots (one randomly selected from each stand) in Fig. 2. In the Huron forest, the mean (±SD) plot-level height ranges of *Quercus* and *Acer* were 8·7 ± 3·2 m and 7·3 ± 0·4 m, respectively. At UMBS, the analogous ranges were 5·4 ± 3·4 m and 5·8 ± 2·4 m. These height ranges are conservative because some of the shorter ramets came from genets having additional shorter, slower-growing but similar-aged ramets. Mean ages of individuals at the extremes of the height ranges on a plot were not statistically significantly different for all species–study-area combinations (Table 3). Power to detect a mean difference of ±2 years (at alpha = 0·05) was high for all comparisons, except *Acer* at UMBS (Table 3).

There was less variability in the heights of *Populus* within plots. In the Huron forest, the mean (±SE) height at the time of sampling of the 20 *Populus* used in stem analysis was 24·5 ± 0·5 m. The mean height of the additional *Populus*, estimated with a clinometer, was 25·2 ± 1·2 m. The mean difference between estimates was not significantly different from zero (paired *t*-test, $P = 0{\cdot}773$). In the UMBS forest, the mean height of the 16 sampled *Populus* was 21·7 ± 0·3 m, while the mean height of the additional *Populus* was also 21·7 ± 0·5 m. Again, the paired heights were not significantly different ($P = 0{\cdot}970$).

Many plots had at least one *Quercus*, and some had an *Acer*, that approached the height of *Populus* at 70 years (see Fig. 2).The potential for *Quercus* and *Acer* to attain dominant canopy positions was assessed by tabulating the number of individuals on each plot that were within 2 m of (or exceeded) *Populus* in height at the time of sampling (Table 4). In the Huron forest, 37% of the *Quercus* ramets had total heights that approached or exceeded the heights of *Populus*, compared to 13% for *Acer*. At UMBS, 53% of the *Quercus* ramets approached or exceeded the heights of the *Populus*, while only 6% of the *Acer* ramets were this tall.

Similarity in height growth rates of *Populus* and dominant *Quercus* and *Acer* (the tallest stem from each of the plots that contributed individuals to Table 4) was assessed by comparing mean cumulative heights between species pairs at 10 year stand age intervals (Fig. 3). There were only three plots with dominant *Acer* at UMBS, too few to be included in these analyses. However, the mean total height of these individuals at the time of sampling was only 0·5 m less than *Populus* from the same plots (Fig. 3).

Time–species effects were non-significant in both *Populus–Quercus* comparisons (Huron, $P = 0{\cdot}086$; UMBS, $P = 0{\cdot}935$), and in the *Populus–Acer* comparison in the Huron forest ($P = 0{\cdot}077$), indicating that the shapes of the cumulative height trajectories were similar between species pairs. Overall species effects were non-significant in both *Populus–Quercus* comparisons (Huron, $P = 0{\cdot}302$; UMBS, $P = 0{\cdot}550$), indicating a similarity in heights at each 10-year plot-age interval. Power to detect a 1-m mean height difference (at $\alpha = 0{\cdot}05$) was high for both comparisons (Huron = 0·87; UMBS = 0·94). Overall species effect was significant for the *Acer–Populus* comparison in the Huron forest ($P = 0{\cdot}006$), although height differences were clearly minor (Fig. 3). For example, heights within time periods were significantly different only at 20 and 30 years after plot initiation ($P < 0{\cdot}05$). However, power to detect a 1 m mean height difference (at $\alpha = 0{\cdot}05$) was moderately low (0·29).

Mean ages of *Populus* and the other species in each of the above comparisons were similar (Table 5). The age difference between *Populus* and the small number of dominant *Acer* at UMBS was also minimal (Table 5). The age similarities, combined with the similarity of heights between species at a plot age of 10 years (Fig. 3), indicates that juvenile height growth rates were similar between species. In other words, dominant *Quercus* and *Acer* were initially shorter and then simply caught up later in stand development.

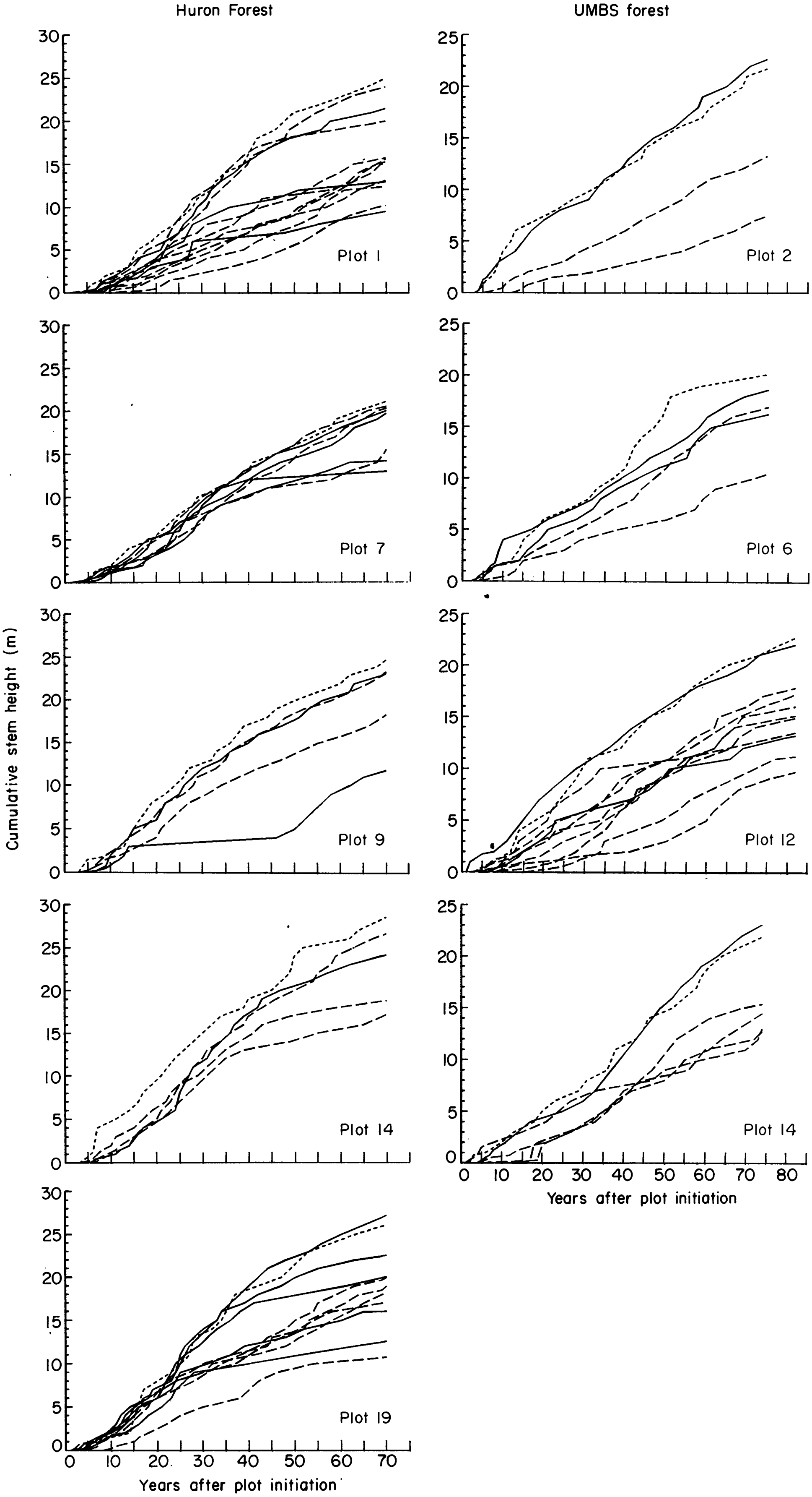

Fig. 2. Height growth reconstructions of *Populus grandidentata* (----), *Quercus rubra* (———) and *Acer rubrum* (– – – –) within randomly selected plots from the Huron and the UMBS forests. Each line represents an individual stem.

Table 3. Mean (±SE) ages of individual *Quercus rubra* and *Acer rubrum* at the extreme height ranges on plots at the Huron and UMBS forests in northern Lower Michigan, USA. These were compared statistically using paired *t*-tests, except the UMBS *Quercus* data, for which a Wilcoxon test was used. The power to detect a mean age difference of ±2 years (at α = 0·05), P(±2 years), was also calculated

	Age (years)				
	Tall	Short	*n*	*P*	P(±2 year)
Huron					
Quercus	65·5 ± 0·3	65·6 ± 0·5	16	0·837	0·940
Acer	66·2 ± 0·4	64·8 ± 0·6	19	0·099	0·780
UMBS					
Quercus	72·5 ± 1·5	72·1 ± 3·9	8	>0·10	0·800
Acer	72·9 ± 1·6	70·0 ± 1·2	15	0·156	0·50

Table 4. Mean (±SE) number of genets ha^{-1} and total number of *Quercus rubra* and *Acer rubrum* genets sampled (pooled across plots, in parentheses) in Huron Forest ($n = 20$ plots) and UMBS forest ($n = 16$ plots) in northern Michigan, USA. Genets are grouped according to height class: dominant *Quercus* and *Acer* were those that exceeded or equalled the height of *Populus grandidentata* on the same plot (≥*Populus*) or approached that height by within 0·5–1 m or 1–2 m; subdominant *Quercus* and *Acer* were more than 2 m shorter than *Populus* on the same plot

	Genet density (ha^{-1})	
Height class	*Quercus*	*Acer*
Huron forest		
dominant	52 ± 10 (28)	22 ± 6 (12)
≥*Populus*	24 ± 9 (13)	12 ± 5 (6)
0·5–1 m	10 ± 4 (5)	6 ± 3 (3)
1–2 m	18 ± 6 (10)	6 ± 3 (3)
subdominant	84 ± 9 (47)	149 ± 15 (80)
total cohort	136 ± 20 (75)	171 ± 21 (92)
UMBS forest		
dominant	25 ± 6 (19)	5 ± 3 (4)
≥*Populus*	13 ± 5 (10)	4 ± 3 (3)
0·5–1 m	5 ± 2 (4)	—
1–2 m	7 ± 3 (5)	1 (1)
subdominant	25 ± 6 (16)	87 ± 13 (65)
total cohort	50 ± 9 (35)	92 ± 14 (69)

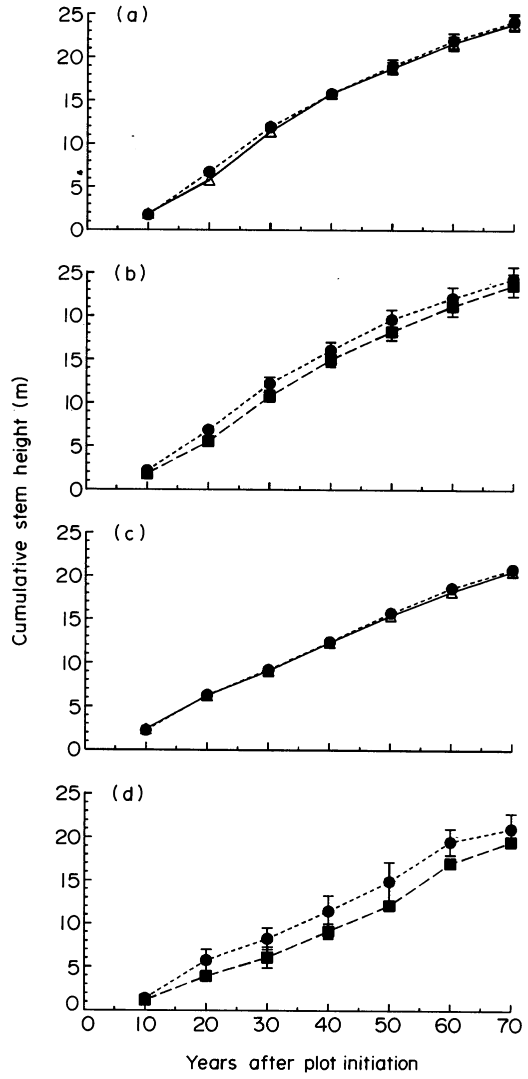

Fig. 3. Heights of *Populus grandidentata* (●) compared to dominant *Quercus rubra* (△) or *Acer rubrum* (■) at 10-year stand-age intervals in the Huron forest (a, b) and the UMBS forest (c, d). Huron values are back-transformed means (±95% confidence intervals) of 16 log(y + 1)-transformed observations for *Q. rubra*, and 10 log(y + 1)-transformed observations for *A. rubrum*. UMBS values are means (±SE) of 13 and 3 observations for *Q. rubra* and *A. rubrum*, respectively.

INDIVIDUAL HEIGHT GROWTH TRAJECTORIES

Each sampled *Populus*, *Quercus* and *Acer* ramet was assigned to one of four categories that described their patterns of individual height growth and reflected changes in an individuals competitive environment or ability. The *suppressed* category included stems that had at least one period of greatly reduced growth. The *released* category included stems that had at least one period of greatly increased growth. The *constant* category included stems showing no periods of major suppression or release in height growth (although actual growth rates were not constant over the entire life of the individual). Finally, the *combination* category included individuals whose cumulative height trajectories indi-

Table 5. Mean (±SE) ages of dominant *Quercus rubra* and *Acer rubrum* compared to the mean (±SE) ages of *Populus grandidentata* ramets on plots at the Huron and UMBS forests in northern Lower Michigan, USA. These were compared statistically using paired *t*-tests, except the UMBS *Quercus–Populus* comparison, which was made using a Wilcoxon test. The power to detect a mean age difference of ±2 years (at $\alpha = 0{\cdot}05$), P(±2 years), was also calculated

	Age (years)	*Populus* comparison	*n*	*P*	P(±2 years)
Huron					
Quercus	65·4 ± 0·3	65·9 ± 0·2	16	0·289	0·990
Acer	66·5 ± 0·5	66·1 ± 0·2	10	0·628	0·900
UMBS					
Quercus	73·0 ± 0·8	72·0 ± 1·2	13	>0·10	0·800
Acer	71·0 ± 4·5	73·3 ± 4·5	3	NA	NA

cated at least one major suppression and release. Examples of suppressed and released stems can be seen in Fig. 2 (e.g. Fig. 2a, Plot 9, the shortest *Quercus* and Fig. 2b, Plot 12, the third-shortest *Acer*).

None of the *Populus* ramets in the Huron forest showed any evidence for a suppression or release (Table 6). Three of the 16 *Populus* ramets (18%) in the UMBS forest did show evidence for a suppression (Table 6). The mean (±SE) growth rate reduction for these stems was 73 ± 9% and began at stem ages of 15, 16 and 47 years. The growth patterns of these stems were unique, relative to suppressed *Quercus* and *Acer* at UMBS (see below), in that the suppressed *Populus* had been growing exceptionally fast prior to suppression, compared to non-suppressed *Populus* from the same stands (e.g. Fig. 2b, Plot 6). These suppressions were therefore more of a reduction of growth rates to a value closer to the norm, rather than an actual inhibition. Three (18%) *Populus* in the UMBS forest showed evidence for a release (Table 6). The mean growth rate increase for these stems was 177 ± 108% and occurred between stem ages of 20 and 40 years.

The majority of dominant *Quercus* and *Acer* at both locations showed no evidence for either suppression or release (Table 6). The few that were suppressed, all *Quercus*, had growth rate reductions of *c.* 60% that began at a stem age of 40 years or later. Only three of the dominant individuals were released (Table 6). The increase in growth rates after release averaged about 120% and occurred early, around a stem age of 15 years.

Between 40 and 72% of the subdominant *Quercus* and *Acer* showed some evidence for large growth-rate changes (Table 6). Most of these were suppressions. The growth-rate reductions averaged around 70% and occurred between stem ages of 30–50 years. The mean height growth rate increase for the released stems, most of which were *Acer*,

Table 6. Height growth patterns of *Populus grandidentata*, *Quercus rubra* and *Acer rubrum* in the Huron and UMBS forests in northern Lower Michigan. The constant category includes ramets with no evidence for major suppression or release; the suppressed category includes ramets with evidence for one major suppression; the released category includes ramets with evidence for one major release; the combination category includes ramets with evidence for one or more major suppressions and releases. Dominant *Q. rubra* and *A. rubrum* were those that exceeded, equalled (±0·5 m) or approached (0·5–2·0 m shorter) the height of *P. grandidentata* from the same plot; subdominant *Q. rubra* and *A. rubrum* were those more than 2 m shorter than *P. grandidentata* from the same plot

		Percentage of total			
		Constant	Suppressed	Released	Combination
Huron forest					
Populus	(*n* = 20)	100	–	–	–
Quercus					
dominants	(*n* = 28)	71	21	4	4
subdominants	(*n* = 47)	28	60	6	6
Acer					
dominants	(*n* = 12)	100	–	–	–
subdominants	(*n* = 80)	49	35	10	6
UMBS forest					
Populus	(*n* = 16)	75	6	6	12
Quercus					
dominants	(*n* = 19)	95	5	–	–
subdominants	(*n* = 16)	50	44	6	–
Acer					
dominants	(*n* = 4)	75	–	25	–
subdominants	(*n* = 65)	61	17	11	11

was over 200%, but was highly variable. Most releases occurred around a stem age of 30 years.

The growth rate potential of suppressed and released *Quercus* and *Acer* from the subdominant height classes was assessed by comparing growth rates of these stems to that of *Populus* from the same plot, over the same stem ages prior to suppression or subsequent to release. Growth rates were considered equivalent if they were within ±0·03 m/year (total heights differing by <2 m at a stem age of 65 years). Approximately 50% (15 stems) of suppressed *Quercus* in the Huron forest and 30% (2 stems) at UMBS were growing at rates equivalent to *Populus* prior to suppression (Table 7). A small percentage (≤16%) of suppressed *Acer* in both forests (3–4 stems) was growing at rates similar to *Populus* prior to suppression (Table 7). Examples of suppressed *Quercus* and *Acer* having initial growth rates equivalent to *Populus* can be seen in Fig. 2. All of the relatively few released *Quercus* in both forests (6 and 1 stems at Huron and UMBS, respectively) had height growth rates after release equivalent to *Populus* (Table 7). Approximately 40% of released *Acer* in both forests (6 stems) had height growth rates equivalent to *Populus* after release. These results suggest that competitive environments or abilities of many subdominant *Quercus* and *Acer* changed over the course of stand development and, in some instances, initial height growth rates prior to suppression, or later growth rate after release, equalled height growth rates of *Populus*.

Discussion

POPULATION HEIGHT STRUCTURES

In both of the forests examined in this study, populations of *Populus grandidentata*, an intolerant, early-successional species were, on average, taller than populations of *Quercus rubra*, a mid-tolerant, relatively later-successional species, which in turn were taller than populations of *Acer rubrum*, a tolerant, later-successional species, at least after the first several decades of stand development. Stratification resulted from species-specific differences in height growth rates, with population age differences having little or no influence on height structures. These results contrast with those from an earlier study which demonstrated that mean age differences among species could influence the development of height stratification in a *Populus* dominated forest that initiated after major disturbance (Palik & Pregitzer 1991).

Although not quantified in this study, differential mortality among species also contributed to height stratification. *Populus* ramet density is known to be high immediately following major disturbance (e.g. >24 000 ramets ha^{-1} following clearcutting and burning; Scheiner *et al.* 1988). Unable to survive even mild suppression (Laidly 1990), most ramets die following the onset of crown differentiation. Thus, in the current study, only dominant–codominant ramets were found in the mature forests. In contrast, many slower growing *Quercus* and *Acer* were able to survive varying degrees of suppression, thereby lowering heights and height growth rates for these species relative to *Populus*.

Table 7. Percentage of suppressed or released subdominant (including all stems more than 2 m shorter than *P. grandidentata* from the same plot) *Quercus rubra* and *Acer rubrum* in the Huron and UMBS forests that had height growth rates equal to or greater than those of *Populus grandidentata* prior to a suppression or subsequent to a release (equivalent growth rate= ±0·03 m/year). Total numbers in the catagory are given in parentheses (note: total may exceed sums of the suppressed+combination or released+combination catagories from Table 3 if a stem in the combination catagory had multiple suppressions or releases

	Quercus	*Acer*
Huron		
suppressed	48 (31)	12 (33)
released	100 (6)	40 (15)
UMBS		
suppressed	29 (7)	16 (19)
released	100 (1)	43 (14)

Within plots, the heights of the surviving *Populus* ramets were often similar. In contrast, a predictable height was not an attribute of surviving stems within *Quercus* and *Acer* populations. Heights often ranged widely and the variation was clearly not related to age. In fact, the ages of individuals differing by up to 15 m in height were similar. Obviously, height growth rates of similar-aged individuals varied widely within *Quercus* and *Acer* populations, so much so that some individuals had height growth rates, including juvenile rates, equivalent to *Populus*. Individual height growth trajectories indicated that many shorter *Acer* and *Quercus* genets in both forests experienced height growth suppression, beyond that which normally develops as a stem ages (Oliver & Larson 1990; Zeide 1991). Some of these stems also had juvenile growth rates comparable to *Populus*.

While these results demonstrate that species-specific differences in height growth rates typically led to stratification of surviving *Populus* over *Quercus* and *Acer*, they also suggest that lower juvenile height growth rates were not inherent attributes of the latter two species *per se*. We suggest that the typically reduced growth rates of *Quercus* and *Acer* resulted from competitive inhibition and/or reduced competitive ability of individual genets. Inhibitory influences were spatially and temporally variable, as indicated by the extreme variation in heights within *Quercus* and *Acer* populations.

Early inhibition was not a consistent feature of

Quercus and *Acer* populations, probably because of spatial variation in competitive environments. For example, local density variation, by its effect on crown exposure, root crowding, or even direct physical abrasion of soft terminal leaders can result in differential plant growth performance both within and among species populations (Cayford 1957; Ross & Harper 1972; Harper 1977; Oliver 1978; Wierman & Oliver 1979; Weiner 1984; Guldin & Lorimer 1985; Silander & Pacala 1985; Kelty 1986; Goldberg 1987; van der Meijden 1989; Hix & Lorimer 1990; Oliver, Clatterbuck & Burkhardt 1990). In the current study, the tallest *Quercus* and *Acer* may have been in relatively uncontested sites throughout stand development. The fact that most dominant *Quercus* and *Acer* were not initially suppressed, but rather, always grew at rates comparable to *Populus* suggests this was the case.

Reduced competitive ability may be a function of mode of regeneration, because within species, sprout-origin individuals characteristically out-grow similar aged seedling-origin individuals (Jensen 1943; Wilson 1968; Oliver 1978; Beck & Hooper 1986). An intermix of seedling- and sprout-origin individuals could lead to height growth-rate variation. However, in the current study, most *Quercus* and *Acer* genets were apparently of sprout-origin. Although some larger *Quercus* had stem morphologies suggesting seedling-origin, no obvious remnant individuals were found in any of the stands that might have acted as seed sources (also true for *Acer*). No cutting has occurred in any of the stands since they initiated, so remnant *Quercus* and *Acer* seed trees, if they existed, should have been apparent. It is likely that few seed-bearing trees existed for either species at the time the stands initiated, given the frequency and extent of post-logging fires in the region (Kilburn 1957, 1960; Pyne 1982, pp. 199–218). Of course, the potential for long-distance dispersal of acorns cannot be ruled out (Darley-Hill & Johnson 1981).

Even if all *Quercus* and *Acer* were of sprout-origin, the age and size of the originating stumps could have influenced early ramet growth rates and therefore competitive ability. For example, in *Quercus*, sprout height growth rate increases with stump diameter (Sander 1971) and size of advanced regeneration (Sander 1972). In *Acer*, younger stumps have higher sprout height growth rates than older stumps (Solomon & Blum 1967). Additionally, ramet number may affect individual growth rates and this in turn may be related to parent stump vigour or size (Solomon & Blum 1967; Johnson 1975; Stroempl 1983). In the current study, *Quercus* and *Acer* genets that always grew slower than *Populus* may have developed from physiologically inferior root systems and were therefore at an initial competitive disadvantage.

The shorter mean height of *Populus*, *Quercus* and *Acer* at UMBS, relative to the Huron forest at comparable stand ages, undoubtedly reflects the influence of differences in site quality on height growth rate (Hix & Lorimer 1990). However, the low number of dominant *Acer* at UMBS, relative to the Huron forest, may not. The Huron plots that were most similar to those at UMBS, in terms of total overstory basal area and density, and *Populus* site index (Palik & Pregitzer, unpublished data), contained fast-growing, dominant *Acer*, while some of the apparently more productive Huron plots did not. These results suggest that inherently slower growth rates of *Acer* populations on the poorer UMBS sites were not solely responsible for the low number of dominants in this forest.

A MODEL FOR THE DEVELOPMENT OF DOMINANCE

Several analyses of secondary forest succession have identified differential growth rates among species as an important factor leading to initial height stratification and early vertical dominance by a particular species (Drury & Nesbitt 1973; Bormann & Likens 1979; Hibbs 1983; Tilman 1985, 1988, 1990). These treatments present a model of mixed-species stratification based on inherently different juvenile height growth rates which, in turn, initiate competitive hierarchies. The implication of such a model for stand development is that a successful early successional species must possess life-history traits which allow it numerically to dominate physical space, but it must also have an inherently fast juvenile growth if it is to gain an early height advantage over less-abundant species. Such a model appears inconsistent with the developmental patterns found in the current study. The potential for *Quercus* and *Acer* to grow in height at rates equivalent to *Populus* clearly demonstrates that some later-successional species have the inherent ability to grow as fast as an early-successional species. We suggest an alternative developmental model in which numerical dominance by *Populus* is a sufficient mechanism in itself to promote vertical stratification, through the inhibition of *Quercus* and *Acer* height growth. Under such a model, species differing in understory tolerance and relative successional status need not have inherently different juvenile height growth rates for stratification to develop.

This model is illustrated stylistically in Fig. 4. In the forests examined, *Populus* was able to gain initial numerical dominance because of its propensity rapidly to saturate soil space with numerous vegetative propagules. Clonal roots of *Populus* are able to extend further than 30 m from an originating genet (Buell & Buell 1959). Following disturbance, the root system from a single clone can rapidly saturate large areas (up to 1 ha in Michigan) with sucker-sprouts, resulting in high density stands (Stoeckeler

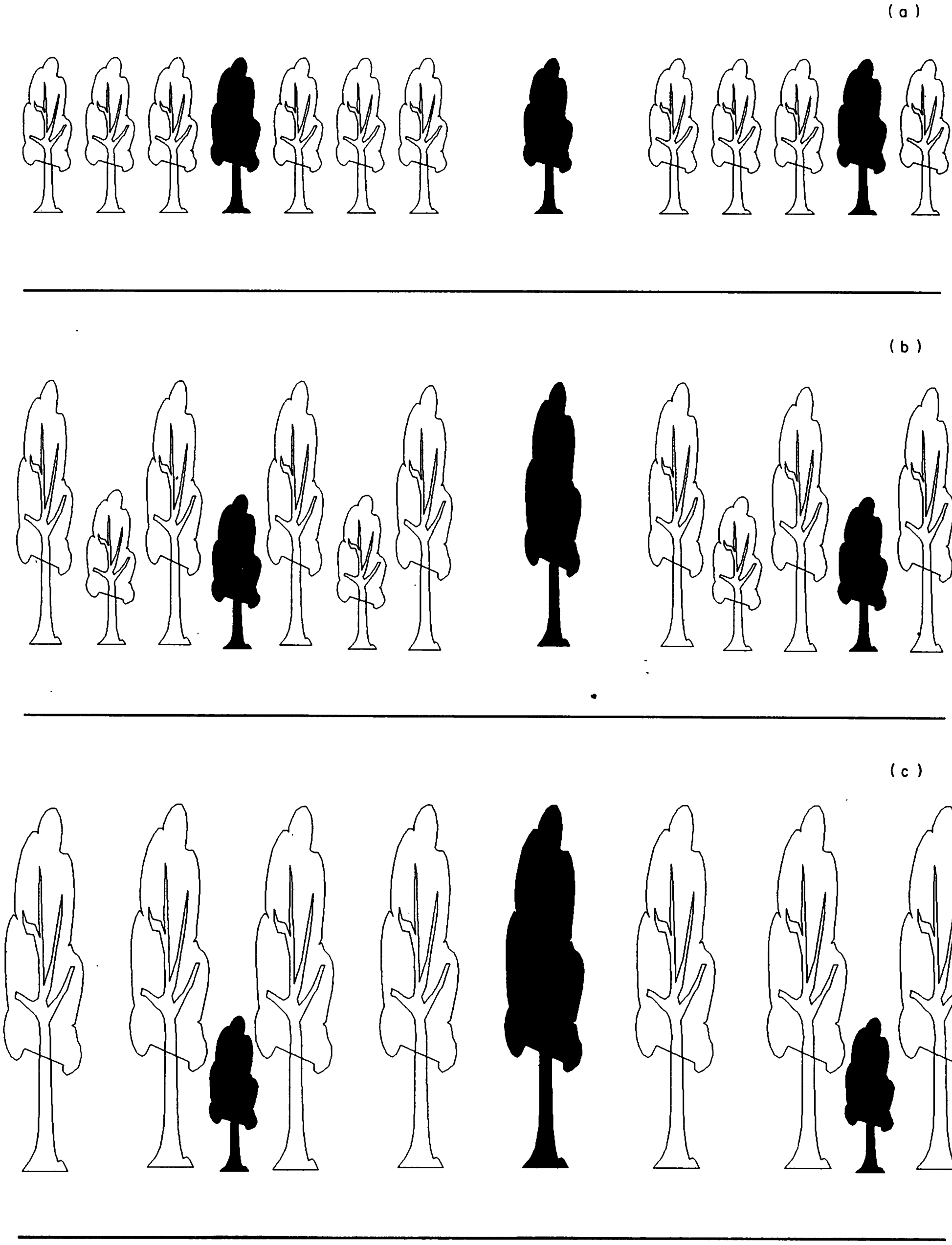

Fig. 4. A model for the development of vertical stratification among tree species differing in understory tolerance and relative successional status in a fully stocked even-aged forest. (a) Immediately following a stand initiating disturbance, initial heights of an intolerant, early-successional species (clear crown) and a relatively more-tolerant, later successional species (filled crown) may be similar. The intolerant species is numerically dominant because of superior dispersal ability. (b) With the onset of crown differentiation, some individuals of both species lapse into suppression. A limited number of individuals of the tolerant species may have early height growth rates similar to the intolerant species, probably because of locally reduced competitive pressure from the intolerant species. The initially low number of stems of the tolerant species reduces the probability that many will occur in competitively favourable neighbourhoods. (c) In the mature forest, the intolerant species is typically vertically dominant over the more-tolerant species although some stems of the tolerant species have maintained growth rates similar to that of the intolerant species. The population-level height growth rate of the intolerant species will be greater than that of the tolerant species because all suppressed stems of the former have died, leaving only fast-growing stems, while slower growing stems of the tolerant species have survived.

& Macon 1956; Zahner & Crawford 1965; Barnes 1966, 1969; Graham, Harrison & Westell 1963; Kemperman & Barnes 1976; Scheiner *et al.* 1988). In contrast, *Quercus* and *Acer* resprout from stumps or root collars (Fowells 1965), restricting the distribution of vegetative propagules of these species to the locations of the originating genets. Many of these genets may be remnant from the presettlement conifer-dominated forests that originally occupied these sites (Palik & Pregitzer 1992b). Neither *Quercus* nor *Acer* were abundant in these forests (Palik & Pregitzer 1992a). Consequently, the number of vegetatively derived individuals in the current forests may have been a function of *Quercus* and *Acer* presettlement abundance.

The large starting capital of *Populus* ramets ensured that this species would continue to dominate most competitive neighbourhoods in the mature forest, despite high, density-dependent mortality early in forest development. Variation in inherent height growth rates among surviving ramets were minimal since most individuals within a given area (for example the plot sizes used) were part of the same clone. The interspecific competitive pressure faced by *Quercus* and *Acer* genets within the *Populus* clonal matrix would have been intense, but spatially variable, probably because of stochastic variation in *Populus* ramet or root density within individual competitive neighbourhoods. Differences in the physiological state of the parent genets may also have influenced height growth potential of individual *Quercus* and *Acer*. In any case, the low number of remnant *Quercus* and *Acer* genets in the early, post-disturbance forests, and the restricted distribution of ramets originating from these genets, ensured that few stems of these species would be vertically dominant in the mature forests. Under this model, vertical stratification develops because of species-specific differences in the ability to achieve maximal potential height growth rates in the face of competitive pressure, not because of inherent differences in juvenile growth rates that initiate competitive hierarchies.

This model of forest development may be characteristic only of forests regenerating predominantly through vegetative means. In such forests, inherently lower height growth rates characteristic of seedlings of more-tolerant species (Loach 1970) may sometimes be compensated for by sprout vigour. Sprout-origin stems occurring in uncontested neighbourhoods would then be able to match height growth rates of less-tolerant species. However, as shown in the current study, most individuals of tolerant species, despite being of sprout-origin, experience suppression to some degree, which in turn leads to species-level height stratification.

A remarkable feature of the forests examined in the current study is that the apparent inhibitory ability of *Populus* has persisted for over 70 years. Not only were the majority of *Quercus* and *Acer* in both study areas suppressed to varying degrees but no individuals from younger cohorts for any species (Palik & Pregitzer 1992b, and unpublished data) have recruited into upper canopy positions. Of course the model we propose needs to be, and can be, examined experimentally in young *Populus* clearcuts. Should it prove valid, this model would account for a pattern of dominance in a forest type (*Populus grandidentata* and *Populus tremuloides* Michx. combined) that covers nearly five million hectares in the northern Great Lakes region of the United States (Jakes 1980; Smith & Hahn 1986; Spencer *et al.* 1988).

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