

# Pin cherry effects on Allegheny hardwood stand development

Todd E. Ristau and Stephen B. Horsley

**Abstract:** Pin cherry (*Prunus pensylvanica* L.) develops an early height advantage over associated species. Data from three long-term studies, extending up to 70 years after complete overstory removal, were used to evaluate the effects of pin cherry density on associates. Survival of seedling-origin stems of black cherry (*Prunus serotina* Ehrh.), red maple (*Acer rubrum* L.), and sugar maple (*Acer saccharum* Marsh.) at age 15 decreased as the density of pin cherry >1.5 m tall at age 3 increased. The regression of pin cherry with black cherry was particularly strong ( $R^2 = 0.632$ ). Height of the tallest black cherry and white ash (*Fraxinus americana* L.) at age 15 also decreased. If the density of pin cherry at age 3 was > 1 stem > 1.5 m tall per 0.0004 ha (high density), the number of black cherry fell below full stocking at age 15. When pin cherry occurred in high density, it lived longer than when it occurred at low density (< 1 stem > 1.5 m tall per 0.0004 ha). High pin cherry density early in stand development delayed the time when shade-intolerant and shade-intermediate species reached a stable proportion of the total basal area. In the long term, pin cherry reduced stand diameter and volume growth, particularly of black cherry.

**Résumé :** Le cerisier de Pennsylvanie (*Prunus pensylvanica* L.) atteint rapidement une hauteur qui lui procure un avantage sur ses espèces associées. Des données provenant de trois études à long terme, qui se sont poursuivies jusqu'à 70 ans après l'enlèvement complet de l'étage dominant, ont été utilisées pour évaluer les effets de la densité du cerisier de Pennsylvanie sur ses associés. La survie des tiges de cerisier tardif (*Prunus serotina* Ehrh.), d'érable rouge (*Acer rubrum* L.) et d'érable à sucre (*Acer saccharum* Marsh.) provenant de semis a diminué à l'âge de 15 ans lorsque la densité du cerisier de Pennsylvanie plus haut que 1,5 m à l'âge de 3 ans a augmenté. La régression du cerisier de Pennsylvanie avec le cerisier tardif a été particulièrement forte ( $R^2 = 0,632$ ). La hauteur des plus hauts cerisiers tardifs et frênes blancs (*Fraxinus americana* L.) à l'âge de 15 ans a aussi diminué. Si la densité du cerisier tardif à l'âge de 3 ans était > 1 tige > 1,5 m de hauteur par 0,0004 ha (ce qui représente une densité élevée), le nombre de cerisiers tardifs tombait en dessous de la densité relative adéquate à l'âge de 15 ans. Lorsque le cerisier de Pennsylvanie présentait une grande densité, il vivait plus longtemps qu'à faible densité (< 1 tige > 1,5 m de hauteur par 0,0004 ha). La présence d'une densité élevée de cerisier de Pennsylvanie tôt au cours du développement du peuplement retardait le moment où les espèces intolérantes et intermédiaires quant à leur tolérance à l'ombre atteignaient une proportion stable de la surface terrière totale. À long terme, le cerisier de Pennsylvanie provoquait une réduction de l'accroissement en diamètre et en volume du peuplement, en particulier chez le cerisier tardif.

[Traduit par la rédaction]

## Introduction

Pin cherry (*Prunus pensylvanica* L.) is a short-lived (20–40 years) tree that may become established following disturbance to forests of the northern United States and Canada (Marks 1974; Wendel 1990). The species is associated with many forest types but has been investigated most frequently in the beech–birch–maple (*Fagus–Betula–Acer*) northern hardwood type. Recruitment occurs primarily from long-lived seeds (Chittenden 1905; Marquis 1975; Auchmoody 1979; Graber and Thompson 1978; Peterson and Carson 1996), though Jobidon (1997) has shown that stems can originate from root suckers. The species is very intolerant of shade (Baker 1949) and grows more rapidly than most

associated species (Elliot 1927). Stem densities as high as about 155 000/ha have been reported in young northern hardwood stands (Marks 1974).

Based on observations in central New Hampshire, Marks (1974) hypothesized that pin cherry density and shade tolerance of associates might be important factors in the dynamics of northern hardwood stand development. He suggested that, as pin cherry density increased, survival and growth, particularly of less shade-tolerant species, would decrease. At the highest pin cherry density, only the most shade-tolerant species such as sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.) would survive. Reports by Jensen (1943) and Longwood (1951) suggested that pin cherry had little or no effect on the early development or species composition of young second-growth northern hardwood stands. However, others have provided support for Marks' (1974) hypothesis. Safford and Filip (1974) reported reduced density of paper birch (*Betula papyrifera* Marsh.) (intolerant) over time in the presence of dominating pin cherry. Leak (1988) found fewer large seedlings (0.9 cm tall to 1.27 cm diameter) of yellow birch (*Betula alleghaniensis* Britton) (intermediate) on 8-year-old

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regeneration plots where pin cherry was present than where it was not present, although neither sugar maple nor white ash (*Fraxinus americana* L.) (intolerant) were affected. In a central New York northern hardwood stand, Heitzman and Nyland (1994) found that the effects of pin cherry were both density dependent and species specific. Permanent regeneration plots with three or more pin cherry per 0.0004 ha at age 3 had fewer black cherry (*Prunus serotina* Ehrh.) (intolerant) and sugar maple  $\geq 2.54$  cm at age 20. Also, there were fewer stems of all species other than pin cherry, the mean diameter at breast height (DBH) of black cherry and white ash was lower, and the basal area of sugar maple was lower than on plots with a lower pin cherry density.

Pin cherry usually do not become established at high densities in the forests of Pennsylvania because it is highly preferred by deer (Jordan 1967), and the state has had an overly abundant deer population since the late 1920s (Redding 1995). Large numbers of pin cherry seeds are found in the forest floor seedbank (Marquis 1975). Under circumstances where deer density is low, forage supply is high, or measures such as a fencing have been used to reduce the impact of deer, large numbers of pin cherry do become established. We have been unable to find any evidence of root sucker origin of pin cherry in our stands (cf. Jobidon 1997). In a recent study (deer density study) of white-tailed deer effects (*Odocoileus virginianus virginianus* (Boddaert)) on vegetation dynamics under controlled low deer densities ( $\leq 7.7$  deer/km<sup>2</sup>) we found that when high densities of pin cherry (greater than about 32 000 / ha at age 3) were present during early regeneration development, there was little regeneration of other species at age 10 (Tilghman 1989; Horsley 1995).

Differences in species composition of advance regeneration in Pennsylvania's Allegheny hardwood forest compared with northern hardwood forests elsewhere obscure the outcome of pin cherry interactions with the remaining species in areas of low deer impact. In this paper, we examine the interaction between pin cherry and its associates using three long-term data sets to determine whether the density of pin cherry that regenerated following complete overstory removal influenced the species composition and pattern of Allegheny hardwood stand development in northwestern Pennsylvania.

## Methods

### The character of Allegheny hardwoods

The northern hardwood stands of Pennsylvania's Allegheny Plateau differ in several respects from those found elsewhere. The second-growth forest became established after a series of early partial cuttings followed by complete overstory removal between 1890 and 1930 (Hough and Forbes 1943; Marquis 1992, 1994). As a result of these cuttings, species with a seedbank regeneration strategy such as pin cherry and black cherry increased substantially in importance among the advance seedlings (Whitney 1990; Peterson and Carson 1996). After overstory removal, slower growing species such as sugar maple and American beech were relegated to intermediate and overtopped crown classes; exceptions were trees left as residuals from the previous stand. Red maple (*Acer rubrum* L.) and the birches grew into codominant and intermediate crown classes. Black cherry became the dominant species in many of these second-growth stands. When its basal area is  $\geq 25\%$ , the cover type is called Allegheny Hardwood (Marquis and Ernst

1992). Common overstory associates are sugar maple, red maple, and American beech. Because of their low crown position in second-growth stands, sugar maple and beech produce little seed, but beech produces root suckers abundantly. Deer density was low during the establishment period of the second-growth forest, and they had little effect on species composition or development of forests cut during the turn-of-the-century period (Redding 1995).

Deer density increased substantially after the 1920s (Redding 1995). In contemporary stands, herbivory by white-tailed deer has virtually eliminated moderately to highly preferred species from the established advance regeneration, including pin cherry, eastern hemlock (*Tsuga canadensis* (L.) Carr) (very tolerant), sugar maple, red maple (tolerant; Loach 1967), white ash, and yellow-poplar (*Liriodendron tulipifera* L.) (intolerant) (Marquis and Brenneman 1981; Horsley 1995). Failure of sugar maple regeneration since at least the 1940s also has contributed to the absence of this species as advance seedlings in contemporary stands (Kolb and McCormick 1993; Long et al. 1997). Black cherry, American beech, and striped maple (*Acer pensylvanicum* L.) (very tolerant) are low to moderate in preference by deer and (or) resilient to repeated browsing. They frequently are present as advance regeneration (Healy 1971; Marquis and Brenneman 1981). At ambient deer densities (15–25 animals/km<sup>2</sup>), most stands cut since the late 1960s have regenerated with a high proportion of black cherry if this species was present in adequate amounts as an advance seedling, or otherwise to ferns, grasses, striped maple, and beech (Horsley and Marquis 1983; Marquis et al. 1992; Horsley 1993).

### Study areas

Since deer browse heavily on pin cherry, we selected stands that developed under low deer impact after complete overstory removal. We used regeneration and growth records from stands in three ongoing long-term research studies (Table 1). Study 1, the deer density study, contains 16 stands at four sites in northwestern Pennsylvania where deer were maintained at densities of 3.9, 7.7, 14.7, or 24.7 animals/km<sup>2</sup> in 13.0 or 25.9-ha enclosures for 10 years. The overstory was removed on 10% of the area and thinned on 30% of the area at the beginning of the study. We used the eight stands where densities had been 3.9 and 7.7 deer/km<sup>2</sup> (stand area = 2.6 and 1.3 ha, respectively). In these stands, deer impact on the species composition and abundance of vegetation was low; differences in species composition between stands treated with 3.9 and 7.7 deer/km<sup>2</sup> were not statistically significant (S.B. Horsley, unpublished data). Pin cherry became the dominant (tallest) species when it was present (Horsley 1995). Study 2, the deer enclosure study, includes nine sites of >10 ha that were cut between 1956 and 1969 (Jordan 1967; Marquis 1974). Each site contained a fenced deer enclosure ranging in size from 0.2 to 3.2 ha, that was erected shortly after cutting. Plots had a wide range of pin cherry densities. Study 3, the weeding study, included four replicate areas (blocks 1–4)  $\geq 6$  ha on the Kane Experimental Forest, where cutting removed the overstory between 1919 and 1923 (Ostrom and Hough 1944; Church 1955). Each block contained twelve 0.08-ha plots, including a 0.04-ha measurement plot. Six plots were designated as controls and received no treatment. Only blocks 1 and 2 remained intact in 1995; the 1936 density of pin cherry was high (49% pin cherry, 31% black cherry) on block 1 and low (9% pin cherry, 17% black cherry) on block 2. Because the shorter term data sets showed significant effects of pin cherry on early stand development, we were interested in whether these effects persisted in the longer term. Availability of the weeding study data set, containing more than 70 years of stand development records, represented an unusual opportunity to investigate this hypothesis.

We compared the six untreated control plots from blocks 1 with those from block 2. Within this new context, the six plots within each block were pseudoreplicates; thus, pin cherry effects were confounded with other site and stand variables. Consideration of

**Table 1.** Study areas used to determine the effects of pin cherry density early in stand development on species composition at a later time.

| Stand name                                  | Ownership and location                                              | Experimental unit size (ha) | Age in 1995 (years) |
|---------------------------------------------|---------------------------------------------------------------------|-----------------------------|---------------------|
| Deer density study                          |                                                                     |                             |                     |
| Fool's Creek, 3.9 deer/km <sup>2</sup>      | Allegheny National Forest, Warren Co., Pa.                          | 2.6                         | 16                  |
| Deadman's Corners, 3.9 deer/km <sup>2</sup> | Allegheny National Forest, Forest Co., Pa.                          | 2.6                         | 16                  |
| Gamelands 30, 3.9 deer/km <sup>2</sup>      | Pennsylvania Game Commission, McKean Co., Pa.                       | 2.6                         | 15                  |
| Wildwood Tower, 3.9 deer/km <sup>2</sup>    | Pennsylvania Bureau of Forestry and National Fuel Gas, Elk Co., Pa. | 2.6                         | 15                  |
| Fool's Creek, 7.7 deer/km <sup>2</sup>      | Allegheny National Forest, Warren Co., Pa.                          | 1.3                         | 16                  |
| Deadman's Corners, 7.7 deer/km <sup>2</sup> | Allegheny National Forest, Forest Co., Pa.                          | 1.3                         | 16                  |
| Gamelands 30, 7.7 deer/km <sup>2</sup>      | Pennsylvania Gamelands 30, McKean Co., Pa.                          | 1.3                         | 15                  |
| Wildwood Tower, 7.7 deer/km <sup>2</sup>    | Pennsylvania Bureau of Forestry and National Fuel Gas, Elk Co., Pa. | 1.3                         | 15                  |
| Deer enclosure study                        |                                                                     |                             |                     |
| Railroad Run                                | Allegheny National Forest, McKean Co, Pa.                           | 0.2                         | 29                  |
| Hemlock Run                                 | Allegheny National Forest, McKean Co, Pa.                           | 0.2                         | 29                  |
| Wolf Run                                    | Kane Experimental Forest, Elk Co., Pa.                              | 3.2                         | 26                  |
| Long Hollow                                 | Allegheny National Forest, Warren Co., Pa.                          | 0.2                         | 30                  |
| Farnsworth                                  | Allegheny National Forest, Warren Co., Pa.                          | 0.2                         | 30                  |
| Kinzua Trail                                | Allegheny National Forest, McKean Co, Pa.                           | 0.2                         | 30                  |
| Chapel Fork                                 | Allegheny National Forest, McKean Co, Pa.                           | 0.4                         | 38                  |
| Cherry Grove                                | Allegheny National Forest, Warren Co., Pa.                          | 0.5                         | 38                  |
| Silver Creek                                | TG Forest Products, Elk Co., Pa.                                    | 0.4                         | 39                  |
| Weeding study                               |                                                                     |                             |                     |
| Weeding block 1                             | Kane Experimental Forest, Elk Co., Pa.                              | 6 × 0.08                    | 72                  |
| Weeding block 2                             | Kane Experimental Forest, Elk Co., Pa.                              | 6 × 0.08                    | 77                  |

site and stand factors at these two blocks convinced us that any differences observed in this analysis would be due mainly to pin cherry density. The two blocks were situated about 3.3 km apart on similar soils. Block 1 was at 585–610 m elevation while that of block 2 was at 606–616 m. Partial cuts on the Kane Experimental Forest during the late 1800s had removed hemlock and the best quality hardwoods. The residual stand located at block 1 received a complete overstory removal cut between 1890 and 1900, then was recut for chemical wood in 1923 (Ostrom and Hough 1944). The effect of this cutting scenario was to greatly increase the proportion of pin cherry in the stand in 1936 when it was 13 years old. The residual stand at block 2 received a complete overstory removal cut in 1919; in 1936 when the stand was 18 years old, the proportion of pin cherry was much lower. A mixture of seedling and stump sprout-origin stems was present at both sites (Ostrom and Hough 1944). Neither block was fenced, but deer density was low during the period of early stand development on the Kane Experimental Forest. (A.F. Hough, unpublished data; Redding 1995).

### Vegetation sampling

Each stand in the deer density study had a systematic grid of 21–25 permanent 0.0004-ha circular sample plots. Detailed surveys of woody regeneration were made 0 or 1, 3, 5, 10, and 15 years after cutting. All stems were counted by species and height class (0.05–0.3, 0.3–0.9, 0.9–1.5, and >1.5 m). On each plot, we recorded heights of the tallest stems of each species. Fifteen years after cutting, data were collected on 0.01-ha plots using the same systematic grid. All stems >1.27 cm DBH were tallied by species and recorded by 2.5-cm diameter classes. The height of the tallest stem of each species was recorded by stem origin (seedling, root sucker, or stump sprout).

In the deer enclosure study, regeneration data were collected on a systematic grid in each enclosure on nine permanently delineated 0.0004-ha circular sample points using the same methods as those

in the deer density study. Inventories were conducted in 1971, 1976, and 1981 when the stands were 2–15, 7–20, and 12–25 years old. In addition, 100% inventories of all stems >1.27 cm DBH were made by 2.54-cm diameter classes on a larger 0.04-ha plot, that enclosed the nine 0.0004-ha plots in 1981, 1988, 1993, and 1995 when stands were 12–25, 19–32, 24–37, and 26–39 years old.

Data collection for the weeding study began in 1936; 100% inventories of stems >1.27 cm DBH by species and 2.54-cm diameter class were made on the 0.04-ha measurement plots at 5-year intervals from 1936 to 1971 and again in 1988, 1993, and 1995. In the 1995 inventory, 72–77 years after overstory removal, we determined the origin (seedling or stump sprout) of each surviving stem.

### Analytical techniques

Data from the deer density study were used to determine trends in species abundance and height development to age 15, and the impact of pin cherry density on other species during this period. The analyses used data expressed on both plot-level and stand-level (stand average) bases.

Plot-level data from repeated measurements of permanent plots were used in regressions to evaluate the effect of early pin cherry density on abundance and height of other species through age 15. By 3 years after overstory removal, all species had become established and differentiation into several height classes had occurred (Table 2, Fig. 1). At age 3, pin cherry density ranged from 0 to 102 stems per 0.0004-ha regeneration plot; stem heights ranged from <0.3 to >1.5 m. Regeneration plots from all eight deer density study stands (175 plots) were pooled and sorted into four new data sets each based on height category (>0.05, >0.3, >0.9, >1.5 m) and abundance of pin cherry (0, 1, 2, ..., *n* pin cherry stems per 0.0004-ha plot). For example, the >1.5 m pin cherry data set was constructed as follows. There were 35 density categories where pin cherry was >1.5 m tall. Plots were sorted into density categories with 0 pin cherry >1.5 m tall, 1 pin cherry >1.5 m tall, ..., *n* pin

**Table 2.** Mean species abundance over time for eight deer density study stands combined.

| Species                | Years after overstory removal |              |                     |                  |                  |                  |                  |                  |               |               |
|------------------------|-------------------------------|--------------|---------------------|------------------|------------------|------------------|------------------|------------------|---------------|---------------|
|                        | 0-1                           |              | 3                   |                  | 3                |                  | 10               |                  | 15            |               |
|                        | <1.5 m                        | >1.5 m       | <1.5 m              | >1.5 m           | <1.5 m           | >1.5 m           | <1.5 m           | >1.5 m           | Seed          | Sprout        |
| American beech         | 16 794<br>(8564)              | 0            | 6699<br>(1631)      | 42<br>(42)       | 4988<br>(1705)   | 438<br>(310)     | 1115<br>(327)    | 1779<br>(464)    | 535<br>(180)  | 26<br>(19)    |
| Black and yellow birch | 9814<br>(2016)                | 0            | 15 104<br>(7806)    | 64<br>(19)       | 9435<br>(2285)   | 866<br>(234)     | 1898<br>(544)    | 2612<br>(686)    | 1529<br>(409) | 4<br>(4)      |
| Black cherry           | 197 287<br>(66 449)           | 112<br>(112) | 67 474<br>(17 856)  | 4050<br>(1769)   | 40 444<br>(8268) | 11 003<br>(4290) | 12 416<br>(3793) | 8453<br>(1608)   | 1461<br>(328) | 567<br>(156)  |
| Pin cherry             | 107 252<br>(26 187)           | 548<br>(548) | 16 760<br>(4844)    | 16 693<br>(6046) | 6201<br>(2195)   | 16 872<br>(5037) | 240<br>(120)     | 9590<br>(2459)   | 3992<br>(742) | 0             |
| Red maple              | 32 033<br>(9913)              | 0            | 23 400<br>(6910)    | 742<br>(366)     | 14 498<br>(3409) | 715<br>(299)     | 7423<br>(1995)   | 551<br>(193)     | 58<br>(32)    | 519<br>(193)  |
| Striped maple          | 11 962<br>(6444)              | 0            | 4563<br>(1906)      | 394<br>(212)     | 2732<br>(947)    | 1281<br>(581)    | 977<br>(451)     | 1467<br>(642)    | 1159<br>(477) | 1<br>(1)      |
| Sugar maple            | 4898<br>(2820)                | 0            | 2037<br>(931)       | 74<br>(74)       | 2234<br>(1467)   | 161<br>(121)     | 118<br>(57)      | 143<br>(90)      | 4<br>(1)      | 28<br>(15)    |
| White ash              | 12 035<br>(8675)              | 0            | 5724<br>(3481)      | 99<br>(99)       | 4859<br>(3162)   | 236<br>(207)     | 2020<br>(1009)   | 406<br>(184)     | 61<br>(25)    | 14<br>(6)     |
| Other                  | 44 030<br>(41 664)            | 0            | 3137<br>(904)       | 185<br>(185)     | 1049<br>(298)    | 483<br>(364)     | 1219<br>(274)    | 301<br>(162)     | 102<br>(46)   | 2<br>(2)      |
| Total                  | 398 414<br>(70 112)           | 660<br>(660) | 144 894<br>(21 958) | 22 369<br>(6020) | 86 440<br>(8772) | 32 055<br>(4606) | 27 426<br>(4027) | 25 303<br>(2315) | 8901<br>(977) | 1162<br>(309) |

**Note:** Each cell shows the mean number of stems per hectare less than or greater than 1.5 m tall, with SE given in parentheses (1–10 years after overstory removal) or by stem origin (15 years after overstory removal) ( $N = 175$  regeneration sample plots (0.0004 ha)). Other species include bigtooth aspen (*Populus grandidentata* Michx.), cucumber tree (*Magnolia acuminata* L.), devil's walking stick (*Aralia spinosa* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), mountain ash (*Sorbus americana* Marsh.), mountain holly (*Nemopanthus mucronata* Raf.), serviceberry (*Amelanchier arborea* Michx. f.), and yellow-poplar (*Liriodendron tulipifera* L.).

cherry >1.5 m tall. Then for each species and stem origin, mean abundance and height were calculated. The same procedure was followed to construct each of the four hierarchical height categories (data sets); the number of density categories varied from 50 in the data set based on plots containing pin cherry >0.05 m tall to 35 in the data set based on plots containing pin cherry >1.5 m tall.

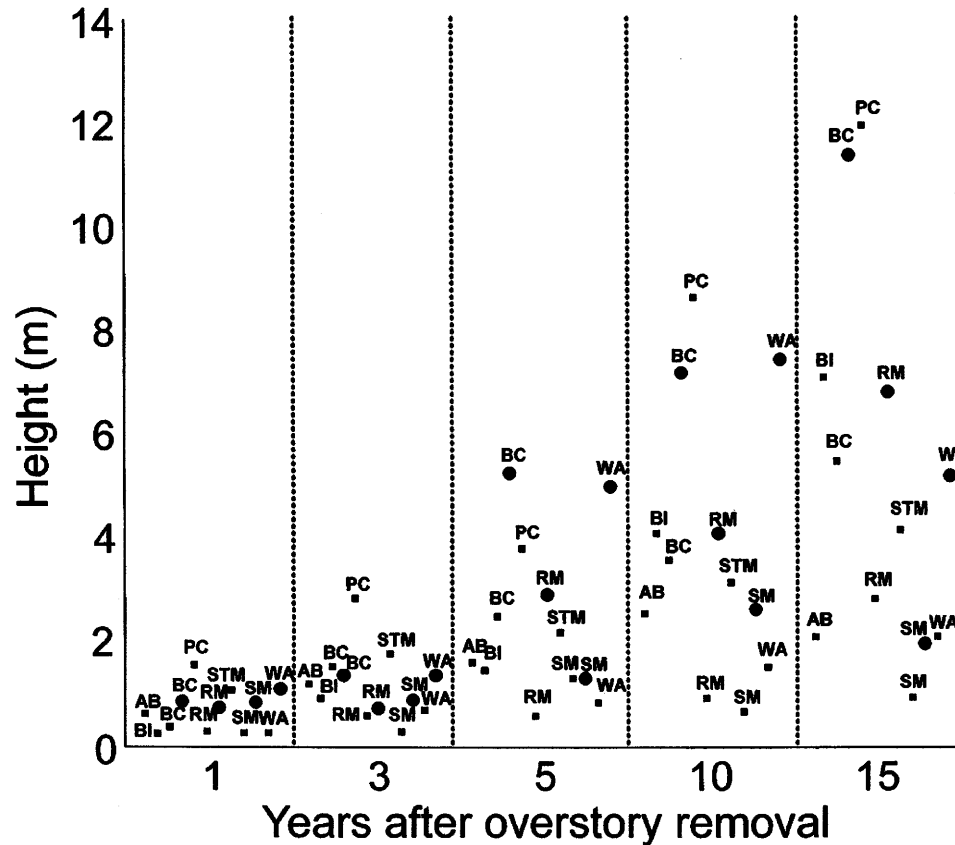
Scatterplots of data suggested a curvilinear relationship between pin cherry density at age 3 ( $x$ ) and species abundance or height ( $y$ ) at age 15. All data were linearized using the  $\log_{10}$  transformation for the  $x$  axis (pin cherry density) in SYSTAT (Wilkinson 1997) after increasing the pin cherry cell densities by one to accommodate zero values in the model. Linear regression analysis was conducted on each pin cherry height category  $\times$  density  $\times$  stem origin data set. American beech root suckers were treated as seedlings in these regressions.

Regressions using the number of pin cherry >1.5 m tall at age 3 generally gave the highest  $R^2$  values. For species with significant ( $P \leq 0.05$ ) regressions and  $R^2 \geq 0.20$ , we determined the threshold density at which pin cherry reduced stocking of other species below the established level for full stocking at age 15. Marquis (1987) determined that two stems >1.27 cm DBH were required on a 0.0011-ha plot at age 10 for the plot to contain at least one stem of acceptable growing stock later when the average stand diameter reached 20 cm. T.E. Ristau and C.A. Nowak (unpublished data) confirmed that a similar relationship (18 stems >1.27 cm DBH on a 0.01-ha plot) was appropriate at age 15. When at least 70% of the plots meet this condition, the stand would likely have 300–500 dominant or codominant stems at age 60 (Marquis 1987). To determine these thresholds, we set  $y = 17$  (the point at which stocking falls below Ristau and Nowak's critical level) and solved the regression equation for pin cherry density at age 3 ( $x$ ).

Potential long-term effects of pin cherry on species composition and growth were evaluated in two ways: (i) stand-level data from the complete set of 29 stands were combined and used to calculate relative species proportion (RSP), a parameter that allows evaluation of changes in stand composition by species or species groups over the 70-year period represented by the data; and (ii) trends in stand diameter and volume were compared using the two blocks from the weeding study, where pin cherry density early in stand development was above (block 1) or below (block 2) the threshold density for effects on other species.

Species composition and development of stands that have grown beyond the regeneration stage commonly are evaluated using basal area. Comparison of stands that still are in the regeneration stage with those beyond this stage is difficult because stem diameter and basal area are not measured on seedling-size stems. Large (tall) stems are the most likely to survive and take a place in the emerging stand and the probability that this will occur increases with the number of large stems. We devised the RSP to bridge this gap and allow continuous comparison of species composition from the regeneration stage through later stages of stand development. In stands that had grown beyond the regeneration stage, RSP was calculated as the proportion of the total stand basal area represented by each species or species group; it was calculated in this way for age 15 stands in the deer density study, for stands older than age 13–26 in the deer enclosure study, and for all stands in the weeding study. For stands that were still in the regeneration stage (stems <2.54 cm DBH), RSP was calculated for each species or species group from the number of stems >1.5 m tall and the mean height of the tallest stem. RSP was calculated through age 15 in the deer density study and through age 13–26 in the deer enclosure study as follows:

**Fig. 1.** Height differentiation over time by species and origin in the deer density study. Seedling origin stems are shown as squares (■); stump sprouts are shown as circles (●). Within a time period, the absolute height of the tallest stem by species and origin is plotted. AB, American beech; BC, black cherry; BI, black and yellow birch; PC, pin cherry; RM, red maple; SM, sugar maple; STM, striped maple; WA, white ash.



$$RSP_i = \frac{N_i H_i}{\sum_{i=1}^n (N_i H_i)}$$

where  $RSP_i$  is the relative species proportion of species  $i$ ,  $N_i$  is the number of stems of species  $i$  that were  $>1.5$  m tall, and  $H_i$  is the mean height of the tallest stem of species  $i$ . Comparison of RSP values derived separately from regeneration and overstory data in the deer density study and the deer enclosure study collected on the same stands in the same years showed high correlations for most species (American beech:  $r = 0.467$ ,  $p = 0.059$ ; black cherry:  $r = 0.824$ ,  $p < 0.001$ ; birch:  $r = 0.442$ ,  $p = 0.076$ ; pin cherry:  $r = 0.751$ ,  $p = 0.001$ ; red maple:  $r = 0.904$ ,  $p < 0.001$ ; sugar maple:  $r = 0.785$ ,  $p < 0.001$ ; striped maple:  $r = 0.967$ ,  $p < 0.001$ ; white ash:  $r = 0.970$ ,  $p < 0.001$ ).

Trends in RSP over time were evaluated by separating stands into two groups: those that developed with pin cherry densities above the critical threshold described previously and those with less pin cherry. Within each stand in each of the two groups, RSP values were calculated for each species and time of measurement. Then species were grouped by shade-tolerance class, and a mean RSP for each shade-tolerance class and time of measurement was calculated. Stands were grouped by 5-year intervals, except for data at age 3, which was plotted separately. Finally, the RSP for each shade-tolerance class was plotted by 5-year intervals against that for pin cherry. The shade-intolerant class included mostly black cherry. The intermediate-tolerance group was primarily black and yellow birch in the deer density study and mostly red maple in

the deer enclosure study and the weeding study. Shade-tolerant species included American beech, striped maple, and sugar maple.

Stand-level data from the weeding study were used to determine whether pin cherry density early in stand development had long-term implications for growth and yield. We calculated mean merchantable diameter (trees  $>14$  cm DBH) and sawtimber volumes for blocks 1 (high-density pin cherry) and 2 (low-density pin cherry) at intervals using the SILVAH stand analysis and prescription program (Marquis et al. 1992; Marquis and Ernst 1992). Since the six measurement plots in each block were pseudoreplicates, we chose the two-sample  $t$  test in SYSTAT to compare the blocks at each time of measurement. The six 0.04-ha plots in each treatment block were considered cases in the analysis (Wilkinson 1997). For all analyses,  $\alpha \leq 0.05$  was the level of probability used as the nominal indicator of statistical significance. However, tests yielding  $p$  values  $>0.05$  and  $<0.15$  were considered worthy of additional investigation.

## Results

### Early stand development: the deer density study

Sixteen species were represented in the data set, although pin cherry, black cherry, birch, and striped maple accounted for 87% (range 68–97%) of the stems 15 years after treatment (Table 2). Large numbers of pin cherry seedlings were present 1 year after overstory removal (range 3500 to nearly 195 000 stems/ha). On the 0.0004-ha sample plots, pin cherry density ranged from 0 to 710 stems. Overall, the

**Table 3.** Mean height (m) of tallest stems by species, origin, and years since overstory removal.

| Species                | Years after overstory removal |                        |                         |                        |                         |                        |                         |                       |                          |                          |
|------------------------|-------------------------------|------------------------|-------------------------|------------------------|-------------------------|------------------------|-------------------------|-----------------------|--------------------------|--------------------------|
|                        | 1                             |                        | 3                       |                        | 5                       |                        | 10                      |                       | 15                       |                          |
|                        | Seed                          | Sprout                 | Seed                    | Sprout                 | Seed                    | Sprout                 | Seed                    | Sprout                | Seed                     | Sprout                   |
| American beech         | 0.26<br>(0.02)<br>[19]        |                        | 1.01<br>(0.14)<br>[10]  |                        | 1.41<br>(0.12)<br>[27]  |                        | 2.39<br>(0.47)<br>[30]  |                       | 4.05<br>(0.10)<br>[100]  |                          |
| Black and yellow birch | 0.06<br>(0.01)<br>[16]        |                        | 0.75<br>(0.06)<br>[63]  | 0.70<br>—<br>[1]       | 1.29<br>(0.08)<br>[91]  |                        | 3.84<br>(0.34)<br>[80]  |                       | 8.19<br>(0.16)<br>[155]  |                          |
| Black cherry           | 0.13<br>(0.01)<br>[73]        | 0.39<br>(0.05)<br>[7]  | 1.30<br>(0.06)<br>[180] | 1.15<br>(0.44)<br>[8]  | 1.62<br>(0.06)<br>[182] | 4.75<br>(0.30)<br>[11] | 3.29<br>(0.22)<br>[146] | 6.7<br>(1.09)<br>[10] | 6.83<br>(0.21)<br>[146]  | 11.90<br>(0.30)<br>[109] |
| Pin cherry             | 0.76<br>(0.14)<br>[9]         |                        | 2.45<br>(0.11)<br>[110] |                        | 3.4<br>(0.12)<br>[100]  |                        | 8.10<br>(0.39)<br>[93]  |                       | 12.29<br>(0.21)<br>[168] |                          |
| Red maple              | 0.08<br>(0.01)<br>[68]        | 0.33<br>(0.15)<br>[4]  | 0.47<br>(0.05)<br>[111] | 0.58<br>(0.16)<br>[15] | 0.46<br>(0.02)<br>[137] | 2.62<br>(0.34)<br>[15] | 0.85<br>(0.11)<br>[111] | 3.8<br>(1.00)<br>[8]  | 4.64<br>(0.25)<br>[38]   | 8.10<br>(0.20)<br>[86]   |
| Striped maple          | 0.50<br>(0.13)<br>[19]        |                        | 1.51<br>(0.05)<br>[17]  |                        | 1.96<br>(0.37)<br>[10]  |                        | 2.92<br>(0.59)<br>[12]  |                       | 5.73<br>(0.14)<br>[85]   |                          |
| Sugar maple            | 0.07<br>(0.01)<br>[6]         | 0.38<br>(0.06)<br>[10] | 0.2<br>—<br>[1]         | 0.73<br>(0.12)<br>[18] | 1.13<br>(0.45)<br>[5]   | 1.15<br>(0.21)<br>[10] | 0.56<br>(0.23)<br>[5]   | 2.40<br>(0.40)<br>[6] | 3.13<br>(0.26)<br>[15]   | 4.10<br>(0.20)<br>[20]   |
| White ash              | 0.07<br>(0.01)<br>[19]        | 0.52<br>(0.24)<br>[2]  | 0.56<br>(0.09)<br>[42]  | 1.15<br>—<br>[1]       | 0.73<br>(0.08)<br>[50]  | 4.50<br>—<br>[1]       | 1.40<br>(0.18)<br>[34]  | 6.97<br>—<br>[1]      | 4.11<br>(0.30)<br>[36]   | 6.70<br>(1.00)<br>[10]   |

**Note:** Each cell shows the mean height, with SE given in parentheses. In years 1, 3, 5, and 10 after overstory removal in the deer density study, the height of the tallest stem on a plot was recorded by species and origin; only one stem was recorded even if stems of both origins were present. In year 15 after overstory removal, heights of both the tallest seedling and the tallest stump sprout origin stem on each plot were collected, if both were present. Number of observations is shown in brackets.

largest numbers of pin cherry were counted 1 year after overstory removal, but in two of the eight stands there were more pin cherry in year 3 than in year 1. First-year pin cherry stems were <1.5 m tall. By year 3, the stands had nearly 17 000 pin cherry stems/ha >1.5 m tall. After year 5, the numbers declined steadily (Table 2); by year 15, only 4000 stems/ha remained.

Black cherry was present as advance seedlings at all sites (data not shown), and others arose from seed in the forest floor after cutting. In the first year, numbers of black cherry seedlings ranged from 38 000 to 620 000 stems/ha. Many grew to >1.5 m height by year 3. Numbers >1.5 m tall peaked from year 3 to year 10 depending on the stand. By age 15, only 1% (range 1–3%) of the seedlings present at year 1 had grown to >1.27 cm DBH. Twenty-eight percent (range 11–51%) of the black cherry stems present at age 15 were of stump sprout origin.

Most of the birches seeded in after overstory removal; peak numbers ranged from 7500 to 69 500 stems/ha, from the first to fifth year. In some stands, birch reached >1.5 m height by year 3; in others it took 5–10 years after overstory removal. By age 15, 88% (range 72–98%) of the stems present in the year of peak birch density had grown to >1.3 cm diameter; nearly all were of seedling origin.

Striped maple typically was present as an advance seedling (data not shown) in six of the eight stands, but occurred

in large numbers at only two sites. Some striped maple reached >1.5 m height 3 years after overstory removal, but most did not until year 5 or 10. Virtually all striped maple >1.27 cm DBH at age 15 were of seedling origin.

Red maple stems ranged from 8000 to 80 000/ha, but few grew into the >1.5 m height class. By year 15, red maple averaged 577/ha and 90% were stump sprouts. American beech was present in all stands, primarily as root suckers. In the first year, there were 750 – 28 000 beech/ha. By age 15, the number >1.27 cm DBH averaged 561/ha; 90% were root suckers and the remainder were stump sprouts. Sugar maple regeneration ranged from 0 to 23 500 stems/ha in the first year, but nearly 60% had died by age 3. By age 15, only 32 sugar maple stems/ha that were >1.27 cm DBH remained; 90% were stump sprouts. White ash was present in five of the eight stands, ranging from 0 to 72 000 stems/ha the first year. Only 76/ha exceeded 1.27 cm diameter by age 15; 82% were of seedling origin.

Pin cherry was the tallest species (except in year 5) and by year 15 the tallest stems averaged more than 12 m (Fig. 1, Table 3). Black cherry stump sprouts were similar to pin cherry in height from year 5 onward; black cherry seedlings grew more slowly than stump sprouts, reaching only 30–60% of the height of the tallest stems from year 3 onward. Birch seedlings became the third tallest species by year 10 (Table 3). Red maple stump sprouts grew much

**Table 4.**  $R^2$ , with  $p$  values given in parentheses, for linear regressions of pin cherry (PC) height class by density categories at age 3 ( $x$ ) with stem abundance of associated species at age 15 ( $y$ ) in the deer density study.

| (A) Number of seedlings and stump sprouts combined at age 15 |         |         |         |         |         |         |          |          |
|--------------------------------------------------------------|---------|---------|---------|---------|---------|---------|----------|----------|
| PC (age 3)                                                   | STM     | RM      | SM      | BI      | AB      | WA      | PC       | BC       |
| >0.05 m                                                      | 0.152   | 0.003   | 0.002   | 0.008   | <0.001  | 0.013   | 0.236    | 0.153    |
| N = 50                                                       | (0.005) | (0.704) | (0.776) | (0.542) | (0.994) | (0.437) | (<0.001) | (0.005)  |
| >0.3 m                                                       | 0.120   | 0.008   | 0.003   | 0.015   | <0.001  | 0.012   | 0.230    | 0.226    |
| N = 49                                                       | (0.015) | (0.549) | (0.733) | (0.400) | (0.978) | (0.462) | (<0.001) | (0.001)  |
| >0.9 m                                                       | 0.202   | 0.001   | 0.006   | 0.002   | 0.007   | 0.008   | 0.225    | 0.324    |
| N = 43                                                       | (0.003) | (0.863) | (0.636) | (0.799) | (0.607) | (0.570) | (0.001)  | (<0.001) |
| >1.5 m                                                       | 0.090   | 0.009   | 0.021   | 0.056   | 0.014   | <0.001  | 0.099    | 0.545    |
| N = 35                                                       | (0.081) | (0.587) | (0.402) | (0.172) | (0.503) | (0.967) | (0.065)  | (<0.001) |

| (B) Number of seedlings at age 15 |         |         |         |         |         |         |          |          |
|-----------------------------------|---------|---------|---------|---------|---------|---------|----------|----------|
| PC (age 3)                        | STM     | RM      | SM      | BI      | AB      | WA      | PC       | BC       |
| >0.05 m                           | 0.152   | 0.005   | 0.055   | 0.007   | <0.001  | 0.009   | 0.235    | 0.093    |
| N = 50                            | (0.005) | (0.618) | (0.102) | (0.557) | (0.972) | (0.523) | (<0.001) | (0.032)  |
| >0.3 m                            | 0.122   | 0.004   | 0.060   | 0.017   | <0.001  | 0.004   | 0.226    | 0.150    |
| N = 49                            | (0.014) | (0.670) | (0.090) | (0.376) | (0.980) | (0.660) | (0.001)  | (0.006)  |
| >0.9 m                            | 0.202   | 0.001   | 0.112   | 0.002   | 0.007   | 0.001   | 0.224    | 0.257    |
| N = 43                            | (0.003) | (0.851) | (0.028) | (0.802) | (0.594) | (0.828) | (0.001)  | (0.001)  |
| >1.5 m                            | 0.089   | 0.224   | 0.294   | 0.055   | 0.016   | 0.004   | 0.098    | 0.632    |
| N = 35                            | (0.081) | (0.004) | (0.001) | (0.176) | (0.469) | (0.709) | (0.068)  | (<0.001) |

| (C) Number of stump sprouts at age 15 |         |         |         |         |
|---------------------------------------|---------|---------|---------|---------|
| PC (age 3)                            | RM      | SM      | WA      | BC      |
| >0.05 m                               | 0.002   | 0.005   | 0.006   | 0.132   |
| N = 50                                | (0.757) | (0.627) | (0.579) | (0.009) |
| >0.3 m                                | 0.009   | 0.005   | 0.035   | 0.118   |
| N = 49                                | (0.520) | (0.616) | (0.200) | (0.016) |
| >0.9 m                                | 0.002   | 0.009   | 0.022   | 0.055   |
| N = 43                                | (0.787) | (0.554) | (0.343) | (0.129) |
| >1.5 m                                | 0.001   | 0.027   | 0.062   | 0.029   |
| N = 35                                | (0.857) | (0.341) | (0.149) | (0.329) |

**Note:** The form of the equations was abundance = constant +  $\log_{10}$  (PC density + 1).  $N$ , number of pin cherry density classes in each pin cherry height category. Number of plots = 175 for all categories. Regressions were conducted for seedling- and sprout-origin stems combined and separately. STM, striped maple; RM, red maple; SM, sugar maple; BI, black and yellow birch; AB, American beech; WA, white ash; BC, black cherry.

faster than red maple seedlings, maintaining a mean height of 40–60% of the tallest species from year 5 onward; red maple seedlings were among the shortest stems at any age. Striped maple was nearly as tall as pin cherry in the first year, but from year 5 onward its height was only about 40% of the tallest species. American beech root suckers and stump sprouts, white ash seedlings, and sugar maple seedlings and stump sprouts were among the shortest at any age. However, white ash stump sprouts were 55% of pin cherry height by age 15.

#### Pin cherry impacts on species abundance and height: the deer density study

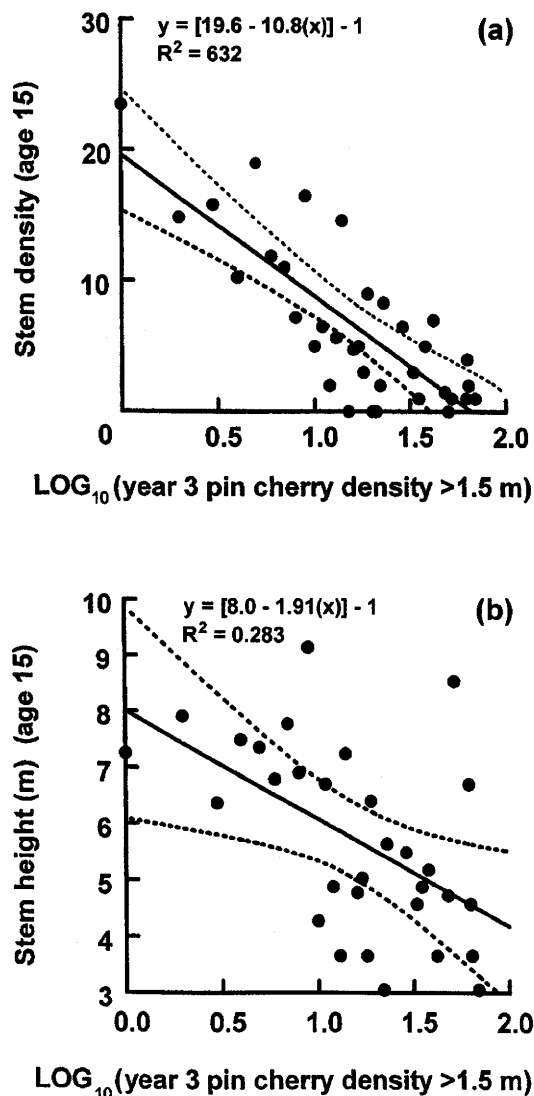
Pin cherry density at age 3 had a negative relationship with abundance of some associated species at age 15 and a positive relationship with 15-year pin cherry abundance (Fig. 2a, Table 4). The effect depended on the stem origin of associates and on the height of pin cherry entered into the regressions. We used  $p \leq 0.05$  and  $R^2 \geq 0.20$  as combined criteria for detecting pin cherry effects. Regressions using

data for stems of seedling and stump sprout origin combined showed effects only on pin cherry, black cherry, and striped maple (Table 4A). However, abundance of pin cherry at age 3 had a negative relationship with abundance of seedling-origin striped maple, red maple, sugar maple, and black cherry at age 15 (Table 4B). Stump sprouts of these species were unaffected (Table 4B).

The highest  $R^2$  values for regressions generally were obtained when the density of only the largest pin cherry (>1.5 m tall) were included in the regressions (Fig. 2a, bottom row in Tables 4A–4C). Smaller numbers of age 15 red maple ( $R^2 = 0.224$ ), sugar maple ( $R^2 = 0.294$ ), and black cherry ( $R^2 = 0.632$ ) seedlings were related to increasing pin cherry density at age 3 (Fig. 2a, Table 4). Striped maple decreased with increases of pin cherry >0.9 m tall. The density of birches, American beech, and white ash was not related to pin cherry density.

Density of pin cherry at age 3 also was correlated with the height of the tallest stem of some associates at age 15 (Fig. 2b, Table 5). The height of the tallest white ash and

**Fig. 2.** Linear regressions for  $\log_{10}$  (density of pin cherry seedlings over 1.5 m tall at age 3) with density of black cherry seedlings at age 15 (a) and height of the tallest black cherry seedling at age 15 (b). Year 3 data were taken on 0.0004-ha plots in the deer density study; year 15 data were taken on 0.01-ha plots using the same plot centers.



black cherry stems of seedling origin decreased as age 3 pin cherry density increased; stump sprouts and other species of seedling origin were unaffected. The  $R^2$  value for the relationship between black cherry seedlings and pin cherry density was highest when pin cherry >1.5 m tall at age 3 were used in the regression, though the proportion of the variance accounted for by the height relationship ( $R^2 = 0.283$ ) (Fig. 2b, Table 5) was less than that for black cherry abundance ( $R^2 = 0.632$ ) (Fig. 2a, Table 4). White ash was not well represented in the data set (Table 2) and inspection of the data showed that at age 3 most plots with white ash coincidentally had pin cherry >1.5 m tall. Since pin cherry height categories were hierarchical, white ash regressions were similar for all height categories (Table 5).

Age 15 stocking was adequate to calculate a critical threshold of pin cherry density only for black cherry. When

there was more than one pin cherry >1.5 m tall per 0.0004-ha plot at age 3 ( $x$ ) fewer black cherry than required for full stocking at age 15 ( $y$ ) were present ( $y = (19.6 - 10.8x) - 1$ ,  $R^2 = 0.632$ ).

#### Long-term impacts of pin cherry on growth and yield: all data bases

Density of pin cherry early in stand development had long-term consequences for stand growth and yield, although species composition was similar. In stands with low pin cherry density (Fig. 3a), RSP for pin cherry peaked at age 10 and then declined to zero about 30 years after overstory removal. Without interference from pin cherry, RSP of shade-intolerant species (mostly black cherry) peaked at about 95% three years after overstory removal and then declined rapidly to a more consistent 40–55% of total RSP after about 10 years. RSP for shade-intermediate species (birch seedlings and red maple stump sprouts) steadily increased for about 20 years and then stabilized at 30–40% of total basal area. The RSP for shade-tolerant species (sugar maple, American beech, striped maple) increased to 5–10% of total basal area by 15 years and then leveled off.

In stands with a high density of pin cherry (Fig. 3b), RSP of pin cherry peaked at about 70% by age 3 and declined to zero at age 40–45. RSP for shade-intolerant species reached a small peak at age 5 and then increased to 40–50% by 35 years. Similarly, RSP stabilized at about 35% after 35 years for the shade-intermediate species.

Trends in RSP were corroborated by measures of growth and wood production over a 70-year period in stands where pin cherry density was high or low early in stand development (Table 6). Mean merchantable diameter (>14 cm DBH) was similar in high and low pin cherry density blocks through year 28 after overstory removal. Between year 28 and year 38, mean merchantable diameter was greater on the low than on the high pin cherry density block ( $p = 0.008$ ); seventy years after cutting, it was 3.3 cm greater for low than high pin cherry density stands ( $p = 0.098$ ) (Table 6). All stands first had sawtimber volume (trees >29 cm DBH) 38 years after cutting, but stands with low pin cherry density had nearly twice the volume ( $p = 0.077$ ) of high pin cherry density stands. This difference persisted through year 70 ( $p = 0.071$ ). Much of the difference was attributable to black cherry (Table 7). In stands with a high density of pin cherry, black cherry averaged 5.2 cm less in DBH ( $p = 0.046$ ), and 6.0 m<sup>2</sup>/ha less in basal area ( $p = 0.250$ ) at age 70. Also, the proportion of seedling-origin black cherry was lower ( $p = 0.090$ ).

#### Discussion

Our results support the effects of high-density pin cherry on other species hypothesized by Marks (1974). They show that with a high pin cherry density, survival, and (or) height growth of seedling-origin black cherry, red maple, sugar maple, white ash, and striped maple are significantly less in the short term. Growth of the birches and stump sprouts of all species was not affected. Effects on seedling origin black cherry were particularly strong (Fig. 2, Tables 4 and 5) and long lasting (Tables 6 and 7), with a plot-level threshold of >1 pin cherry >1.5 m tall at age 3 per 0.0004 ha. Stands with

**Table 5.**  $R^2$  values, with  $p$  values given in parentheses and number of observations given in brackets, for linear regressions of pin cherry (PC) height class by density categories at age 3 ( $x$ ) with height of the tallest stem of associated species at age 15 ( $y$ ) in the deer density study.

| (A) Height of seedlings and stump sprouts combined at age 15 |                          |                          |                         |                          |                          |                          |                          |                          |
|--------------------------------------------------------------|--------------------------|--------------------------|-------------------------|--------------------------|--------------------------|--------------------------|--------------------------|--------------------------|
| PC (age 3)                                                   | STM                      | RM                       | SM                      | BI                       | AB                       | WA                       | PC                       | BC                       |
| >0.05 m                                                      | 0.065<br>(0.152)<br>[33] | 0.124<br>(0.129)<br>[20] | 0.005<br>(0.894)<br>[6] | 0.071<br>(0.073)<br>[46] | 0.003<br>(0.734)<br>[40] | 0.384<br>(0.002)<br>[23] | 0.052<br>(0.110)<br>[50] | 0.085<br>(0.047)<br>[47] |
| >0.3 m                                                       | 0.054<br>(0.201)<br>[32] | 0.145<br>(0.081)<br>[22] | 0.005<br>(0.894)<br>[6] | 0.032<br>(0.238)<br>[46] | 0.004<br>(0.710)<br>[41] | 0.332<br>(0.005)<br>[22] | 0.050<br>(0.123)<br>[49] | 0.101<br>(0.028)<br>[48] |
| >0.9 m                                                       | 0.006<br>(0.695)<br>[27] | 0.123<br>(0.167)<br>[17] | 0.025<br>(0.801)<br>[5] | 0.023<br>(0.335)<br>[40] | 0.014<br>(0.509)<br>[34] | 0.364<br>(0.003)<br>[21] | 0.225<br>(0.001)<br>[35] | 0.117<br>(0.035)<br>[31] |
| >1.5 m                                                       | 0.046<br>(0.393)<br>[18] | 0.085<br>(0.310)<br>[14] | 0.066<br>(0.623)<br>[6] | 0.082<br>(0.133)<br>[29] | 0.052<br>(0.242)<br>[28] | 0.363<br>(0.004)<br>[21] | 0.014<br>(0.502)<br>[35] | 0.106<br>(0.075)<br>[31] |
| (B) Height of seedlings at age 15                            |                          |                          |                         |                          |                          |                          |                          |                          |
| PC (age 3)                                                   | STM                      | RM                       | SM                      | BI                       | AB                       | WA                       | PC                       | BC                       |
| >0.05 m                                                      | 0.065<br>(0.152)<br>[33] | 0.008<br>(0.701)<br>[20] | 0.005<br>(0.894)<br>[6] | 0.071<br>(0.073)<br>[46] | 0.003<br>(0.734)<br>[40] | 0.366<br>(0.002)<br>[23] | 0.053<br>(0.109)<br>[50] | 0.104<br>(0.027)<br>[47] |
| >0.3 m                                                       | 0.054<br>(0.201)<br>[32] | 0.032<br>(0.424)<br>[22] | 0.005<br>(0.894)<br>[6] | 0.032<br>(0.238)<br>[46] | 0.004<br>(0.710)<br>[41] | 0.308<br>(0.007)<br>[22] | 0.050<br>(0.122)<br>[49] | 0.084<br>(0.045)<br>[48] |
| >0.9 m                                                       | 0.003<br>(0.786)<br>[27] | 0.061<br>(0.338)<br>[17] | 0.025<br>(0.801)<br>[5] | 0.023<br>(0.355)<br>[40] | 0.014<br>(0.509)<br>[34] | 0.340<br>(0.004)<br>[23] | 0.031<br>(0.260)<br>[43] | 0.183<br>(0.007)<br>[38] |
| >1.5 m                                                       | 0.046<br>(0.393)<br>[18] | 0.126<br>(0.213)<br>[14] | 0.066<br>(0.623)<br>[6] | 0.082<br>(0.133)<br>[29] | 0.052<br>(0.242)<br>[28] | 0.308<br>(0.009)<br>[21] | 0.014<br>(0.502)<br>[35] | 0.283<br>(0.002)<br>[31] |
| (C) Height of stump sprouts at age 15                        |                          |                          |                         |                          |                          |                          |                          |                          |
| PC (age 3)                                                   | RM                       | SM                       | WA                      | BC                       |                          |                          |                          |                          |
| >0.05                                                        | 0.002<br>(0.779)<br>[39] | 0.019<br>(0.654)<br>[13] | 0.086<br>(0.573)<br>[6] | 0.063<br>(0.133)<br>[37] |                          |                          |                          |                          |
| >0.3 m                                                       | 0.005<br>(0.663)<br>[38] | 0.017<br>(0.674)<br>[13] | 0.086<br>(0.573)<br>[6] | 0.064<br>(0.132)<br>[37] |                          |                          |                          |                          |
| >0.9 m                                                       | 0.026<br>(0.351)<br>[36] | 0.026<br>(0.598)<br>[13] | 0.091<br>(0.561)<br>[6] | 0.068<br>(0.137)<br>[34] |                          |                          |                          |                          |
| >1.5 m                                                       | 0.060<br>(0.240)<br>[25] | 0.035<br>(0.607)<br>[10] | 0.064<br>(0.629)<br>[6] | 0.006<br>(0.697)<br>[26] |                          |                          |                          |                          |

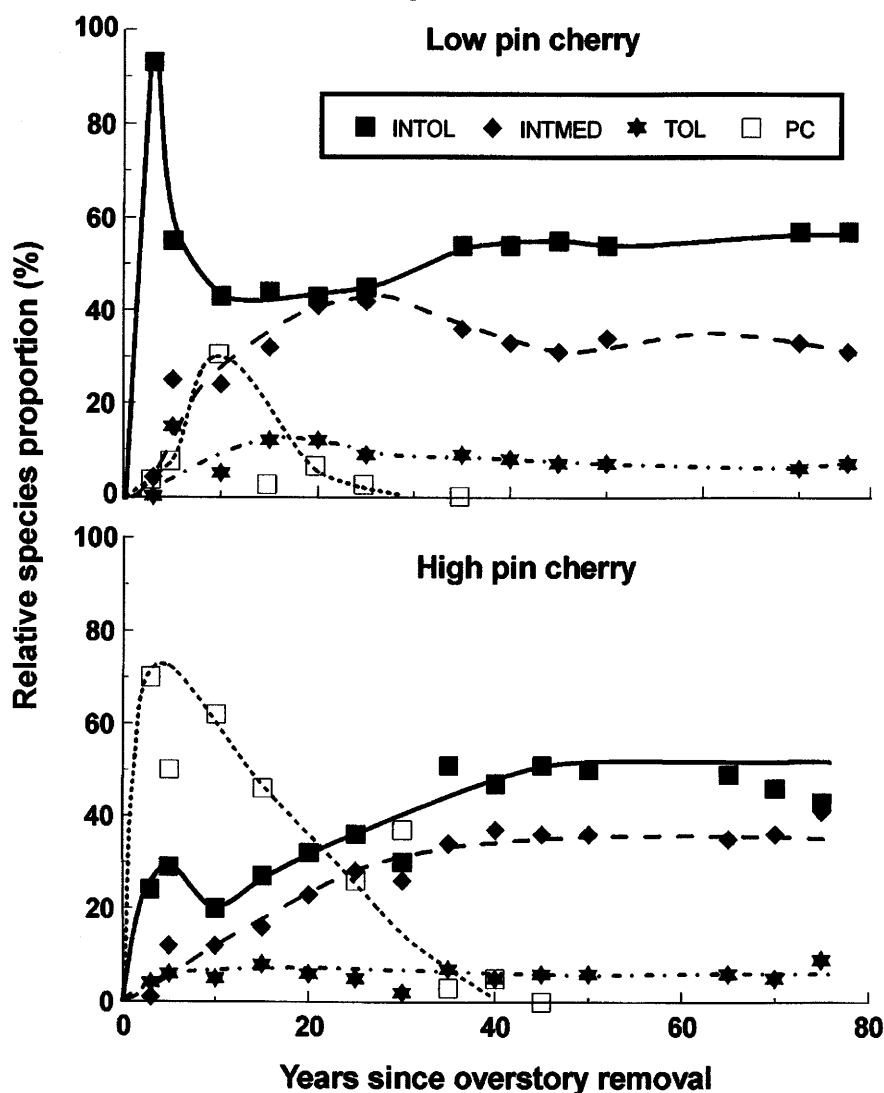
**Note:** The form of the equations was height = constant +  $\log_{10}$  (PC density + 1). Regressions were conducted for seedling and sprout origin stems combined and separately. STM, striped maple; RM, red maple; SM, sugar maple; BI, black and yellow birch; AB, American beech; WA, white ash; BC, black cherry.

that minimum number of pin cherry became understocked with seedling-origin black cherry and other affected species. Also, the rate of stand development was significantly slower and stands had a larger proportion of stump sprouts, particularly of black cherry.

Our results are similar to those of Heitzman and Nyland (1994) for a central New York northern hardwood stand. We

extended their findings by showing differential sensitivity of seedlings and stump sprouts. Heitzman and Nyland's (1994) threshold for pin cherry interference was  $\geq 3$  pin cherry of all sizes per 0.0004-ha plot. We found that pin cherry >1.5 m tall at age 3 accounted for the largest amount of the variance in seedling abundance and height. Our results and those of Heitzman and Nyland differ from findings of Leak (1988)

**Fig. 3.** Relative species proportion for pin cherry, shade-intolerant, -intermediate, and -tolerant species over time for stands with low (a) or high (b) pin cherry seedling density early in stand development.



**Table 6.** Stand productivity over time for weeding study stands where pin cherry density was above the critical threshold (high) or below this threshold (low).

| Pin cherry density                    | Years since overstory removal |       |       |       |       |       |       |
|---------------------------------------|-------------------------------|-------|-------|-------|-------|-------|-------|
|                                       | 18                            | 23    | 28    | 38    | 43    | 48    | 70    |
| Mean merchantable diameter (cm)       |                               |       |       |       |       |       |       |
| High                                  | —                             | 17.5  | 19.1  | 20.7  | 21.9  | 23.1  | 28.6  |
| Low                                   | 6.6                           | 17.0  | 18.9  | 22.6  | 25.3  | 26.5  | 31.9  |
| <i>p</i>                              |                               | 0.558 | 0.878 | 0.008 | 0.019 | 0.035 | 0.098 |
| Sawtimber volume (m <sup>3</sup> /ha) |                               |       |       |       |       |       |       |
| High                                  | —                             | —     | —     | 4.6   | 7.8   | 13.6  | 46.5  |
| Low                                   | —                             | —     | —     | 8.9   | 20.9  | 28.0  | 70.3  |
| <i>p</i>                              |                               |       |       | 0.077 | 0.025 | 0.024 | 0.071 |

and Safford and Filip (1974) for northern hardwood stands in New Hampshire. There, pin cherry had a negative effect on survival and growth of paper birch and yellow birch during the regeneration stage of stand development. Neither we nor Heitzman and Nyland (1994), found an effect on black

birch or yellow birch. The reason for this discrepancy is not apparent.

Our data do not show mechanistically how pin cherry interferes with growth and development of black cherry or other Allegheny hardwood species. We hypothesize that the

**Table 7.** Comparison of stand level parameters by species for weeding study stands where pin cherry density was above the critical threshold (high) or below this threshold (low) at age 70.

| Species                | Mean no. of stems/ha |     |          | Percent seedling origin in 1995 <sup>a</sup> |     |          | Basal area (m <sup>2</sup> /ha) |      |          | Mean diameter (cm) |      |          |
|------------------------|----------------------|-----|----------|----------------------------------------------|-----|----------|---------------------------------|------|----------|--------------------|------|----------|
|                        | High                 | Low | <i>p</i> | High                                         | Low | <i>p</i> | High                            | Low  | <i>p</i> | High               | Low  | <i>p</i> |
| Black cherry           | 292                  | 292 | 1.000    | 59                                           | 74  | 0.125    | 18.0                            | 24.0 | 0.250    | 30.4               | 35.6 | 0.046    |
| Red maple              | 321                  | 346 | 0.707    | 28                                           | 23  | 0.653    | 13.5                            | 12.8 | 0.811    | 27.1               | 24.0 | 0.177    |
| Sugar maple            | 148                  | 202 | 0.622    | 54                                           | 87  | —        | 0.9                             | 1.4  | 0.641    | 10.3               | 9.9  | 0.873    |
| Black and yellow birch | 8                    | 45  | 0.02     | 100                                          | 100 | —        | 0.2                             | 1.5  | 0.058    | 15.2               | 22.3 | 0.516    |

<sup>a</sup>Values shown for the high pin cherry density overestimate the proportion of seedling origin stems. Single-stemmed stump sprouts could not unequivocally be differentiated from seedling origin stems in 1995. The weeding study also contains data on stem origin for trees selected as "crop trees" in 1936 and their survival through 1971 when they were 48–53 years old. On high pin cherry density plots, survival of 97 seedling-origin crop trees was 38% in 1971; survival of 24 stump sprout origin crop trees was 64%. On low pin cherry density plots, 63% of 66 seedling-origin crop trees and 50% of eight stump sprout origin crop trees survived in 1971.

similarity of resource requirements between black cherry and pin cherry may play a role in development of black cherry dominated Allegheny hardwood stands in Pennsylvania. Both species are shade intolerant, although pin cherry is the more intolerant of the two. Both species require high nutrient levels, particularly nitrogen (Marks 1974; Auchmoody 1982), and have shallow root systems capable of capturing large quantities of nutrients (Marks 1974; Safford and Filip 1974).

Rapid growth of pin cherry early in stand development puts seedling-origin black cherry at a competitive disadvantage to capture above- and below-ground resources; many black cherry seedlings succumb at this time. Stump sprouts of black cherry grow as rapidly as pin cherry (Fig. 1, Table 3), so they are not exposed to the reduced light levels and have well-established root systems. Later, as nutrients (particularly nitrogen and phosphorus; Auchmoody 1982) become more limiting, growth of the more shade-tolerant species such as the birches and red maple is reduced (Fig. 3).

In stands where the density of pin cherry is low, typically there are large numbers of seedling-origin black cherry in the dominant crown class, pin cherry is short lived, and black cherry stems are well spaced. When a large proportion of the stand has pin cherry above the critical threshold density, seedling-origin black cherry do not occupy the dominant crown position; most dominant black cherry are of stump sprout origin and have the spacing of the older stems from which they originated. Seedling-origin black cherry that survive are smaller because they developed in a subordinate crown position. In stands with high pin cherry density, the longevity of pin cherry is greater, and the turnover of resources to surviving stems probably occurs at a later time. Thus, stand growth is slower and yield is less (Tables 6 and 7) than in stands with low pin cherry density.

Land managers should consider the implications of interference from pin cherry seed stored in the forest floor of current second-growth Allegheny hardwood stands. Some pin cherry remains viable in the seedbank for about 125 years from the date of overstory removal (Marquis 1975; Peterson and Carson 1996). Much of the pre-settlement forest on the Allegheny Plateau was removed between 1890 and 1930. Considering that pin cherry seed typically is produced for about 35 years after overstory removal (Peterson and Carson 1996) and the density of viable pin cherry in the seedbank

begins to decline about 65 years after disturbance (Marquis 1975), current second-growth Allegheny hardwood stands have a high potential to regenerate to pin cherry for some time to come. The amount of pin cherry in the seedbank varies considerably from stand to stand; thus pin cherry stocking likely will range from high to low, with important consequences in stands where a high proportion of the area regenerates to >1 pin cherry >1.5 m tall at age 3 per 0.0004 ha.

In Pennsylvania, herbivory by white-tailed deer determines whether pin cherry survive and develop. Currently, a high density of pin cherry develops only in protected areas or areas of low deer impact (Horsley 1995). In such areas, seedbank size can be reduced substantially by making a shelterwood seed cut several years prior to final overstory removal and keeping the residual stand above 60% relative density (Horsley and Marquis 1983). The disturbance will trigger germination of some pin cherry seed and the seedlings will die in the shade of the shelterwood overstory within a year or two (Horsley and Marquis 1983). Alternately, Auchmoody (1979) found that pin cherry seed germination is stimulated by the application of nitrogen-containing fertilizers in uncut stands. There, too, seedlings will die due to low light levels. Afterward, an appropriate method can be used to regenerate more desirable species.

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