Variability in early height growth rate of forest trees: implications for retrospective studies of stand dynamics

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Abstract: Retrospective studies of forest stand dynamics may rely on estimates of tree ages. In some of these studies, trees are aged near the stem base, while in other studies trees may be aged at breast height. An age correction may be added to breast-height ages in an attempt to account for average time to reach breast height and thus provide better estimates of total ages. Aging at breast height can provide estimates of stem and stand ages that are sufficient and appropriate for many studies of stand dynamics, for example, those focusing on the dynamics of canopy recruitment. However, the various aging methodologies will provide similar interpretations of actual stand age structures only if early height growth rates are not variable among stems, an assumption not likely to be true. Thus, aging at breast height, with or without a correction factor, may be inappropriate in studies that rely on accurate determination of tree establishment times. In the present study, variability of early height growth rates for several tree species common to *Populus grandidentata* Michx. forests is quantified by determining the number of years to reach breast height. Interpretations of stand age structures and dynamics are made based on total tree ages, breast-height ages, and corrected breast-height ages. The results are compared to explore the implications of ignoring variability in early height growth rates when interpreting development of the stands. For the study populations, early height growth rates were highly variable. Some variability was accounted for by differences in understory tolerance, establishment times, and regenerative modes. Intolerant species establishing early grew faster than more tolerant, later establishing species. Sprout-origin stems grew faster, and had much less variable growth rates, than did seed-origin stems. In the understory, hardwood regeneration grew faster than pine regeneration. Even after accounting for these factors, early height growth rates were still variable. Within replicate plots, cumulative establishment distributions based on breast-height ages always differed from those based on total ages, leading to different interpretations of stand age structures. Cumulative establishment distributions based on breast-height ages corrected for aging height differed 44% of the time from those based on total ages. The timing of understory reinitiation, an important dynamic in even-aged forests, was determined using the three aging methods and compared. The timing of understory reinitiation based on breast-height ages differed significantly from that derived using total ages, while that derived using corrected breast-height ages did not differ from the latter. These results suggest that interpretations of stand age structures and past dynamics based on breast-height ages should be viewed cautiously if the objectives of a study require accurate estimates of tree establishment times.

Résumé : Les études de la dynamique passée des peuplements forestiers peuvent s'appuyer sur l'âge des arbres. Dans certaines de ces études, l'âge est estimé à la souche, alors que dans d'autres il l'est à hauteur de poitrine. Dans ce dernier cas, pour tenter de mieux estimer l'âge total, on corrige l'âge à hauteur de poitrine en lui ajoutant l'âge moyen que met l'arbre pour atteindre la hauteur de poitrine. L'âge à hauteur de poitrine peut être suffisant et adéquat à plusieurs études de la dynamique des peuplements, par exemple, celles sur la dynamique du couvert. Cependant, les diverses estimations d'âge n'aboutissent aux mêmes interprétations des structures d'âge que si la variation inter-arbre de la croissance en hauteur juvénile n'est pas élevée. Comme cette hypothèse n'est pas toujours remplie, l'estimation de l'âge à hauteur de

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poitrine avec ou sans correction peut être inappropriée aux études exigeant une estimation précise de la durée de la phase juvénile. Dans la présente étude, le nombre d'années pour atteindre la hauteur de poitrine est utilisé pour analyser la variation de la croissance en hauteur juvénile de plusieurs essences communes aux peuplements de *Populus grandidentata* Michx. Les analyses de la structure d'âge et de la dynamique des peuplements s'appuient sur l'âge total, l'âge à hauteur de poitrine et l'âge à hauteur de poitrine corrigé. On détermine en particulier les conséquences d'ignorer la variation de la croissance en hauteur juvénile sur l'interprétation du développement des peuplements. Pour les peuplements étudiés, la croissance en hauteur juvénile est très variable. Une partie de cette variation est causée par les différences de tolérance à l'ombre, les durées d'installation et les modes de régénération. Les essences intolérantes croissent plus vite que les essences plus tolérantes dont l'installation est plus tardive. Les tiges de rejet de souche poussent plus vite et ont les taux de croissance moins variables que les tiges de semis. Dans le sous-bois, les feuillus se régénèrent plus vite que les pins. Même en tenant compte de ces facteurs, la croissance en hauteur juvénile demeure variable. Dans chacune des placettes mesurées, les distributions cumulées d'installation bassées sur l'âge à hauteur de poitrine diffèrent toujours de celles basées sur l'âge total, causant ainsi les différences d'interprétation de la structure d'âge. Les distributions cumulées d'installation basées sur l'âge à hauteur de poitrine corrigé diffèrent de 44% de celles basées sur l'âge total. On compare en outre l'effet des méthodes d'estimation d'âge sur l'évaluation de la durée de réinstallation du sous-bois, facteur important de la dynamique des peuplements équiennes. Basée sur l'âge à hauteur de poitrine, cette durée diffère significativement de celle basée sur l'âge total, alors que celle basée sur l'âge à hauteur de poitrine corrigé ne diffère pas de celle basée sur l'âge total. Ces résultats suggèrent que les analyses des structures d'âge et de la dynamique passée basées sur l'âge à hauteur de poitrine devraient être entreprises avec prudence si leurs objectifs exigent une estimation précise des durées d'installation de diverses essences.

[Traduit par la Rédaction]

Introduction

Quantifying tree ages or times of seedling establishment are integral components of some studies of forest stand structure and dynamics. In retrospective studies, tree ages are determined through examination of increment cores or stem sections taken at some standard height on the bole. When increment cores or stem sections are taken as close to tree bases as is practical (e.g., Muir 1993; Parker and Peet 1984) they can provide a reasonable reflection of true stand age structure. However, increment cores (and sometimes stem sections) may be extracted at breast height, or some other height well above the tree base. In some of these latter studies, the assumption is that trees are "born" at breast height. Alternatively, a fixed age may be added to breast height ages in an attempt to account for time spent growing to breast height (e.g., Golley et al. 1994; Tyrrell and Crow 1994). Age corrections may be derived from published estimates of mean number of years to reach breast height for a particular species.

Aging at breast height, with or without a correction, will provide an accurate interpretation of stand age structure (i.e., the relative age differences among stems) only if early height growth rates are similar among stems. Such an assumption is not likely to be true, particularly for mixed-species stands and for populations of species that survive for extended periods in low resource environments of the forest understory. For the latter, early height growth rates may be highly variable among stems, depending on the degree of variation in local competitive environments (Stoll et al. 1994). Failure to account for variability in early height growth rates in some retrospective studies of forest stands may lead to errors in interpretations of stand age structure, as well as the timing of specific structural dynamics during stand development. If the objectives of a retrospective study depend on having accurate determinations of tree and stand ages, then use of the appropriate aging methodology is warranted.

In this paper we examine variation in early tree height growth rates by determining the number of years to reach breast height for populations of several tree species that are characteristic of bigtooth aspen (*Populus grandidentata* Michx.) dominated ecosystems in the northern Great Lakes region. Our objectives are to (1) quantify variability in early height growth rates of the study populations and (2) explore the implications of ignoring this variability when interpreting stand age structures and past dynamics within the study forest.

Study site

This research was conducted at the University of Michigan Biological Station (UMBS) in northwestern Lower Michigan (45°40′N, 84°40′W). Surficial geology of the study area consists of outwash sands (Lapin 1990). Soils throughout the majority of the study area are classified as Entic Haplorthods of the Rubicon series; soil textures of upper horizons are dominated by coarse and medium sands (65–75%), with little (<5%) clay and silt (USDA Soil Conservation Service 1991).

The study forest is even aged, having originated following logging and wildfire 75–80 years prior to sampling (Palik and Pregitzer 1993*a*). Overstory vegetation is dominated by bigtooth aspen, with lesser amounts of northern red oak (*Quercus rubra* L.) and red maple (*Acer rubrum* L.) (Palik and Pregitzer 1992). Site index for bigtooth aspen in the study area ranges from 16.0 to 17.0 m (50-year base; B. Palik, unpublished data). Sapling- and seedling-layer vegetation is dominated by eastern white pine (*Pinus strobus* L.) and red maple, with lesser amounts of red pine (*Pinus resinosa* Ait.) and red oak (Palik and Pregitzer 1993*b*). Most red oak and red maple in the overstory appear to be of vegetative origin (see Palik and Pregitzer 1993*a*), as determined by (1) the presence of multiple stems; (2) highly convoluted or crescent-shaped stem bases, which may be indicative of development around remnant stumps; (3) rapid early radial growth rates (B.J. Palik and K.S. Pregitzer, unpublished data), which can be indicative of vegetative origin (Sander 1990).

Stand development of the study area conforms loosely to the model described by Oliver (1981) for forests developing after major disturbance. The initial post-disturbance cohort of trees resprouted during a 10- to 15-year period (stand initiation). In most stands, a subsequent period of reduced establishment or survival (stem exclusion) followed, but the length of stem exclusion and, thus, the timing of understory reinitiation, was highly variable among stands (Palik and Pregitzer 1993*b*).

Methods

Sampling

This study was conducted using data collected for a comprehensive examination of stand development in the UMBS forest (Palik and Pregitzer 1992, 1993*a*, 1993*b*, 1994). For this previous work, trees were sampled on 16 circular 475-m^2 plots. Plots were located randomly within four stands (four plots per stand) belonging to the same ecological land type (Lapin 1990). For the present study, plots were used as replicates in all statistical analyses. On each plot, all trees ≥1.5 m tall that were species other than bigtooth aspen were destructively sampled. Only the tallest ramets were sampled from multistemmed genets. For bigtooth aspen, one individual on each plot from the dominant or codominant crown classes was randomly selected and destructively sampled. Most bigtooth aspen ramets were in dominant or codominant classes. Sampling intensity for bigtooth aspen was lower than that for other species because little height variation was observed among dominant–codominant ramets within plots and little age variation was expected.

Stems were felled at 0.5 m or ground level (depending on size). Stem sections were cut at ground level and at 1.4 m (breast height) from larger individuals, generally those taller than 2.5 m. The stem sections were sanded to a smooth surface and wetted with water to aid ring examination. Ages of all sections were determined by counting ring numbers on at least two radii that differed in orientation by 90–180° under a dissecting microscope. The oldest age of each section was recorded when the counts differed. 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.

Age chronologies developed from the cross sections were not cross-dated. Failure to cross-date may have introduced errors into estimates of plot age structures because of the occurrence of false or absent rings in some trees. However, false rings were identified easily based on cell structure and general appearance. We do not believe that they represent a significant source of error in our age estimates. Further, we believe the potential for aging errors resulting from locally absent rings (those absent from part of a cross section) was minimized by aging sections on at least two radii. Highly suppressed trees of low understory tolerance may be missing rings across the entire cross section. However, we believe that the effect of missing rings on our results was minimal because a ring would likely be missing from stem sections taken at both the tree base and breast height and, thus, comparisons between stand age structures based on the two methods would not be compromised.

Small stems of red maple and red oak, usually those <2.5 m tall, were aged at the base and 1.4 m by counting the number of terminal bud scale scars preceding each height interval. Small stems of white pine and red pine were aged by counting annual branch whorls. The accuracy of bud scale and branch whorl counts was checked by counting rings on the basal stem sections from a subsample of stems under a dissecting microscope. Age determinations for the two methods seldom differed by more than ±2 years and then only on individuals >2 cm basal diameter.

Analysis

Terminal bud scale counts, branch whorl counts, and ring counts on stem sections were used to determine total stem ages and ages at breast height. Differences in mean number of years to reach breast height were compared among species using ANOVA. Individual means were separated using Bonferroni contrasts (Gill 1978). Differences in mean number of years to reach breast height were compared between sprout- and seedling-origin stems and between pines and hardwoods using paired *t*-tests. For all parametric statistical analyses, residuals were judged to be distributed normally (Shapiro–Wilk test, $p = 0.10$) and variances were judged to be homogeneous (F-max test, $p = 0.25$).

A third age estimate was determined for each stem by adding a fixed number of years to breast-height ages as a correction factor. Aging height corrections were determined by averaging the number of years to reach breast height from the entire population of sampled stems, stratified within species-regenerative mode classes. The age corrections (number of years) were as follows: bigtooth aspen = 3; sprout red oak = 5; sprout red maple = 9; seed red oak = 14; seed red maple = 16; white pine = 21; red pine = 16.

The three age determinations for each stem were used to estimate establishment times (years after plot initiation). Time of plot initiation (years before sampling) was based on the mean age of all individuals establishing within the first 10 years of post-disturbance development. The timing of understory reinitiation (sensu Oliver 1981) was determined using the three age determinations on each plot and compared using paired *t*-tests.

We caution that nonrandom mortality across time introduces a potential source of error in our estimate of timing of understory reinitiation. Probability of mortality is a positive function of stem age and physiological stress. Therefore, older suppressed stems that established in the

Table 1. Summary statistics for number of years to reach breast height.

	Total[a]			Sprout[b]			Seed[c]		
Plot	Mean (years)[d]	CV (%)	Range (years)	Mean (years)[d]	CV (%)	Range (years)	Mean (years)[d]	CV (%)	Range (years)
1	16 (7)	44	28	5 (3)	60	7	17 (6)	35	24
2	14 (6)	43	22	5 (3)	60	7	15 (5)	33	21
3	14 (6)	43	28	3 (1)	33	3	15 (6)	40	26
4	13 (6)	46	24	8 (5)	63	12	14 (6)	43	23
5	21 (7)	33	28	5 (3)	60	11	23 (4)	17	21
6	17 (6)	35	31	5 (3)	60	7	19 (5)	26	24
7	12 (6)	50	26	6 (4)	66	10	13 (6)	46	26
8	18 (8)	44	28	6 (4)	66	12	23 (4)	17	14
9	20 (6)	30	30	6 (3)	50	8	21 (4)	19	21
10	17 (5)	29	27	8 (5)	63	12	18 (4)	22	20
11	16 (5)	31	24	10 (8)	80	22	17 (4)	24	19
12	19 (5)	26	27	11 (6)	55	17	20 (4)	20	21
13	18 (6)	33	34	5 (3)	60	8	19 (5)	26	30
14	18 (7)	39	32	13 (5)	38	11	18 (7)	39	29
15	24 (10)	42	37	6 (5)	83	18	28 (6)	21	25
16	21 (7)	33	31	9 (9)	100	23	22 (5)	23	22

Note: Standard deviation is given in parentheses.

[a] All stems combined by plot.

[b] Stems of vegetative origin (all species combined).

[c] Stems of seed origin (all species combined).

[d] Mean number of years to reach breast height (1.4 m).

understory, either at the end of initial post-disturbance establishment or at the beginning of understory reinitiation, may have died prior to sampling. Such errors would have the effect of overestimating the length of stem exclusion and, thus, the timing of understory reinitiation. Interpretation of results from our study are not compromised by this source of error, since its effect would be manifest similarly in stem age distributions based on all three aging methodologies.

Cumulative establishment distributions were constructed by plot (pooling all species) using both stem ages as determined at the base and at breast height. For each plot, shapes of the cumulative establishment distributions (differences in location, dispersion, skewness, etc.) were compared using a Kolmogorov–Smirnov two-sample test (Sokal and Rohlf 1981). Similarly, the breast-height age distributions, corrected for aging height, were compared with those based on total ages using Kolmogorov–Smirnov two-sample tests. The cumulative establishment distributions provide relative measures of plot age structures that are directly comparable to each other, since the time of establishment of the oldest stem in each plot is set to zero, thus defining the beginning of plot initiation for each distribution. If all aging methodologies capture the true relative age structure of a plot, then cumulative establishment distributions based on each methodology should not differ significantly.

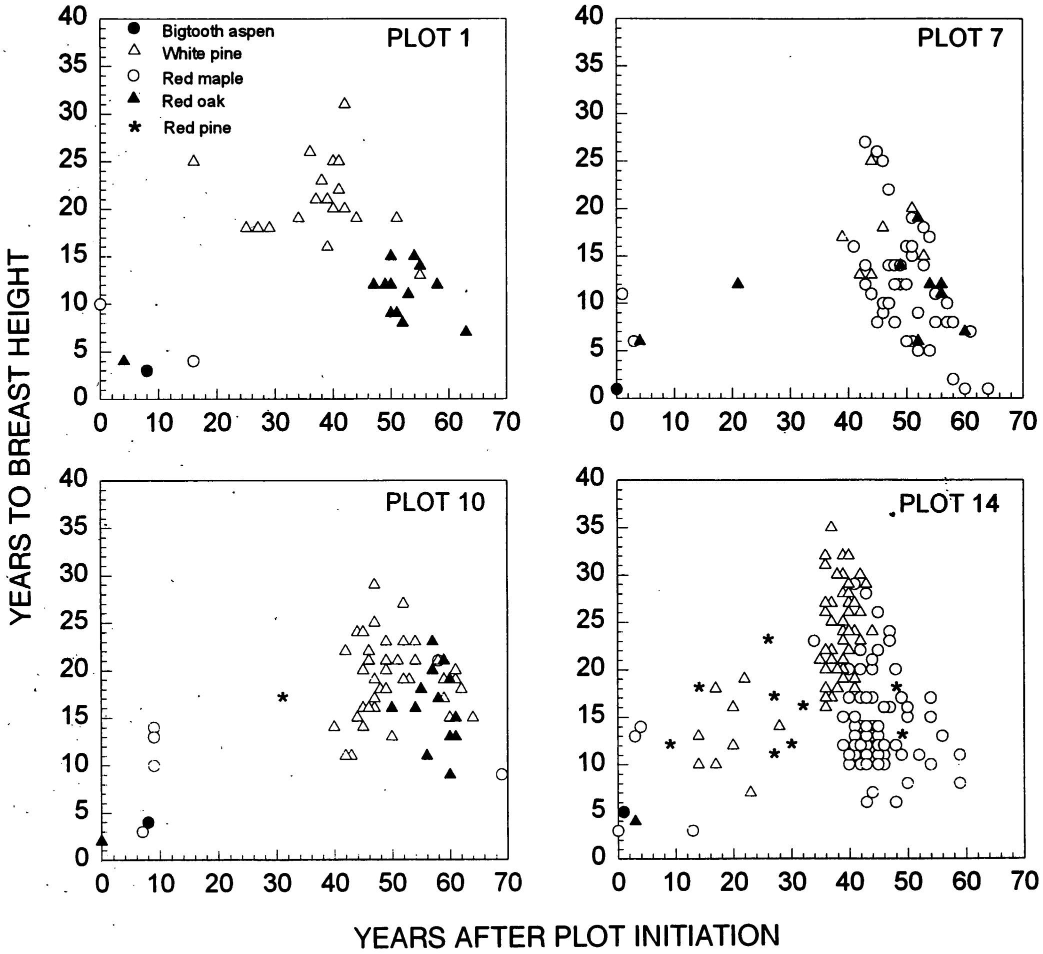
Results

Variation in early height growth rates

Mean number of years to reach breast height, pooling all stems and species, varied from 12 to 24 years among plots, while the coefficient of variation ranged from 26 to 50% of the mean (Table 1). The range in number of years to reach breast height within plots varied from 22 to 37 among plots (Table 1). Examining cohorts separately, mean number of years to reach breast height in the sprout cohort varied from 3 to 13 among plots, while the coefficient of variation ranged from 33 to 100% of the mean (Table 1). The range in number of years to reach breast height varied from 3 to 23 among plots (Table 1). Within the seed-origin cohort, mean number of years to reach breast height varied from 13 to 28 among plots, while the coefficient of variation ranged from 17 to 46% of the mean (Table 1). The range in number of years to reach breast height among seed-origin stems varied from 14 to 30 among plots (Table 1).

The selected plots in Fig. 1 illustrate some factors that had a strong influence on early height growth rates of the sampled stems. Within the sprout-origin cohort, there was a significant species effect on early height growth rate (pooling all stems within each of three species in each of 16 plots; randomized block ANOVA, $\mathrm{MS}_{\mathrm{plot}} = 5.820$, $\mathrm{MS}_{\mathrm{species}} = 133.761$, $\mathrm{MS}_{\mathrm{error}} = 4.010$, $p < 0.0001$; where MS represents mean square). Specific contrasts (Bonferroni *t*-tests), comparing pairs of species of decreasing understory tolerance, indicated that the mean (±SE) number of years for red maple to reach breast height was significantly greater than that for red oak (9 ± 0.6 vs. 5 ± 0.6 years; $t_{\mathrm{b}} = 5.665$, $p < 0.01$), while red oak and bigtooth aspen (3 ± 0.4 years) did not differ significantly ($t_{\mathrm{b}} = 2.260$, $p > 0.05$). Mean (±SE) number of years to reach breast height was significantly greater for seed-origin stems (19 ± 1 years) than for sprout-origin stems (7 ± 0.5 years) within a plot (pooling all species separately within the

Fig. 1. Number of years to reach breast height (1.4 m) as a function of time of establishment (years after plot initiation) for all stems in four selected plots. (Note that each plot contained an additional 15–35 bigtooth aspen ramets of similar age as the sampled stem.)



sprout- and seed-origin cohorts; paired *t*-test; $t_p = -11.459$, $p < 0.0001$, $n = 16$). Within the seed-origin cohort, mean (±SE) number of years to reach breast height was significantly greater for white pine (20 ± 1 years) than for hardwood species (15 ± 0.8 years; paired *t*-test, $t_p = 4.228$, $p = 0.0014$, $n = 12$ plots containing ≥3 stems of both taxa). Red maple and red oak were combined in the hardwood category, since early height growth was not significantly different between these two species (paired *t*-test, $t_p = 2.514$, $p = 0.07$, $n = 5$ plots containing ≥3 stems of both species).

Early height growth rates were variable in the understory cohort, even after accounting for the influence of species-specific growth rates (Fig. 1). For red maple, the coefficient of variation in number of years to reach breast height varied from 33 to 50% of the mean among plots, while the range in number of years to reach breast height for red maple stems within each plot varied from 17 to 26 (Table 2). For white pine, the coefficient of variation in number of years to reach breast height varied from 13 to 39% of the mean among plots, while the range in number of years to reach breast height among stems within plots varied from 12 to 28 (Table 2). The coefficient of variation in number of years to reach breast height varied from 13 to 38% of the mean among plots for red oak and 20 to 29% for red pine, while the ranges in number of years to reach breast height among stems within plots varied from 4 to 21 for red oak and 7 to 16 for red pine (Table 2).

Interpretations of stand age structures

All 16 comparisons between establishment distributions based on total ages and those based on breast-height ages were significantly different ($p < 0.01$; Table 3). Selected plots are illustrated in Fig. 2. For these plots, cumulative establishment across time, as inferred from breast-height ages, lagged behind that based on total stem ages, beginning 10–40 years after plot initiation. Further, on three of the four plots (7, 10, 14), the establishment periods lasted longer when based on breast-height ages. The establishment distributions based on breast-height ages suggest that plot age distributions had a greater skew towards younger individuals than was actually the case. The results were similar for the 12 additional plots.

Seven of the 16 comparisons between cumulative establishment distributions based on total ages and those based on breast-height ages plus a correction factor were significantly different ($p < 0.05$–0.01; Table 3). For example, on plot 14 (Fig. 2), cumulative establishment based on corrected breast-height ages began to lag behind that based

Table 2. Summary statistics for number of years to reach breast height for species in the seed cohort[a] of stems.

	Red maple			Eastern white pine			Northern red oak			Red pine		
Plot	Mean (years)[b]	CV (%)	Range (years)	Mean (years)[b]	CV (%)	Range (years)	Mean (years)[b]	CV (%)	Range (years)	Mean (years)[b]	CV (%)	Range (years)
1	—	—	—	21 (4)	19	18	12 (3)	25	8	—	—	—
2	15 (5)	33	21	—	—	—	13 (5)	38	14	—	—	—
3	15 (6)	40	26	18[c]			14 (5)	36	21	—	—	—
4	14 (5)	36	23	18 (7)	39	15	13 (5)	38	12	—	—	—
5	21 (7)	33	17	23 (3)	13	13	—	—	—	—	—	—
6	24 (9)	38	21	19 (3)	16	12	14[c]			—	—	—
7	12 (6)	50	26	17 (4)	24	12	12 (4)	33	13	—	—	—
8	—	—	—	23 (4)	17	14	—	—	—	—	—	—
9	—	—	—	21 (4)	19	21	—	—	—	19 (4)	21	7
10	15[c]			19 (4)	21	18	16 (4)	25	14	16[d]		
11	16 (6)	38	20	18 (3)	17	13	13 (4)	31	15	16[d]		
12	8[d]			20 (4)	20	20	18[c]			—	—	—
13	15[d]			20 (5)	25	26	15 (2)	13	4	14 (4)	29	16
14	15 (5)	33	23	23 (6)	26	28	—	—	—	15 (3)	20	12
15	—	—	—	28 (5)	18	24	18[c]			13[c]		
16	—	—	—	22 (5)	23	21	—	—	—	15 (4)	27	11

Note: Standard deviation is given in parentheses.

[a] Stems of seed origin.

[b] Mean number of years to reach breast height (1.4 m).

[c] Only two stems were measured.

[d] Only one stem was measured.

Table 3. Summary statistics for Kolmogorov–Smirnov comparisons of cumulative establishment distributions based on different stem-aging methodologies.

Plot	Total age vs. breast-height age[a] (D[c])	Total age vs. corrected breast-height age[b] (D[c])	N	$D_{0.05}$[d]	$D_{0.01}$[d]
1	0.421 05**	0.157 89	38	0.311 56	0.373 40
2	0.709 68**	0.403 23**	62	0.243 90	0.292 30
3	0.679 25**	0.226 42	53	0.263 82	0.316 18
4	0.450 00**	0.216 67	60	0.247 95	0.297 16
5	0.776 47**	0.423 53**	85	0.208 32	0.249 67
6	0.527 78**	0.222 22	36	0.320 11	0.383 63
7	0.655 74**	0.163 93	61	0.245 91	0.294 72
8	0.647 06**	0.205 88	34	0.329 39	0.394 76
9	0.745 28**	0.264 15**	106	0.186 55	0.223 57
10	0.698 41**	0.174 60	63	0.241 98	0.290 00
11	0.719 10**	0.247 19*	89	0.203 59	0.249 91
12	0.720 43**	0.193 55	93	0.199 16	0.238 69
13	0.776 79**	0.250 00**	112	0.181 48	0.217 50
14	0.710 34**	0.400 00**	145	0.159 50	0.191 15
15	0.671 43**	0.385 71**	70	0.229 56	0.275 12
16	0.666 67**	0.212 12	66	0.236 41	0.283 33

[a] Cumulative establishment distributions based on total ages and ages at breast height (1.4 m).

[b] Cumulative establishment distributions based on total ages and ages at beast height plus a correction for years to reach breast height.

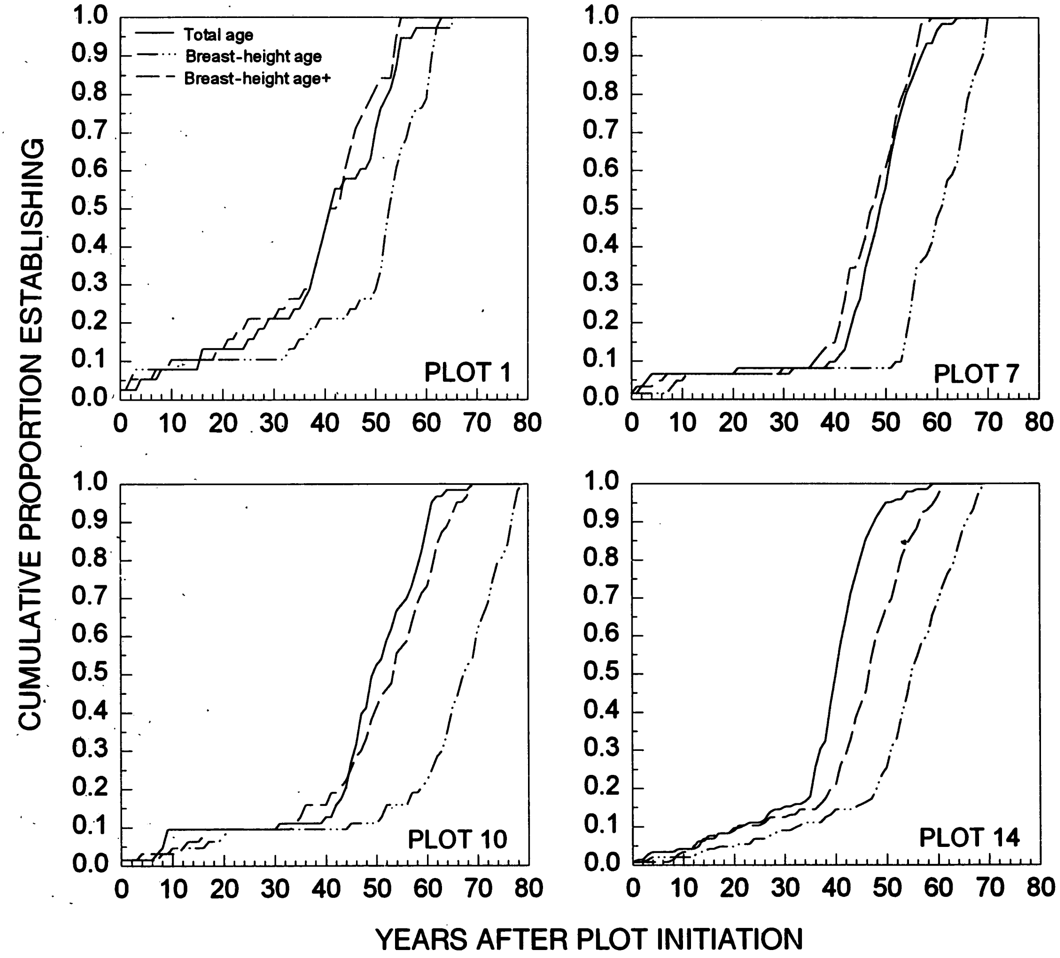
[c] Test statistic for Kolmogorov–Smirnov two-sample test.

[d] Critical values for type I error probabilities of 0.05 and 0.01.

*$p \le 0.05$.

**$p \le 0.01$.

Fig. 2. Cumulative establishment distributions of four selected plots based on total stem ages, ages at breast height (1.4 m), and ages at breast height plus a correction for number of years to reach breast height (breast height age+).



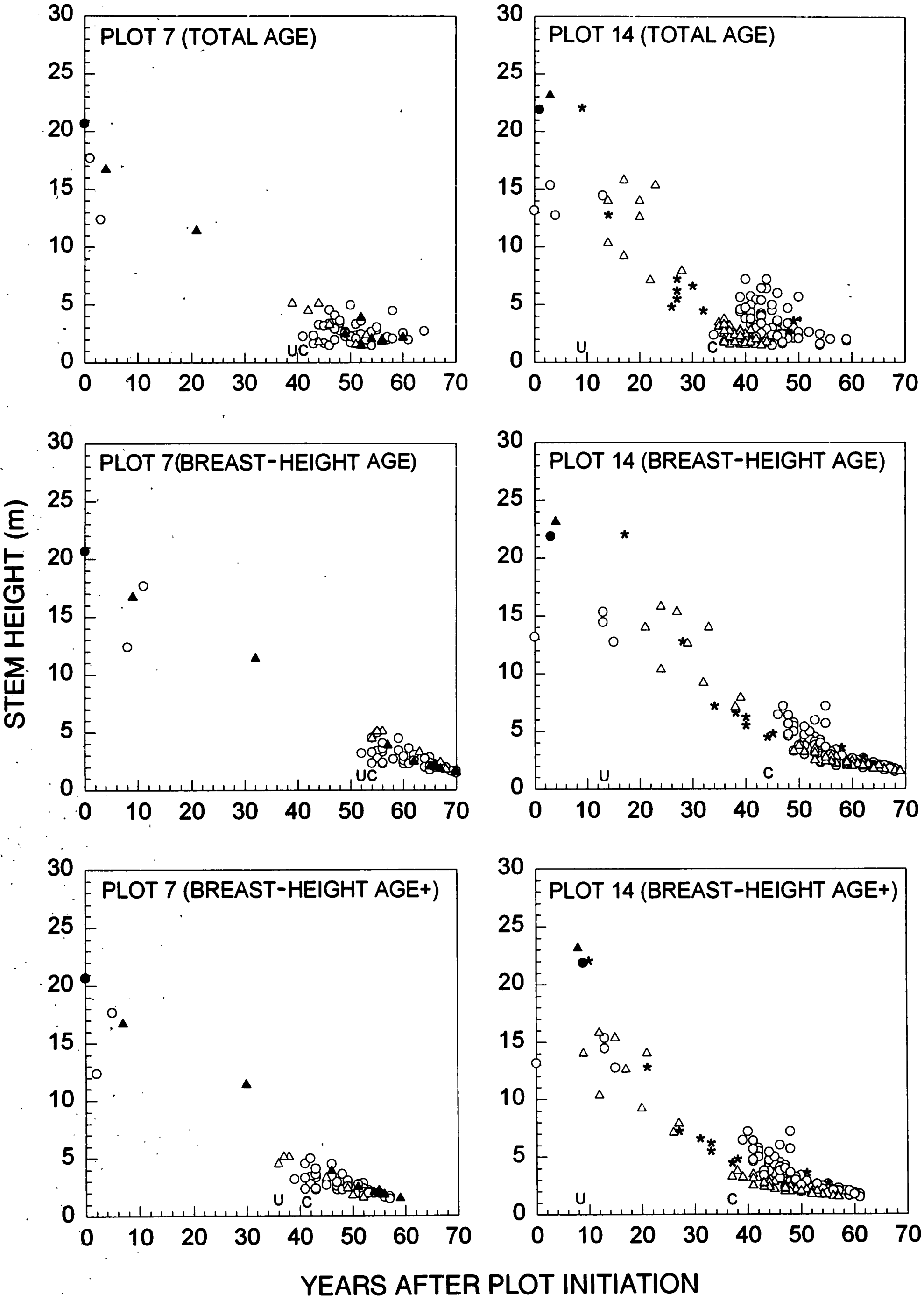
on total stem ages beginning 30 years after plot initiation, implying a younger age structure than was actually the case. In contrast, for the other three illustrated plots, distributions based on corrected breast-height ages matched closely those based on true stem ages.

Interpretations of stand development patterns

In previous work, the timing of understory reinitiation was determined for the 16 plots examined in the current study (Palik and Pregitzer 1993*b*). For each plot, time of plot initiation (years before sampling) was based on the mean age of all individuals that established within the first 10 years of post-disturbance development. Time of understory reinitiation was defined as the stand age (years after stand initiation) after which at least two new individuals established every 5 years for at least a 20-year period (see Fig. 3 for examples). Establishment was defined as survival to the time of sampling. Additionally, a second, more conservative estimate of timing of understory reinitiation was defined as the number of years until at least one individual established every year, or two individuals established every 2 years, for at least a 10-year period, or to the time of sampling (Fig. 3). This latter estimate was termed continuous understory establishment. Determinations of the timing of both understory reinitiation and continuous understory establishment are not biased by exclusion of stems <1.5 m tall (as in the current study), since the maximum ages of these individuals rarely approached the age of individuals ≥1.5 m tall that defined the start of understory reinitiation and continuous understory establishment (Palik and Pregitzer 1993*b*). As reported previously (Palik and Pregitzer 1993*b*), mean (±SD) time to understory reinitiation for the 16 study plots was 25 ± 12 years after plot initiation, while mean time to continuous understory establishment was 34 ± 7 years after plot initiation.

For the current study, timing of understory reinitiation and continuous understory establishment were estimated, as above, but by using plot age structures determined from breast-height ages, both with and without an aging height correction (see Fig. 3 for examples). These two determinations were compared, separately, with the original estimates based on total tree ages using paired *t*-tests. Both mean (±SD) time to understory reinitiation (39 ± 12 years) and mean time to continuous understory establishment (48 ± 7 years), as determined using breast-height ages, were significantly greater than respective estimates based

Fig. 3. Age–height distributions for all sampled stems on two selected plots based on total stem ages, breast-height ages (1.4 m), and breast-height ages plus a correction factor for number of years to reach breast height (breast-height age+). (Note that each plot contained an additional 15–35 bigtooth aspen ramets of similar age as the sampled stem.) The U near the *x*-axis in each plot marks the start of understory reinitiation (at least two stems establishing every 5 years for a minimum of 20 years). The C near the *x*-axis in each plot marks the start of continuous understory establishment (at least one stem establishing every year, or two every 2 years, for a minimum of 10 years or to the time of sampling). Species symbols are as in Fig. 1.



on total ages (understory reinitiation: $t_p = -9.792$, $p < 0.0001$; continuous establishment: $t_p = -10.661$, $p < 0.0001$; $n = 16$). In contrast, mean time to understory reinitiation (24 ± 15 years) and mean time to continuous understory establishment (34 ± 7 years) based on breast-height ages plus an aging height correction factor did not differ significantly from estimates based on total tree ages (understory reinitiation: $t_p = 0.899$, $p = 0.383$; continuous establishment: $t_p = -0.677$, $p = 0.509$; $n = 16$).

Discussion

The results of this study illustrate, in a quantitative way, the variability in early height growth rates that can be a feature of tree populations in forest stands. Some of this variability reflects growth rate differences among species. In the overstory of the study forest, bigtooth aspen and red oak, both early successional, intolerant species, often had greater early height growth rates than did more tolerant red maple. In the understory, white pine had a slower early height growth rate than hardwood species. Differences in growth rates among species often are related to morphological and physiological traits (Canham and Marks 1985; Kozlowski et al. 1991).

Some variability in early height growth rates can be attributed to times of stem establishment. Greater early height growth rates, and much lower variability of growth rates among stems, within the initial post-disturbance cohort likely reflects greater resource availability during establishment, compared with understory stems. Also, mode of regeneration between these two cohorts may be a contributing factor, since vegetative stems often have faster early height growth rates than do seed-origin stems (Wilson 1968). Within species and cohorts, the remaining variability in early height growth rates is likely related to a combination of factors, including variation in competitive environments, microclimate, herbivory, and genotype.

Failure to account for variability in early height growth rates of forest trees by aging at beast height may lead to errors in interpretation of stand age structures, as illustrated by our example. For the study forest, cumulative establishment distributions, as determined from breast height stem ages, differed consistently from those based on total stem ages, the former implying younger plot age structures than was actually the case. Thus, breast-height ages do not capture the relative age differences among stems in the study forest. Cumulative establishment distributions based on breast-height ages plus an aging height correction differed 44% of the time from distributions based on total stem ages. This result implies that differences in early height growth rates among the species – age cohort combinations that were used to determine aging height corrections sometimes had a stronger influence on defining stand age structures than did variation within species – age cohort combinations. However, the ability to capture true relative stand age structures using corrected breast-height stem ages was not consistent. Further, successful determination of stand age structures using corrected breast-height ages will depend on having reasonable estimates of time to reach breast height for each important species – age cohort combination of a study ecosystem. Such estimates are seldom available in the literature.

This study also illustrates the importance of having an accurate determination of stand age structure when attempting to interpret past dynamics of an even-aged stand. The differing estimates of timing of understory reinitiation and continuous understory establishment, depending on stem aging methodology, serve as an example. Misinterpretation of past stand dynamics as a result of aging methodology may obscure the search for mechanisms that cause patterns in stand development. For example, in previous work (Palik and Pregitzer 1993*b*), we hypothesized that the timing of continuous understory establishment in the study forest was caused by an increase in resource availability in the understory occurring in response to a wave of mortality (perhaps natural thinning) within bigtooth aspen populations. In contrast, we hypothesized that the timing of early understory reinitiation was related to the local availability of seed from tolerant species (Palik and Pregitzer 1993*b*, 1994). Evidence to support our hypothesis that continuous understory establishment is controlled by increased resources was provided by way of radial growth increases in co-occurring overstory red oak and red maple. These radial growth increases coincided with the start of continuous understory establishment on most plots. The strength of this argument would have been lessened had stem establishment patterns been reconstructed using breast-height stem ages rather than total stem ages, because of the significantly longer period of stem exclusion that was estimated using the former aging methodology.

We recognize that the results of our study have application to a narrowly defined subset of stand dynamics studies; i.e., those that rely on accurate determination of tree "birth" dates and stand ages. In contrast, for many retrospective studies, estimates of tree establishment dates are of less interest than are dates of release from understory suppression or of canopy recruitment. Additionally, the objectives of many studies may be met simply by defining a window of establishment, for example, establishment within a specific decade. Defining a window of establishment may be necessary in some studies because of the difficulty associated with aging large, old trees from increment cores and because of the restrictions placed on cutting such trees in preserves. Also, our study does not address the distinction between root-collar ages and stem ages, which can differ by many decades. Thus, our results have application only for interpreting development following the most recent stand initiating disturbance and cannot address the cumulative influence of multiple past disturbances on stand development.

In conclusion, we suggest that for the subset of retrospective studies that do depend on accurate determination of tree and stand ages, every effort should be made to age trees as close to ground line as possible. Further, when correcting ages for coring or cutting at some height well above the stem base, age corrections should be based on estimates of early height growth rates that incorporate knowledge of growth rate variation as related to species, regenerative modes, and times of establishment. Finally, for studies similar to ours, interpretations of stand age structures based on breast-height ages should be made cautiously, since use of breast-height ages may result in different interpretations than those based on actual tree ages.

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