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Early cohort development following even-aged reproduction method cuttings in New York northern hardwoods

Ralph D. Nyland, David G. Ray, Ruth D. Yanai, Russell D. Briggs, Lianjun Zhang, Robert J. Cymbala, and Mark J. Twery

Abstract: We described a general pattern of cohort development following two types of even-aged reproduction methods in northern hardwoods. Three clearcut sites initially had divergent numbers of stems, because of variable amounts of advance regeneration. By 10 years, total stem densities became quite similar across sites. Three sites treated by shelterwood seed cutting lacked advance regeneration. Compared with the clearcuts, seedlings became established at much higher stem densities there, and even early cohort development followed a consistent pattern. By 20–25 years, both the clearcut and shelterwood sites supported 7600–8900 total stems/ha. Stems ≥2.54 cm diameter at breast height peaked at about 6000, but by age 15 following clear-cutting, and not until age 20 after shelterwood seed cutting. The time lag likely reflects initial differences in advance regeneration, and possibly other factors between sites. Basal area at the clearcut sites reached 26 m^2/ha within about 25 years. At the shelterwood sites it reached 22 m^2/ha by age 25. The quadratic stand diameter increased consistently across sites and treatments. Regression models describe changes in numbers of total stems, numbers of saplings, stand basal area, and quadratic stand diameter for each treatment.

Résumé : Les auteurs décrivent un patron général de développement des cohortes suite à l'application de deux types de méthodes de régénération équiennes chez les feuillus nordiques. Initialement, trois sites coupés à blanc avaient un nombre différent de tiges dû à des quantités variables de régénération préétablie. Au bout de 10 ans, la densité totale des tiges était devenue très semblable dans ces sites. Trois sites qui avaient subi une coupe progressive de régénération n'avaient pas de régénération préétablie. Dans ces sites, les semis se sont établis à des densités beaucoup plus élevées que dans les sites coupés à blanc et même le développement initial des cohortes a suivi un patron cohérent. Vers l'âge de 20 à 25 ans, les sites qui avaient subi une coupe à blanc ou une coupe progressive supportaient un total de 7600 à 8900 tiges à l'hectare. Le nombre de tiges de 2,54 cm de diamètre ou plus à hauteur de poitrine a atteint un maximum d'environ 6000, mais seulement vers l'âge de 15 ans dans le cas de la coupe à blanc et pas avant l'âge de 20 ans dans le cas de la coupe progressive. Ce décalage dans le temps reflète probablement les différences initiales entre les sites dans la régénération préétablie et possiblement d'autres facteurs. La surface terrière a atteint 26 m^2/ha dans les sites coupés à blanc après environ 25 ans. Elle a atteint 22 m^2/ha à 25 ans dans les sites soumis à la coupe progressive. Le diamètre quadratique du peuplement a augmenté de façon similaire dans tous les sites et avec tous les traitements. Des équations de régression décrivent les variations dans le nombre total de tiges, le nombre de gaules, la surface terrière du peuplement et le diamètre quadratique du peuplement pour chaque traitement.

[Traduit par la Rédaction]

Introduction

The general descriptive model for development of even-aged northern hardwood stands presented by Bormann and Likens (1979) portrays the most important stages of cohort development based upon the accumulation of biomass over time. Oliver (1981) presented a similar model that empha-sizes the change in numbers of trees. Both describe an early chaotic phase when herbaceous vegetation dominates a site, followed by a gradual increase in importance of the tree component. Following tree canopy closure, biomass accumulates to a peak over several decades, and then declines as mortality eventually exceeds ingrowth and accretion (Bormann and Likens 1979). During this same period, mortality reduces stem numbers from a maximum near the time of canopy closure, to a low at the time when biomass reaches an upper limit (Oliver 1981; Oliver and Larson 1990). Yet, these conceptual models do not quantify numbers or sizes of stems, nor the time of transition from one stage to another. This limits their use in simulation modeling or in planning the management of developing even-aged tree communities.

Relative density guides represent another kind of conceptual model for even-aged stand development. They provide a quantitative index to the growing space used by individual trees, and sum these to characterize conditions in the stand

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as a whole. The one initially developed for oak (*Quercus* spp.) stands by Gingrich (1967), and later presented in the context of a management guide by Roach and Gingrich (1968), used the tree-area ratio approach developed by Chisman and Schumacher (1940). The resulting line for full stocking (100% relative density) shows the pattern of change for numbers of trees and total basal area as a stand matures. Later hardwood guides by Leak et al. (1969), Roach (1977), and Tubbs (1977) have a similar format. Each describes a consistent relationship between basal area and numbers of trees, with the line for 100% relative density representing the expected long-term pattern of development for single-cohort communities.

The guide by Roach (1977) demonstrated that species composition affects stocking in Allegheny hardwood stands (a variant of northern hardwoods). For any given stem density and quadratic stand diameter (QSD), the amount of total stand basal area depends upon the proportion of black cherry (*Prunus serotina* Ehrh.), white ash (*Fraxinus americana* L.), and tulip-tree (*Liriodendron tulipifera* L.) in the community. Similarly, Tubbs (1977) needed separate relative density guides to effectively differentiate stands with an important component of basswood (*Tilia americana* L.) or eastern hemlock (*Tsuga canadensis* (L.) Carr.) from other northern hardwood communities of the Upper Lake States. The work by Stout and Nyland (1986) confirmed this hypothesis of species effects on total stand basal area, and they proposed the use of three general species groups for describing relative density in Allegheny hardwoods.

None of these relative density guides predict changes in stand characteristics as a factor of stand age or site quality. In fact, Chisman and Schumacher (1940) demonstrated that adding a measure of site quality or age had no effect on the tree-area ratio. Later researchers used that evidence in their work, suggesting that their guides should apply to stands growing on a wide variety of sites. Also, none of the hardwood guides reflect the age when stands should reach different levels of stocking. They use change in number of trees as a surrogate for stand age. Experience suggests that stands on the better sites should follow along the suggested developmental pathway at a faster rate (Nyland 1996).

Our past work has demonstrated that in the absence of intensive herbivory or a dense understory of interfering plants, northern hardwoods in New York regenerate to well-stocked new cohorts following a variety of reproduction method cuttings. Clear-cutting has proven suitable for northern hardwood stands having abundant advance regeneration (Nyland and Irish 1971; Walters and Nyland 1989). Similarly, shelterwood method seed cutting produced high stem densities following herbicide treatments to reduce understory American beech (*Fagus grandifolia* Ehrh.) (Kelty and Nyland 1981; Ray et al. 1999). Both clearcutting and shelterwood method led to abundant tree regeneration and a high proportion of stocked plots at all sites. Canopy closure occurred within the new cohort around the end of the first decade (Wang and Nyland 1993; Ray et al.1999). Species importance values shifted over time, through at least 20 years in the clearcuts (Wang and Nyland 1993). Also, the proportion of more rapidly growing species of lower shade tolerance influenced the early patterns of basal area development and the rate of increase in QSD. However, that earlier

work did not model changes in numbers of trees or stand basal area over time or determine whether all stands followed a common trajectory of development.

The research reported here tested the hypothesis that young even-aged northern hardwood cohorts develop in a consistent pattern and that we could quantify stem density as a function of time after an even-aged reproduction method cutting. We used data from three long-term study sites in central New York to model changes in numbers of trees and basal area through 25–30 years following clear-cutting. We then compared the findings with those by Ray et al. (1999), who recently presented a model depicting early cohort development following shelterwood seed cutting in New York's Adirondacks.

Methods

Clearcut sites

For this research we used three clearcut stands located on state-owned forest land in Cortland (CC-1), Onondaga (CC-3), and Oneida (CC-2) counties in central New York. These ranged from 3 to 26 ha. Prior to cutting, all areas supported well-developed northern hardwood communities containing sawtimber-sized trees. All had a history of past partial cuttings that left irregular multiaged structures generally dominated by poor-quality trees. Basal areas ranged from 24 to 30 m²/ha, with sugar maple (*Acer saccharum* Marsh.) and American beech the most abundant species. Other species included white ash, trembling aspen (*Populus tremuloides* Michx.), large-toothed aspen (*Populus grandidentata* Michx.), black cherry, yellow birch (*Betula alleghaniensis* Britton), basswood, black birch (*Betula lenta* L.), grey birch (*Betula populifolia* Marsh.), red maple (*Acer rubrum* L.), eastern hemlock, hop hornbeam (*Ostrya virginiana* (Mill.) K. Koch), choke cherry (*Prunus virginiana* L.), shadbush (*Amelanchier arborea* (Michx. F.) Fern), and striped maple (*Acer pensylvanicum* L.). Clear-cutting felled all stems larger than 5 cm DBH. Because of poor markets for smaller diameter material, trees <30 cm DBH were left on site, and heavy slash covered much of the regeneration areas.

All three clearcut sites are located in hilly uplands at elevations between 396 and 579 m and with gently sloping terrain. The soils originated in glacial till composed of sandstone, siltstone, and shale. They are medium in texture, strongly acid, and generally well drained (Seay 1961; Hutton and Rice 1977). Season of logging varied, but none of the sites had frozen soil or snow cover during the harvesting operations.

Permanently located milacre plots (0.0004 ha) were established along transect lines situated no closer than 30 m apart within each regeneration area (Walters and Nyland 1989). Plots were located at 15-m intervals along these transects. Regeneration samples were taken prior to clear-cutting at two of the three sites, and immediately after cutting in all areas. Approximately 15 years after the regeneration cuttings, milacre plots were increased to 2 m radius plots (0.0012 ha) to reduce variability in stem counts as self-thinning progressed. Similarly, 0.02-ha plots were installed at two of the sites at 25–27 years. Total stems (stems ≥0.3 m tall) and saplings (≥2.5 cm DBH) were tallied at each measurement period. This periodic monitoring provided data to document stand development for up to 27 years following clear-cutting.

Neither deer browsing nor interfering plants seemed to preclude effective regeneration at these sites. But because main skid trails and log landings often do not regenerate promptly following cutting and may remain essentially devoid of tree cover for many decades (Walters and Nyland 1989; Oswald and Brown 1993), we limited our plots to the intertrail spaces. Further, the proportion of treatment area affected by skid trails and landings can vary widely

between stands. Thus, by locating plots only between the skid trails we eliminated their unpredictable influence on our evaluation.

Data analysis and modeling

Overall F tests indicated significant differences in total stem counts among clearcut sites at each point in time but with the differences diminishing with cohort age. We separated stand-level means using the Bonferonni procedure. For total stems (stems ≥30 cm tall), we detected no significant differences between CC-1 and CC-2 at age 10. By age 17, CC-2 and CC-3 also had similar total stem counts. Also at age 25, total stems at CC-2 and CC-3 could be combined. Differences in the amounts of advance regeneration in the clearcut stands made statistical comparisons of their pre- and early post-treatment status impractical.

For saplings, analysis of variance revealed no significant differences among the clearcut sites between ages 4 and 5 ($P = 0.21$) or between ages 10 and 13 ($P = 0.92$). At ages 17 and 20, significant differences were identified among all stands within the sapling class. However, by age 25, CC-2 and CC-3 were once more indistinguishable. CC-1 had significantly fewer saplings at age 27 than either of the other two areas.

We used dummy variables in the regression analysis to test for coincidence, equal slopes, and equal intercepts of the regression lines (Myers 1990; Rawlings et al. 1998). Slope parameters for total stems did not differ significantly beyond age 10. Results for the sapling size class suggested that the slope parameters for those regressions did not differ ($P = 0.55$) beyond age 15. In all instances, we rejected tests for the intercepts and coincidence of the regressions at $\alpha = 0.05$ level.

We developed predictive models for the clearcuts using nonlinear regression techniques following the approach taken with three shelterwood stands in the Adirondacks (Ray et al. 1999). Total stems and saplings were modeled using the following equation (Ratkowsky 1990):

$$[1] \quad Y = X^a e^{(b-cX)}$$

where Y is stem density (number/ha) for either size class; X is time since treatment; e is the base of the natural logarithm; and a, b, and c are regression coefficients estimated by size class.

We also used dummy variable analysis to justify a single model of basal area (BA) development for the clearcuts. Stand level BA (m²/ha) was modeled using

$$[2] \quad BA = \sqrt{mX - b}$$

where m is an estimated regression coefficient and b is the intercept. Trials with other models (Ratkowsky 1990) indicated that eq. 2 best represented BA development for these stands.

Since numbers of saplings and their associated BAs exhibited significant within-treatment consistency, we also fitted models for QSD development (a composite of those measures). We fitted simple linear regressions with time since treatment as the predictor variable, using the stand level means for QSD as determined for both treatments. For all the analyses we used the Statistical Analysis System (SAS Institute, Inc. 1990).

Comparing clearcut and shelterwood sites

Shelterwood seed cutting had occurred at three sites located on the Huntington Wildlife Forest in Hamilton and Essex counties in the central Adirondack Mountains of New York State. Ray et al. (1999) described those stand conditions and detailed the methods for articulating patterns of cohort development for up to 25 years following the shelterwood seed cutting. Hunting had reduced browsing at all three shelterwood sites. Yet, they differed from the clearcuts in one noteworthy respect. Dense interfering understory beech was reduced by herbicide prior to seed cutting (Tierson 1967; Kelty and Nyland 1981). As a consequence, the shelterwood

sites lacked advance regeneration at the time of seed cutting. Also, widely spaced seed trees remained in place through the time of the last sampling at two of the sites, representing conditions associated with reserve shelterwood method. This produced two-aged stands with widely spaced large overstory reserve trees, and an understory of the new cohort. At the times of the last measurement the reserve trees accounted for 8 m²/ha (age 16) in one stand, and 15 m²/ha (age 20) in the other. Yet our observations indicate that because of the wide spacing between reserve trees and their large diameters, the understory remained well illuminated. We believe the reserve trees had no clear effect on the patterns of cohort development through the time of the last measurement (Ray et al. 1999). Results reported here support that assertion.

The consistent protocol for sampling at the clearcut and shelterwood sites allowed us to compare patterns of development and changes in stem densities following the two reproduction methods. We also used the same model form to evaluate cohort development after both the clearcutting and shelterwood seed cutting treatments (Ray et al. 1999). To compare these different sets of data, we initially plotted mean stem counts against time by size class. Subjective assessments indicated a common response within and between the shelterwood and the clearcut treatments. Subsequently, we used analysis of variance and mean separation procedures to test for significant differences in stem counts for stands within a common treatment (three clearcuts and three shelterwoods), and by size class (total stems and saplings). Time since clear-cutting or seed cutting provided the grouping criteria for those analyses. We used dummy variables to test for differences in the slope and intercept of regression lines describing the stem numbers by size class over time. Line segments representing similar time periods were tested using this methodology.

Results

Total stems (stems ≥30 cm tall)

Advance regeneration varied widely among the clearcut sites prior to treatment, ranging from 7700 to 47 600 / ha before cutting (Table 1). First-year stem counts also varied widely among the three clearcut sites. Because of a lack of remeasurement data between ages 2 and 10, the pattern of change for total stems over that period remains uncertain. As a consequence of these factors, we did not model the first decade of cohort development for the clearcuts. Total stems at the three sites had become more similar by year 10, and we used a nonlinear model (Fig. 1, solid line) to depict cohort development beyond that time. Total stems further converged among these sites between ages 10 and 27.

The model for the Huntington Wildlife Forest shelterwood sites (from Ray et al. 1999) also appears in Fig. 1 (broken line). At those sites, total stems peaked at approximately 95 000 / ha at age 5, then declined rapidly, dropping below 20 000 / ha by age 20. As shown, lines for the clearcut and shelterwood sites begin to converge to a common level by about 25 years.

Saplings (stems ≥2.5 cm DBH)

Numbers of advance saplings also varied among the clearcut stands, ranging from 0/ha at CC-2 to 560/ha in CC-3 at age 1 (Table 1). Sapling abundance was lowest 2 or 3 years following cutting, either as a direct result of the logging operations and (or) due to losses following cutting. Sapling ingrowth had increased again by age 5, and numbers climbed rapidly through year 10 (Fig. 2). As shown, the

Table 1. Stem densities over time by size class following clearcutting in three central New York State northern hardwood stands.

| Time (years post cut)	Total stems/ha ($\geq$0.3 m tall)		Saplings/ha ($\geq$2.54 cm DBH)	
	Mean $\times$ 10^3	SE $\times$ 10^3	Mean $\times$ 10^3	SE $\times$ 10^3
CC-1				
0	7.7	2.5	—	—
1	37.0	3.4	0.23	0.08
2	—	—	0.16	0.05
4	—	—	0.50	0.12
13	11.5	1.0	5.56	0.70
20	7.7	0.5	5.70	0.19
27	4.7	0.3	3.07	0.12
CC-2				
1	15.9	2.7	0.00	0.00
3	—	—	0.00	0.00
5	—	—	1.13	0.58
10	17.2	1.9	5.51	0.84
17	19.3	1.6	6.73	0.40
25	8.7	0.5	5.07	0.37
CC-3				
0	47.6	12.5	—	—
1	12.3	1.5	0.03	0.03
3	—	—	0.08	0.05
5	—	—	0.60	0.18
11	27.9	1.8	5.93	0.72
18	21.6	1.1	8.31	0.40
25	9.9	0.4	6.53	0.23

Fig. 1. Total stem densities (stems $\geq$30 cm tall) over time following clear-cutting and shelterwood seed cutting in New York northern hardwoods.
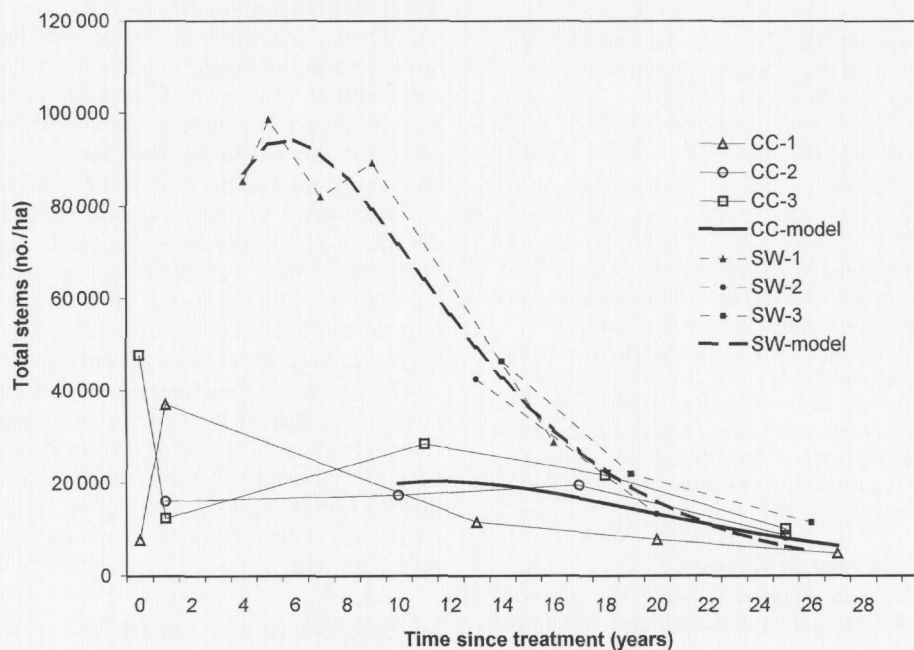
model predicts peak numbers of about 6500 saplings/ha approximately 15 years following clear-cutting.

Notable sapling ingrowth did not occur at the shelterwood sites until age 10, when stem count reached approximately 1000/ha. Sapling abundance increased rapidly through age 15 at these sites ($\cong$4000/ha), peaking at around 6100/ha by age 20.The model for the shelterwood sites shows the same developmental pattern as after clear-cutting, but with the curve reaching its maximum approximately 5 years later (Fig. 2).

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Fig. 2. Sapling densities (stems $\geq$2.54 cm DBH) over time following clear-cutting and shelterwood seed cutting in New York northern hardwoods.
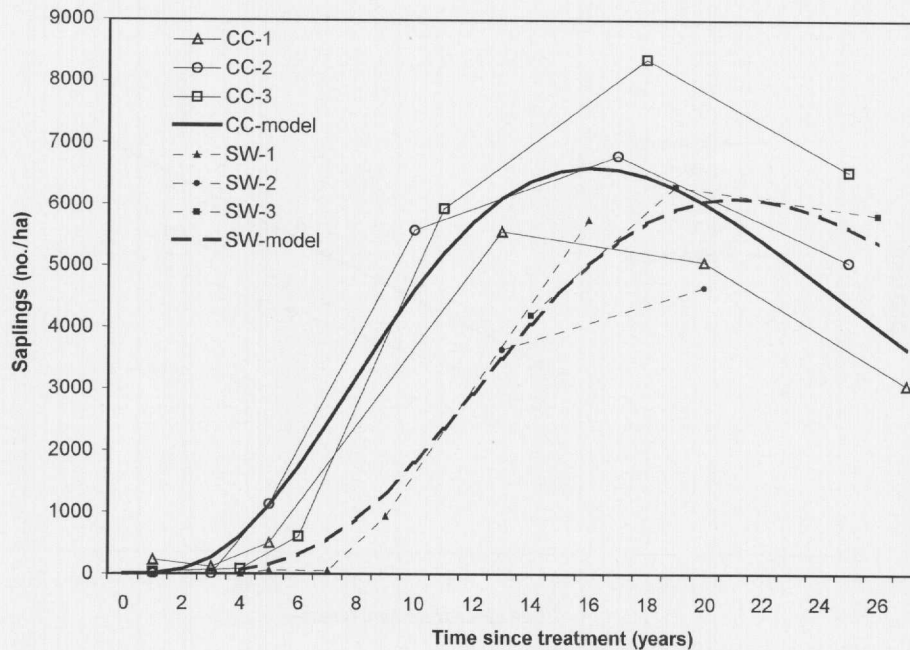
Fig. 3. Basal area development (saplings) over time following clear-cutting and shelterwood seed cutting in New York northern hardwoods.
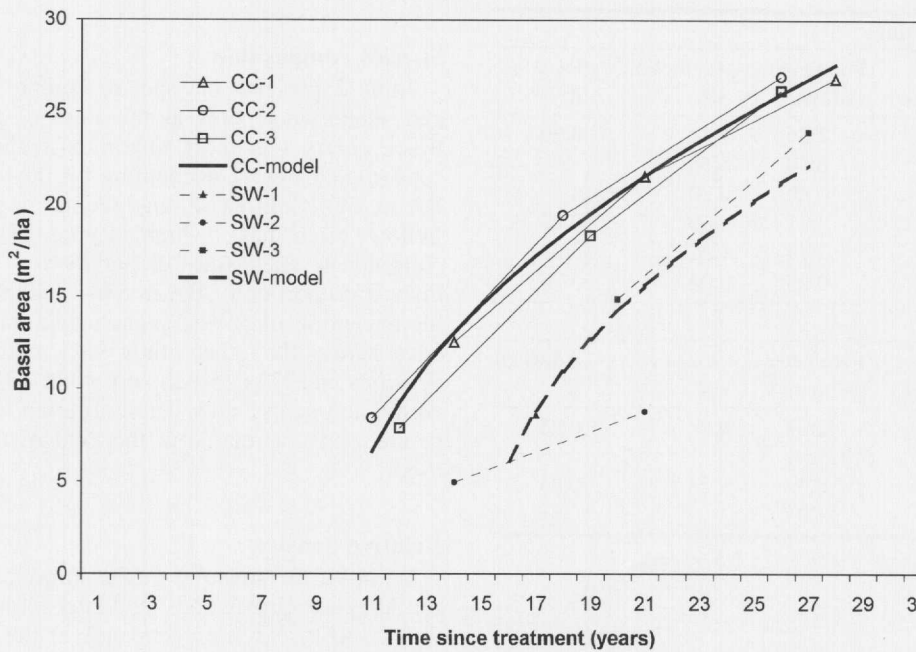

Basal area and QSD development

Basal area and QSD exhibited consistent trends of development. Dummy variable analysis failed to identify significant differences in the regressions of BA versus stand age in the clearcuts ($P = 0.54$), justifying a single model based on the combined data (Fig. 3). Stand level basal area reached approximately 9 m²/ha at age 10, 17 m²/ha by age 15, 22 m²/ha by age 20, and 26 m²/ha by age 25. Following shelterwood method seed cutting, basal area reached approx-

imately 9, 17, and 22 m²/ha, by ages 16, 21, and 26, respectively.

Quadratic stand diameter exhibited a somewhat divergent trend over time, particularly for the clearcut stands (Fig. 4). Initially, 10–13 years following clearcutting, QSDs were similar among sites, ranging from 4.1 cm at CC-3 and 4.3 cm at CC-2 to 5.3 cm at CC-1. The magnitude of that difference increased through time, ranging from 7.1 to 10.7 cm at ages 25 to 27 years. The shelterwood sites had

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Fig. 4. Quadratic stand diameter (QSD) development (saplings) over time following clear-cutting and shelterwood seed cutting in New York northern hardwoods.
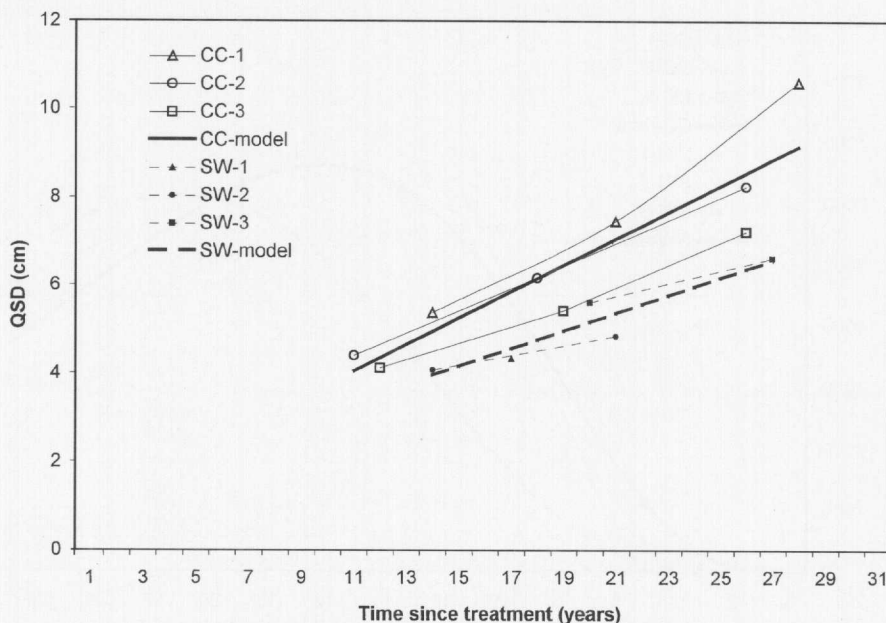
Table 2. Summary of regression coefficients and related statistics for early cohort development models following clear-cutting in New York northern hardwoods.

(A) Total stems and saplings

Model	Parameter	Parameter estimate	Asymptotic SE	Pseudo R^2
Total stems	a	2.36	3.22	0.90
	b	6.50	5.55	
	c	0.20	0.20	
Saplings	a	3.71	0.69	0.97
	b	2.19	1.22	
	c	0.23	0.04	

(B) BA and QSD

Model	Parameter	Parameter estimate	CV	Adjusted R^2
BA	m	42.04	9.07	0.98
	b	−377.01		
QSD	m	0.3	8.28	0.83
	b	1.04		

Note: Total stems or saplings = $X^a e^{(b-cX)}$; BA = $\sqrt{mX - b}$; QSD = $mX - b$.

consistently lower QSDs, ranging from 4.0 cm at age 13 to 6.6 cm by age 26.

Regression parameters and statistics

Table 2 shows the estimated regression parameters and selected statistics for the various models representing clearcut sites as presented in Figs. 1–4. Model residuals were normally distributed for the regressions. Predictions are valid over the range of the data used to construct them, as follows: (*i*) total stems from ages 10–27 for the clearcuts and ages 4–26 for the shelterwoods; (*ii*) saplings from age 0–26 and 27

for the shelterwoods and clearcuts, respectively; and (*iii*) basal area from ages 10–27 in the clearcuts, and ages 14–26 in the shelterwoods.

Species composition

Table 3 presents the species composition at the clearcut and shelterwood sites at the time of last remeasurement. Black cherry was more important at the central New York sites (the clearcuts), accounting for the highest proportion of BA in CC-1 and CC-2, and second to pin cherry in CC-3. Yellow birch has a high degree of importance at the Adirondack sites (the shelterwoods), accounting for the highest proportion of BA in SW-1 and SW-3. With the notable exception of SW-1, sugar maple had a consistent presence across the other study sites both in terms of stem densities and BAs. Beech and white ash vary in importance within and across sites. These differences appear regional in nature, and not related to the kind of reproduction method used.

Relative density

We used the stocking guide introduced by Roach (1977) for Allegheny hardwoods, and later refined by Marquis et al. (1984), to assess site occupancy at the time of last remeasurement at these sites. By age 25, the clearcuts had an average of 4900 saplings/ha, 26 m²/ha of BA, a QSD of 8.4 cm, and 40% of the basal area in black cherry and white ash. Based on those figures, new cohorts at the clearcut sites had reached 100% relative density. The shelterwood sites averaged approximately 5700 saplings/ha, 22 m²/ha of BA, a QSD of 6.4 cm, and had 20% of the basal area in black cherry and white ash. Extrapolating slightly below the minimum QSD represented in the stocking guide (7.6 cm), the new cohorts at the shelterwood sites also had approached 100% relative density.

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Table 3. Densities of total stems and saplings, and basal areas for saplings of commonly occurring species at the time of last measurement at the clearcut sites.

Species	CC-1 Age 27 Total/ha	Saplings/ha	BA (m²/ha)	CC-2 Age 25 Total/ha	Saplings/ha	BA (m²/ha)	CC-3 Age 25 Total/ha	Saplings/ha	BA (m²/ha)
Aspen	7	7	0.22	44	44	0.92	35	178	2.88
Beech	988	403	1.27	1295	499	0.53	1757	1038	1.47
Black cherry	509	479	14.39	682	613	6.46	865	744	4.94
Pin cherry	22	54	1.00	591	591	4.74	633	956	6.38
Sugar maple	2533	1673	6.94	3773	1841	4.29	3232	1851	3.58
White ash	35	86	0.84	568	432	4.62	623	502	2.87
Yellow birch	35	42	0.53	638	546	3.77	148	269	1.43
Other*	621	324	1.56	1067	499	1.52	1144	993	2.55
Total	4750	3068	26.75	8658	5065	26.85	8437	6531	26.10

*Other species include: basswood, black birch, choke cherry, gray brich, hemlock, hophornbeam, red maple, red spruce, shadbush, and striped maple. The listed species accounted for at least 5% of total stand BA in at least one stand at the time of last measurement.

Discussion

Limiting the analyses to data gathered within the intertrail spaces likely improved the consistency of findings among stands, providing a better estimate of the ecological potential of the different sites. The resulting model indicates that, by the time of canopy closure (approximately 10 years), the new cohort at three central New York northern hardwood sites treated by clear-cutting began to show a common pattern of development. Likewise, shelterwood seed cutting at three sites in the Adirondack Mountains also led to a consistent pattern of cohort development, but with stem densities initially much higher than at the clearcut sites.

Past research indicates that size–density relationships define an upper limit to the numbers and sizes of trees that can occupy a given area (sensu Reineke 1933). Our data suggest that once canopy closure occurred, appreciable mortality had begun to reduce total tree density in these even-aged cohorts (Kelty and Nyland 1981; Walters and Nyland 1989; Wang and Nyland 1993; Ray et al. 1999). By 20 years the total stem density at the shelterwood sites had converged with that at sites treated by clear-cutting. Evidently, the processes acting to regulate stem densities brought these communities to a fairly homogeneous condition over a relatively short time period (within 20–25 years) after cohort initiation. This evidence supports our hypothesis of a consistent pattern of early development within young even-aged cohorts. Also, the decrease in stem density at all sites by 10 years indicates that the aggradation (Bormann and Likens 1979) or stem exclusion (Oliver 1981) phase of cohort development had begun by that time.

At neither the clearcut nor shelterwood sites did interfering plants or animal browsing appreciably influence cohort establishment and development. For the clear-cutting, contractors felled all stems larger than 5 cm DBH, while for the shelterwood seed cutting they removed mid- and low-level shade as well as the majority of upper-canopy trees. This left a reserve of widely spaced dominants at the shelterwood sites (Ray et al. 1999). The seed trees remained at two shelterwood sites throughout the measurement period and could have influenced development of the young cohort. Even so, available data clearly show that all of the cuttings

created ecological conditions conducive to the establishment and subsequent development of new even-aged cohorts comprised of tree species with a wide range of shade tolerances. Also, we saw a consistent pattern of development and a consistent level of stem density at shelterwood sites where reserve trees remained in place and where cutting removed the seed trees after 10 years. The latter site had the longest lapse time after seed cutting but a pattern of development and stem density similar to the sites with reserve trees still in place. Based upon these observations, we hypothesize that the reserve trees had little influence over site-level stem densities and that the shelterwood equation will serve as a useful model to describe early patterns of cohort development following regular shelterwood method or after a two-aged reproduction method cutting that leaves a low density of older trees.

Lack of data between ages 1 and 10 prevented us from describing cohort development over that period for the clear-cuts. Pre- and immediate postcut data showed that the three sites had widely divergent numbers of advance seedlings, also precluding meaningful modeling of those early years. Yet by 10 years, all clearcut sites supported fairly similar numbers of total stems, suggesting the onset of a process of stem exclusion that reduced total numbers to some ecologically based level of stocking. For the shelterwood sites, equations suggest that total stems in the new cohort had reached a peak number by 5 years after seed cutting and then declined. This agrees with findings by other investigators, who earlier reported that total stem densities reached peak levels between 2 and 4 years following even-aged reproduction method cuttings in northern hardwoods (Bormann and Likens 1979; Hibbs 1983; Metzger and Schultz 1984; Marquis 1987).

Based on those findings and ours, we expect that total stem counts reached a maximum prior to age 10 at the clearcut sites, as they did after shelterwood seed cutting. Yet clearcut sites probably had fewer trees at the time of peak stem density. We also believe that the lack of advance regeneration at the shelterwood sites made ground-level conditions favorable to a higher rate of new seedling establishment than occurs in the presence of well-developed advance regeneration like that found prior to the clear-cutting. That advance

stocking at the clearcut sites likely limited early stem numbers and shortened the time to canopy closure to some degree, making the reduction in numbers less dramatic than at the shelterwood sites.

We also observed a common pattern of sapling development and a consistent maximum sapling stem density after the two reproduction methods. Yet the models predict that numbers of saplings in the clearcuts peaked 5 years earlier than at the shelterwood sites, and also that they began to decline sooner. Eventually, numbers of saplings also converged to a fairly common level across all sites. Based upon this evidence, we believe that the presence of abundant advance regeneration, perhaps coupled with the higher proportion of faster growing species that regenerated after the clearcuts, contributed to the earlier transitions within the sapling size class. As suggested by Ray et al. (1999), the model depicting development of the sapling size class actually portrays dynamics within the main crown canopy by ages 15–20 at the shelterwood sites. Current findings suggest the same relationship for the clearcuts but beginning by ages 10–15 after that treatment.

Basal area developed in a strikingly similar way among the clearcut sites, while data from the shelterwood sites showed a less consistent pattern. Basal area at the shelterwood sites remained lower than that after clear-cutting, consistent with differences in the timing of ingrowth into the sapling size class between treatments, and possibly influenced by the shorter growing season in the Adirondacks. The observed variability in basal area growth among the shelterwood sites most likely reflects differences in species composition, and possibly some influence of the widely spaced residual seed trees that remained in two of the sites. We found more of the slower growing sugar maple and American beech at SW-2, but more yellow birch at SW-1. Also, a more diverse species mixture developed at SW-3. Patterns of development for QSD appeared similar within and between treatments (Fig. 4), but with the shelterwood sites having a smaller QSD for any given age. The rate of increase in QSD tended to diverge over time, indicating that the growth of fewer but larger saplings resulted in comparable levels of basal area in these stands, particularly for the clearcuts.

Since our models of early stand development fit so well with conditions for 100% relative density in Allegheny hardwoods, we believe that our equations may serve as a useful device for portraying the early development of fully stocked even-aged northern hardwood cohorts leading to the time when they reach minimum conditions delineated by an appropriate relative density guide.

Conclusions

Data from these study sites allowed us to construct models depicting various aspects of early cohort development following two different even-aged reproduction method cuttings in New York northern hardwoods. The total abundance (total stems and saplings) and associated BAs and QSDs proved predictable over the first quarter century of cohort development in these communities. Forest managers and researchers can use our models to anticipate patterns of early stand development under similar conditions.

We believe both the status of advance regeneration prior to cutting and subtle differences in species composition between areas influenced the timing of developmental responses at the treatment level. Rates of development for sites without advance regeneration (shelterwoods) lagged approximately 5 years behind ones with advance regeneration (clearcuts). However, the numbers of total stems and the numbers of saplings converged towards similar stem densities by 20–25 years across all sites, indicating a common kind of response and an ecologically determined maximum stem density for young even-aged cohorts within this forest type.

Our results quantify the rate and magnitude of even-aged cohort development, providing previously unavailable information and filling a gap in understanding of even-aged stand dynamics for northern hardwood forests. Findings show that differences in species compositions influence the development of basal area and QSD but have less effect on the number of stems.

Acknowledgements

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