Canadian Science Publishing

ARTICLE

Long-term evolution of composition and structure after repeated group selection over eight decades

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Abstract: In northeastern North America, group selection is frequently used in northern hardwood forests to maintain uneven-aged stand structure and promote regeneration of tree species spanning a range of shade tolerances. For this study, long-term application of group selection at the Bartlett Experimental Forest, New Hampshire, USA, provided a unique opportunity to address cohort- and stand-level progression after 80 years of treatment. Cohort-level evolution reflected successional and developmental dynamics associated with even-aged forest systems, whereas aggregate stand-level conditions were consistent with expectations for uneven-aged systems. As cohorts aged, diameter distributions progressed towards descending monotonic forms and species composition transitioned from shade-intolerant species to shade-tolerant species. Standing deadwood and downed woody material in cohorts followed trajectories of aging even-aged stands through time. Although American beech (*Fagus grandifolia* Ehrh.) was a primary species across cohorts and at the stand level, stand-level regeneration included a mixture of ecologically and commercially valuable species. These long-term results offer important insights into emergent cohort- and stand-level conditions and processes that may affect continued recruitment of desirable compositional and structural conditions in stands managed using group selection over numerous cutting cycles.

Key words: group selection, uneven-age management, northern hardwood, silviculture.

Résumé : Dans le nord-est de l'Amérique du Nord, le jardinage par groupe est fréquemment utilisé dans les forêts de feuillus nordiques pour maintenir la structure inéquienne des peuplements et favoriser la régénération d'espèces d'arbres couvrant une gamme de tolérances à l'ombre. Dans cette étude, l'application à long terme du jardinage par groupe à la forêt expérimentale de Bartlett, située au New Hampshire, États-Unis, a fourni une occasion unique de documenter la progression arborescente aux échelles de la cohorte et du peuplement après 80 ans de traitement. Les changements temporels à l'échelle de la cohorte reflétaient la dynamique de succession et de développement associée aux systèmes forestiers équiennes, tandis que les conditions globales à l'échelle du peuplement étaient cohérentes avec les attentes reliées aux systèmes inéquiennes. Avec le vieillissement des cohortes, la distribution des diamètres progressait vers des formes monotones descendantes alors que la composition des espèces passait d'espèces intolérantes à l'ombre à des espèces tolérantes à l'ombre. Les arbres morts sur pied et les débris ligneux au sol dans les cohortes ont suivi les trajectoires de peuplements vieillissants de structure équienne au fil du temps. Bien que le hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.) soit une espèce primaire dans toutes les cohortes et à l'échelle du peuplement, la régénération à l'échelle du peuplement comprenait un mélange d'espèces désirées des points de vue écologique et commercial. Ces résultats de longue durée fournissent des renseignements importants sur les conditions et les processus aux échelles de la cohorte émergente et du peuplement qui peuvent affecter le recrutement continu des conditions souhaitables de composition et de structure dans les peuplements aménagés à l'aide du jardinage par groupe appliqué sur plusieurs rotations. [Traduit par la Rédaction]

Mots-clés : jardinage par groupe, aménagement inéquienne, feuillus nordiques, sylviculture.

Introduction

Uneven-aged silvicultural systems have long been applied to a great range of forest types and ownerships throughout temperate regions of the globe (Meyer 1952; O'Hara 2002; Kerr 2014). Early forms of uneven-aged management using selection-based methods were developed in Europe during the 1800s in response to overexploited forests and subsequently diminished wood supplies (Schutz 1999; Puettmann et al. 2009). These systems closely regulated age classes and diameter distributions, assuming regeneration replaced older, larger trees removed during harvest, creating a multiage stand structure and sustained yield over time (Baker 1934; Smith et al. 1997; Lundqvist 2017). In addition to more consistent growth and yield, uneven-aged systems also addressed noneconomic objectives, including protection of soil and water quality by maintaining continuous forest cover (Troup 1928; Miller and Kochenderfer 1998).

The distinct age class structure associated with uneven-aged management is achieved by removing single trees or groups of trees, creating small canopy gaps of <0.1 ha or 0.2–0.8 ha in size, respectively (Leak et al. 1987; Schutz 2001; Ontario Ministry of Natural Resources 2015). Removals are guided by compositional and stocking goals, tree quality, and target residual diameter

Received 20 July 2020. Accepted 15 November 2020.

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Can. J. For. Res. **51:** 1080–1091 (2021) dx.doi.org/10.1139/cjfr-2020-0339

distributions (Smith et al. 1997; Nyland et al. 2016). Commonly applied guides, including the BDq approach and Arbogast guide, encourage the development of reverse-J diameter distributions over time (Arbogast 1957; Guldin 1991; O'Hara and Gersonde 2004). However, additional diameter distributions such as the rotated-sigmoid and increasing-*q* have also been recognized in managed uneven-aged forests (Janowiak et al. 2008).

Single-tree selection maintains consistent forest cover following harvest, resulting in stands dominated by shade-tolerant species (Neuendorff et al. 2007; Keyser and Loftis 2013). More shade-intolerant species can be managed with single-tree selection if cutting cycles and residuals basal areas are carefully chosen (Schulte and Buongiorno 1998), yet maintaining a spectrum of shade tolerances, especially in mixed-species stands, is generally regarded as a benefit of group selection (Murphy et al. 1993). By removing trees as aggregates at each entry, group selection results in greater canopy disturbance, creating light conditions suitable for a wider range of species, depending on opening size and gap orientation (Leak et al. 1987; Diaci et al. 2005). When openings exceed 0.8 ha up to 2.0 ha, as with patch selection, groups are intended to act as small clearcuts recruiting similar levels of species diversity (Meadows and Stanturf 1997; Leak 1999). However, compared with larger clearcuts, patch cuts and large group opening retain a higher composition of shade-tolerant species. Group selection, and to a greater extent patch selection, increases heterogeneity relative to single-tree selection by creating a series of small even-aged "stands" that cumulatively form an uneven-aged condition (Murphy et al. 1993; Smith et al. 1997). Increased heterogeneity has recognized benefits but can pose operational challenges and diminish stand-level growth rates if removals are too heavy (Roach 1974; Murphy et al. 1993; Franklin et al. 2007; Lundqvist 2017).

Today, selection-based silvicultural systems remain a viable form of management for many forest types, balancing timber production, aesthetics, and ecological values (Franklin et al. 2002; Pommerening and Murphy 2004; Kern et al. 2017*a*). However, the degree to which selection systems, particularly group selection, have been adapted as a common management practice varies globally (Boncina 2011; O'Hara et al. 2018). In North America, selection methods are valued for their ability balance traditional forestry objectives, including sustained yield, economic returns, and structural and compositional regulation, with evolving policy mandates and changing public preferences (LeDoux 1999; Franklin et al. 2002; Fahey et al. 2018). Increasingly, selection methods are also used to meet contemporary ecological objectives and capture a wider range of ecosystem services, such as retention of coarse woody material, scenic value, and resiliency to changing climate conditions (Keeton 2006; D'Amato et al. 2011; Gamfeldt et al. 2013).

In northern hardwood forests in northeastern North America, selection methods have been widely applied to meet past and contemporary management objectives (Leak et al. 1987; Nyland 1998). These treatments largely mimic the frequent, partial canopy disturbances common in the region and have historically been successful in sustaining dominance of desired commercial species, namely sugar maple (*Acer saccharum* Marsh.) (Seymour et al. 2002; Lorimer and White 2003). In addition, the lower harvesting intensity of these methods relative to other silvicultural systems is consistent with the objectives of the family forest owners who own much of the region's land base (Costello et al. 2000; Kelty et al. 2003).

Long-term studies across the range of northern hardwood forests have shown single-tree selection can successfully regenerate sugar maple and other species that rely on advance regeneration, particularly on more fertile soils (Eyre and Zillgitt 1953; Gilbert and Jensen 1958; Bedard and Majcen 2001; Webster and Jensen 2007). Nonetheless, long-term application has generally led to forest conditions dominated by shade-tolerant species in all canopy layers (Lamson and Smith 1991; Niese and Strong 1992). This transition is in stark contrast to the diversity of canopy species and tolerances characterizing natural, unmanaged examples of these forests (Lorimer 1977; Woods 2004; Angers et al. 2005; Cain 2011). The decline in species diversity over time, including the loss of ecologically and commercially important mid-tolerant canopy species, such as yellow birch (*Betula alleghaniensis* Britt.), has been a major critique of single-tree selection (Kochenderfer et al. 2004; Webster and Jensen 2007). This issue has become increasingly problematic in stands with a heavy component of American beech (*Fagus grandifolia* Ehrh.). American beech is the most shade-tolerant species of northern hardwood and often becomes dominant with repeated single-tree selection cuttings, especially on sites with moderate fertility (Jones et al. 1989; Nyland et al. 2006; Canham 1989). With the arrival of beech bark disease (*Cryptococcus fagisuga*/*Neonectria* spp. complex) in the early 1900s, few healthy American beech remain in northeastern forests (Morin et al. 2007). Instead, what were originally single stems of American beech have been replaced by dense thickets of diseased root suckers with limited economic and ecological value (Ostrofsky 2005). The negative effects of American beech on regeneration of desired species, like sugar maple and yellow birch, are further exacerbated by high populations of white-tailed deer (*Odocoileus virginianus).* Deer favor maple and birch species for browse but find American beech less palatable, further shifting the competitive edge to American beech (Godman et al. 1990).

In the context of current regeneration challenges and the silvicultural preferences of regional land owners, group selection provides an opportunity to balance economic feasibility and structural flexibility with maintenance of species diversity and traditional uneven-aged forest characteristics (Leak and Gottsacker 1985; Niese and Strong 1992; Poznanovic et al. 2013; Nyland et al. 2016). Early research on northern hardwood silviculture acknowledged that maintaining yellow birch specifically would require integration of larger openings into forest stands (Gilbert and Jensen 1958). More recent studies indicate application of larger openings (>0.04 ha) is critical for providing a competitive advantage for less-tolerant species relative to American beech, especially if advance regeneration is removed and soils are scarified at the time of group removals (Shields et al. 2007; Leak et al. 2014).

One of the longest continuously maintained studies of group selection in the USA is at the Bartlett Experimental Forest in Bartlett, New Hampshire, where group selection has been repeatedly applied to a 46 ha northern hardwood stand since the late 1930s (Leak and Filip 1977). Relative to the initial stand composition, results from the first 61 years of the study showed an increased component of mid- and intolerant species, yellow birch, paper birch (*Betula papyrifera* Marsh.), and white ash (*Fraxinus americana* L.), in the sapling and small pole size classes (Leak 1999), despite initial American beech dominance. These results have led to an increased reliance on group selection harvests across northeastern North America to serve as a technique to transition even-aged forests to uneven-aged conditions (Kelty et al. 2003) and to maintain compositional diversity in uneven-aged forests dominated primarily by shade-tolerant species like beech and sugar maple (Falk et al. 2010; Kern et al. 2017*b*).

Despite the broad application of group selection, key knowledge gaps remain regarding the long-term outcomes of this approach on stand-level structure and composition. Specifically, uncertainty remains about the long-term structural and composition outcomes of this approach across group cohorts as well as whether group selection is able to continuously regenerate ecological and economically desired species over time. This study takes advantage of the unique abovementioned long-term research at the Bartlett Experimental Forest to examine the outcomes of eight decades of group selection harvests on stand evolution and individual cohort status. Much of our knowledge regarding the outcomes of repeated group selection emphasizes stand-level changes, leaving a limited understanding of within-stand variability, particularly structural and compositional conditions. Given group selection is often applied by extending even-aged concepts of area regulation to allocating and tracking within-stand cohort area and distribution, there is

Table 1. Attributes for managed cohorts and matrix.

Cohort	Years between harvest	Area (ha) Average	Minimum	Maximum	Total	No. of sample plots
1 (1937–1940)	NA	0.13	0.0	0.3	3.4	10
2 (1951)	14–11	0.24	0.1	0.3	6.4	16
3 (1960)	9	0.32	0.1	0.8	3.2	8
4 (1992–1994)	32–34	0.30	0.1	0.9	5.8	16
5 (matrix)	NA	NA	NA	NA	26.4	31
Managed cohorts	NA	0.20	0.0	0.9	18.8	50

Note: In this table, "Area" stands for area of groups in hectares (ha). NA, not applicable.

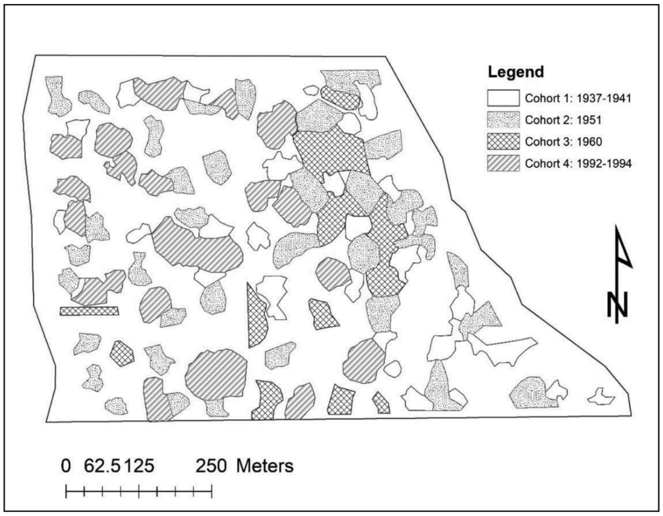
value in understanding the influence of cohort-level conditions on overall stand conditions. With this work, we undertook a detailed analysis of gap cohorts relative to the surrounding matrix and the stand as a whole. Specifically, we classify changes in compositional and structural attributes, and regeneration of cohorts created by group selection over time. This work will address three hypotheses regarding emergent stand and cohort properties. (*i*) After 80 years the overall stand will reflect characteristics traditionally associated with uneven-aged management (reverse-J diameter distribution for overstory trees), while containing compositional characteristics associated with group selection in northern hardwood forests of the northeast. This includes representation of shade-intolerant to -tolerant species in the overstory and regeneration of commercially desirable species competitive with regeneration of American beech. (*ii*) Group selection creates compositionally and structurally unique cohorts driven by decreasing species richness and increasing structural complexity as cohorts age. Decreasing species richness is primarily from the loss of intolerant and mid-tolerant species over time. Increasing structural complexity reflects diversity in diameter distributions and accumulation of coarse woody material over time. (*iii*) Attributes of uneven-aged stands managed with group selection reflect the aggregate of even-aged "microstands".

Materials and methods

Study site

This research was conducted on a 46 ha tract of uneven-aged northern hardwood forest at the Bartlett Experimental Forest (BEF) in Bartlett, New Hampshire (44°17′N, 71°3′W), during the summer of 2017. Group selection has repeatedly been applied to this stand, known as Compartments 5 and 6, since 1937. The initial harvest occurred between 1937 and 1940. Over the duration of the study, the cutting cycle has been variable (Table 1) with subsequent entries in 1951, 1960, and between 1992 and 1994. The location of group openings was designed to capture economically overmature trees or to release advance regeneration (Leak and Filip 1977). The size of group openings has varied within entries and across time, reflecting the changing forest condition and management objectives (Leak and Filip 1977; Leak et al. 2014). Across the study period, group openings ranged from 0.04 to 0.8 ha, with the average opening 0.2 ha in size (Fig. 1). Following the harvest in the early 1990s, 41% of the stand had been treated with group selection (Table 1).

Fig. 1. Group openings in Compartments 5 and 6 at the Bartlett Experimental Forest, New Hampshire, USA. Different patterns represent different cohorts created by application of group selection from 1937 to 1994. The matrix cohort is all area outside of groups.



The areas examined are at approximately 427 m in elevation and soils are primarily sandy loam podzols derived from glacial drift (Leak 1999). Climate is characterized by moderate summers and cold winters with snow coverage from December through mid-April (Leak 1999). Documentation of the stand prior to the first harvest is limited, but previous publications note the stand was "old-growth" northern hardwoods (cf. Gilbert and Jensen 1958) with a basal area of between 24 and 28 $m^2 \cdot ha^{-1}$ in stems 12.7 cm diameter and greater. Composition was approximately 70% tolerant species (American beech, sugar maple, eastern hemlock (*Tsuga canadensis* (L.) Carr.), and red spruce (*Picea rubens* Sarg.), 25% mid-tolerant species (yellow birch, red maple (*Acer rubrum* L.), white ash), and 5% intolerant species (paper birch) (Filip et al. 1960; Leak and Filip 1977). Harvesting in the stand prior to the establishment of this experiment in the late 1930s was limited to light high-grading for softwood species, namely red spruce, at the turn of the century (Leak and Filip 1977).

During the first entry, groups were clustered in areas containing economically mature trees with softwood advance regeneration and saplings up to 15.2 cm diameter at breast height (dbh) were retained where present (Leak and Filip 1977). Later entries were treated as small clearcuts (Gilbert and Jensen 1958), removing nearly all existing woody vegetation within the group, including advance regeneration of beech, with group establishment focused in areas containing trees at or beyond economic maturity (Leak 1999). Harvest entries were completed during the late fall and early winter, but information on snow cover or leaf-on and leaf-off condition was not recorded (W. Leak, personal communication). Tree removal was constrained to group openings, with any cutting in the matrix occurring only for the purpose of accessing the stand and establishing skid trails. No tending of groups after the initial harvest or within the matrix has occurred. Also, there was no additional scarification of the site via site preparation equipment postharvest; however, incidental scarification likely occurred during harvesting operations (Leak et al. 2017)

Plot selection

In 2017, 81 circular, fixed-area sample plots were established across the stand using a stratified sample design. The goal of the sample was to capture 10% by area (ha) of each managed cohort and 5% by area (ha) of the matrix. Managed cohorts and the matrix were sampled using 0.04 ha circular, fixed-area plots with a radius of 11.28 m. Total area occupied by each managed cohort was calculated in ESRI ArcGIS 10.6.1 (https://www.arcgis.com) using digitized maps of group openings generated from past harvest maps (Leak 1999). Area of the matrix was calculated as the difference between the total stand area and area in groups.

The individual groups where sample plots were established were selected using the random point function in ArcGIS 10.6.1. To ensure selected groups captured the variability in gap size within and among cohorts, groups were aggregated into 0.04 ha area classes by cohort. Sample plots were established in the center of each randomly selected group. If a selected group was larger than 0.4 ha, two plots were established with plot centers 75 m apart. Sample plots were established at the center of each group opening to minimize subjectivity in field protocols and create consistency between the type of area being sampled, edge versus gap interior, to the degree possible. The establishment of plots in the center of group openings minimizes the amount of edge area sampled as group openings increases in size. As such, findings from this work may not fully capture regeneration and structural dynamics associated with gap edge environments. To acknowledge the impact of plot placement on results, we calculated the correction between advance regeneration stocking of key species (American beech, sugar maple, yellow birch, other species) and average gap size, in hectares, by cohort (see Statistical Analyses below). Definitions of advance regeneration and stocking are below.

By cohort, once groups from each area class were selected, the remaining plots needed to reach the 10% sample size were randomly selected across all area classes using the random point function in ArcGIS. For the matrix, plot locations were determined using a 40.2 m by 40.2 m grid with a random start. We dropped plots from the final sample if they fell within 20.1 m of a group or the stand edge.

Plot locations determined using ArcGIS were then located in the field with a handheld Garmin 64s GPS unit. Accuracy of the GPS was ±3 m. We visually confirmed the location of plot centers in the field using physical features (i.e., composition and structure) associated with each cohort. Further, we walked group boundaries to ensure the area and shape matched information from ArcGIS and available paper maps.

Plot measurements

Overstory trees (≥10.2 cm dbh) were measured on the 0.04 ha plots, saplings (≥2.5 cm < 10.2 cm dbh) were measured on 0.02 ha nested circular plot, and seedlings were measured in four 0.0004 ha plots. Diameter and species were recorded for all live overstory trees and saplings and dead overstory trees.

Seedling plots were located 5 m out from plot center at azimuths of 0, 90, 180, and 270°. We tallied seedlings by species and size class from 0.3 m in height to 2.54 cm dbh. Size classes were grouped as follows: 0.3 m to 0.9 m, 0.9 m to 1.8 m, 1.8 m to 2.54 cm dbh.

Downed woody material was measured for wood pieces ≥10 cm in diameter and >1 m in length following the line intercept method (Harmon and Sexton 1996). Three 11.3 m transects were established on north (0°), southeast (120°), and southwest (240°) azimuths from plot center. If a piece of coarse material crossed two transects it was recorded twice following established field protocol; however, this situation was rarely encountered in the field (Fraver et al. 2018). For each piece of coarse material intersected, diameter at intercept, species, where possible, and decay class based on Sollins (1982) were noted. Total length of transect sampled for each cohort ranged from 271.1 to 1084.8 m, which is greater than the minimum lengths recommended for generating a precise estimate of deadwood volumes using this method (Fraver et al. 2018).

Statistical analysis

We conducted analysis for this work at the cohort and stand scale. Cohorts were summarized as follows: the 1993 cohort are the group selection harvests created between 1992 and 1994, the 1960 cohort corresponds to the groups created in 1960, the 1951 cohort are the groups established in 1951, the 1938 cohort are the original groups, corresponding to the entry between 1937 and 1940, and the matrix is the surrounding portion of the stand not cut with group selection. This cohort-level grouping was used for a chronosequence analysis where age increases from youngest cohort (1993 cohort) to oldest managed cohort (1938 cohort), and with the matrix representing the oldest, stand condition.

For each cohort, we calculated overstory characteristics related to structure and composition. Difference in structure and composition among cohorts was used to measure development over time. Overstory trees were classified as those ≥10.2 cm at breast height. Overstory structure was assessed using density, basal area, Shannon's diversity index for size classes, and standing dead and downed woody material. Density was calculated as the number of trees per hectare in each 5 cm size class by species group (American beech, sugar maple, yellow birch, eastern hemlock, and other species) and total. Other species largely refers to eastern hemlock in the matrix and 1938 cohort. In younger cohorts, other species includes white ash, red maple, and pin cherry (*Prunus pensylvanica* L.).

Shannon's diversity index was determined for density by diameter class of each cohort using the diversity function in the vegan package of R 1.2.5001 (https://www.r-project.org/). The index is calculated with the formula

$$(1)\qquad H_{\mathrm{Diameter}} = -\sum p_i \log(b) p_i$$

where p_i is the proportional abundance of species i, and b is the base of the logarithm. Greater values of Shannon's diversity index (H_{Diameter}) correspond to greater diversity in size classes.

Standing dead trees per size class were calculated by basal area as well as volume of downed woody material. Size classes were divided into three groups: saplings (2.5–10.1 cm), poletimber (10.2–21.3 cm), and sawtimber (≥21.4 cm). Woody material volume was computed using the formula

$$(2)\qquad V = \left(\frac{\pi^2 \Sigma d^2}{8L}\right) \times 10\,000$$

where V is the volume of coarse woody material ($\mathrm{m}^3\ \mathrm{ha}^{-1}$), d is the intercept diameter of the woody material in metres, and L is the downed woody material sampling transect length in metres (van Wagner 1968).

Change in composition over time was represented by change in composition among cohorts following a chronosequence approach. Compositional change per cohort was measured by Shannon's diversity index (all species) and species importance values calculated for the species groups listed above. Shannon's diversity index (H_{Species}) for species in each cohort was determined following the steps outlined above for H_{Diameter}. Species importance value (IV) was determined from the formula

$$(3)\qquad \mathrm{IV} = (R_{\mathrm{Den}} + R_{\mathrm{Dom}})/2$$

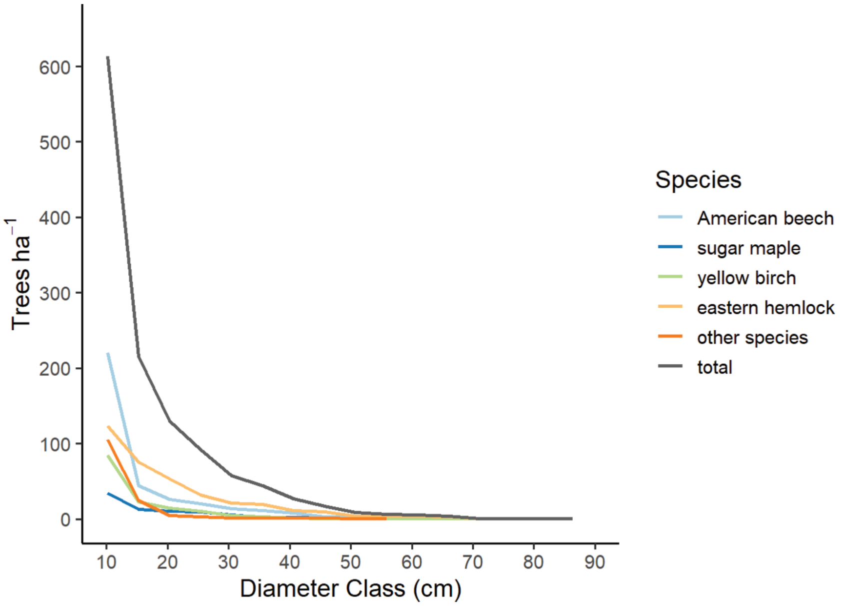
where R_{Den} is the relative density of a single species and R_{Dom} is the relative dominance of a species.

$$(4)\qquad R_{\mathrm{Den}} = \left(\frac{\text{Species density}}{\text{Density of all species}}\right) \times 100$$

Relative density (R_{Den}) was defined as the proportion of a given species (Species density, tree·ha^{-1}) compared with the total number of species in a cohort (Density of all species).

Relative dominance (R_{Dom}) was defined as the basal area (m^2·ha^{-1}) of a given species (Species basal area) compared with total basal area

Fig. 2. Stand-level, live-tree distribution across species. [Colour online.]



in a cohort (Total basal area). Relative density and dominance were expressed as percent of the total.

$$R_{\mathrm{Dom}} = \left(\frac{\text{Species basal area}}{\text{Total basal area}}\right) \times 100 \quad (5)$$

Density and stocking of advance regeneration (seedlings and saplings ≥30.5 cm in height and up to 10.1 cm dbh) of American beech, sugar maple, yellow birch, and all other species was determined for each cohort. Density of advance regeneration was defined as the number of stems, and regeneration stocking was defined as the number of plots where one or more stems of a given species and (or) species group was present relative to the total number of plots. We multiplied decimal values of stocking by 100 to convert to percent stocking. We calculated density of seedlings and stocking for the species and (or) species groups above for trees <30.5 cm in height.

Additionally, we calculated stand-level basal area, density, and standing and downed woody material following the methods outlined above to compare stand evolution with evolution of each cohort. We also determined the stand diameter distribution weighted by cohort to assess the impact of each cohort on overall stand structure. The aggregate diameter distribution was the sum of each cohort, trees per hectare by diameter class, weighted by area. Shape of the stand-level diameter distribution was used to assess structure in the context of hypothesis one. Diameter distribution shape was determined by regressing the base 10 logarithms of trees per hectare on dbh, dbh^2, and dbh^3 following the method by Janowiak et al. (2008). Coefficient signs for the most significant models (highest adjusted R^2 and lowest Akaike information criterion) informed diameter distribution shape.

Results

Stand scale

Total stand basal area was 33.1 ± standard deviation of 18.8 m^2·ha^{-1}, with overstory trees ranging in diameter from 10.2 to 90.0 cm after 80 years of group selection (Fig. 2). The most significant model for determining diameter distribution shape included a negative dbh coefficient, positive dbh^2 coefficient, and negative dbh^3 coefficient (Table 2). As such, the stand diameter shape was classified as rotated-sigmoid (Janowiak et al. 2008). The weighted stand diameter distribution showed the impact of each cohort on overall stand structure (Fig. 3). The 1993 cohort largely contributed trees per hectare to the smaller size classes, whereas larger size classes were primarily composed of trees from the matrix (Fig. 3). Eastern hemlock was the most abundant species across size classes, followed by American beech. Eastern hemlock also had the highest importance values and pin cherry the lowest (Fig. 4). Advance regeneration of beech was found on nearly all plots sampled, while stocking of sugar maple and yellow birch was 51.0% and 36.2%, respectively (Table 3). Density of advance regeneration and seedlings also varied by species, ranging from 817 to 9450 stems of advance regeneration and 4791 to 17 875 seedlings (Table 3). American beech was the most abundant species in the advance regeneration and seedling size classes (Table 3).

Table 2. Model coefficients from the diameter distribution analysis based on Janowiak et al. (2008).

	Estimate	Std. error	P value
Intercept	+540.61	38.86	<0.05
dbh	–91.63	10.17	<0.05
dbh^2	+4.88	0.72	<0.05
dbh^3	–0.08	0.14	<0.05

Cohort scale

At the individual cohort level, overstory basal area ranged from 10 m^2·ha^{-1} in the 1993 cohort to 50 m^2·ha^{-1} in the matrix (Fig. 5). Diameter distributions in the younger cohorts, 1993 and 1960, were composed of a higher number of small stems, with maximum diameters not exceeding 20.0 and 43.0 cm, respectively. In older cohorts, 1951 and 1938, as well as the matrix, diameter distributions transitioned towards a reverse-J shape with larger maximum diameters, 63.0, 67.0, and 88.0 cm, respectively. The diversity in live-tree structure, as measured by Shannon's diversity index, also increased as cohorts aged (Table 4).

Dominance of individual species, defined as the species with the highest importance value, was variable across cohorts, although American beech was the most important species regardless of cohort age (Fig. 4). As cohort age increased, dominance of shade-intolerant species decreased in favor of shade-tolerant species. The

Fig. 3. Average stand-level, live-tree size distribution weighted by cohort area. [Colour online.]

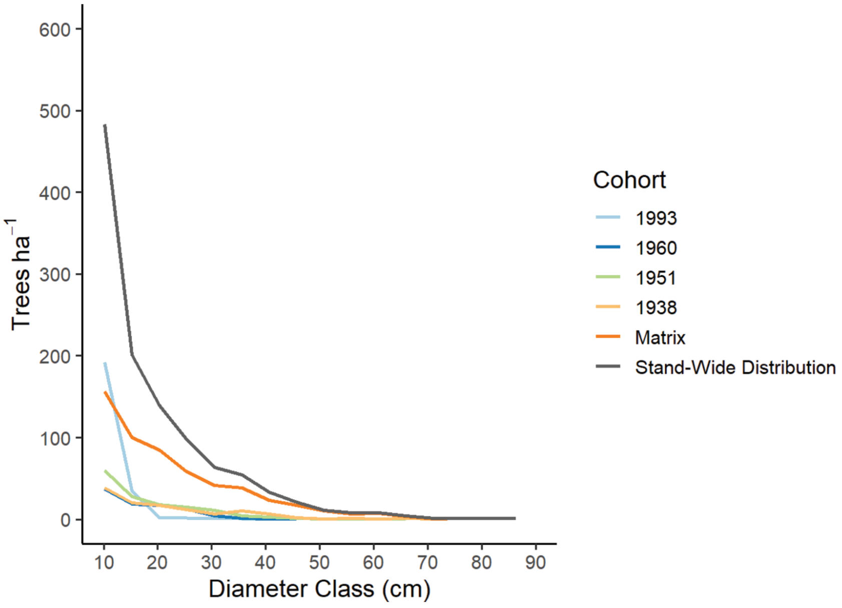


Fig. 4. Species importance value by cohort. For a definition of species importance value see eqs. 3, 4, and 5 in the Materials and methods section. [Colour online.]

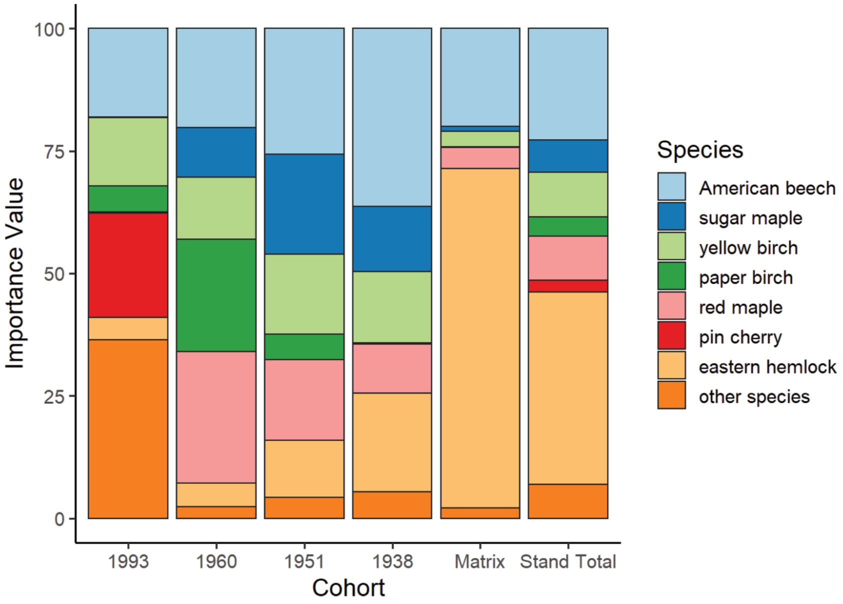


Table 3. Stand regeneration stocking and density by species group of advance regeneration (≥30.5 cm in height and up to 10.1 cm diameter at breast height) and seedlings (<30.5 cm in height).

	American beech	Sugar maple	Yellow birch	Other species
% Stocking	93.6	51.0	36.2	54.9
Advance regeneration density (trees·ha^{-1})	9450	1499	817	5290
Seedling density (trees·ha^{-1})	17 875	4791	7592	15 484

importance of yellow birch was consistent across all cohorts excluding the matrix, while pin cherry and paper birch were most important in younger cohorts (1993 and 1960). Sugar maple importance increased between the 1960 and 1951 cohorts, while eastern hemlock was most prevalent in the matrix. Changes in species composition were also reflected by differences in H_{Species} among cohorts (Table 4). The greatest diversity was in the transitional 1951 cohort, the lowest diversity was in the matrix.

Basal area of standing dead trees increased as cohorts aged, as did proportion of standing dead trees in the sawtimber size class (Fig. 6). In the 1993 cohort, the majority of standing dead trees were in the sapling size class, with a small portion in poletimber.

Fig. 5. Overstory basal area by cohort, with cohort age increasing from left to right; stand wide basal area was 33.1 ± 18.8 $m^2 \cdot ha^{-1}$. The overstory is defined as trees with ≥10.2 cm diameter at breast height.

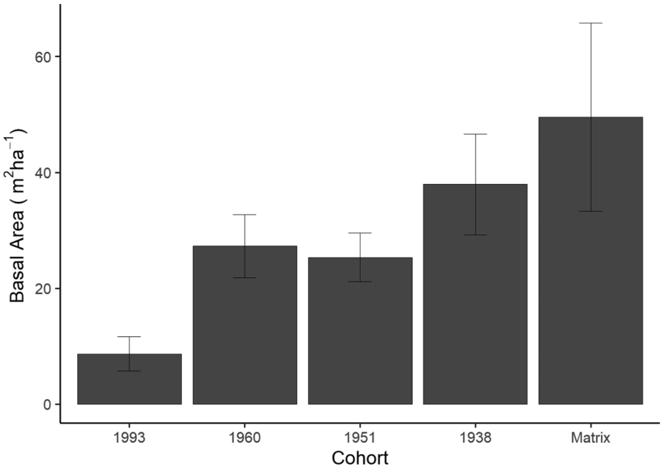
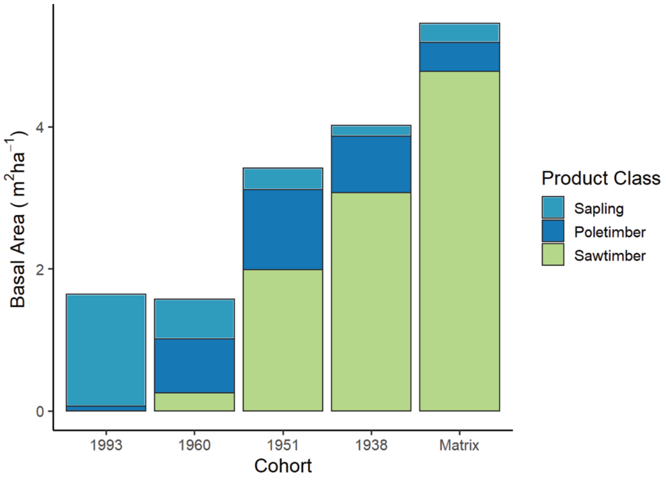


Table 4. Shannon's diversity index (*H*) for diameter class and species by cohort.

Cohort	$H_{Diameter}$	$H_{species}$
1990s	1.04	1.69
1960s	2.14	1.79
1950s	2.40	1.80
1930s	2.68	1.63
Matrix	2.74	0.92

Fig. 6. Basal area of standing dead trees by product class and cohort; stand-wide basal area of snags was 3.6 ± 0.5 $m^2 \cdot ha^{-1}$. Saplings were defined as trees with ≥2.5–10.1 cm diameter at breast height (dbh), poletimber as trees with ≥10.2–21.3 cm dbh, and sawtimber as trees with ≥21.4 cm dbh. [Colour online.]



Downed woody material volume was also lowest in the 1993 cohort. As cohorts aged, the amount of beech downed woody material increased (Fig. 7). Paper birch and pin cherry downed woody material was highest in the 1960 cohort (Fig. 7).

Density of advance regeneration averaged 8855 ± 282 trees per hectare for all cohorts except the matrix for which abundance of regeneration was below 1800 ± 37 $trees \cdot ha^{-1}$ (Fig. 8). American beech was the most prolific species regenerating, although sugar maple and yellow birch advance regeneration was found in all cohorts except the matrix. Stocking of American beech and yellow birch advance regeneration was strongly correlated with average cohort size in hectares (Pearman's correlations = −0.76 and 0.88, respectively). Sugar maple and other species stocking were also significantly correlated with cohort size; however, strength of association was lower (*r* = −0.43 and 0.40, respectively).

Fig. 7. Downed woody material volume by species and cohort; stand-wide volume of downed woody material was 73.5 ± 9.8 $m^3 \cdot ha^{-1}$. [Colour online.]

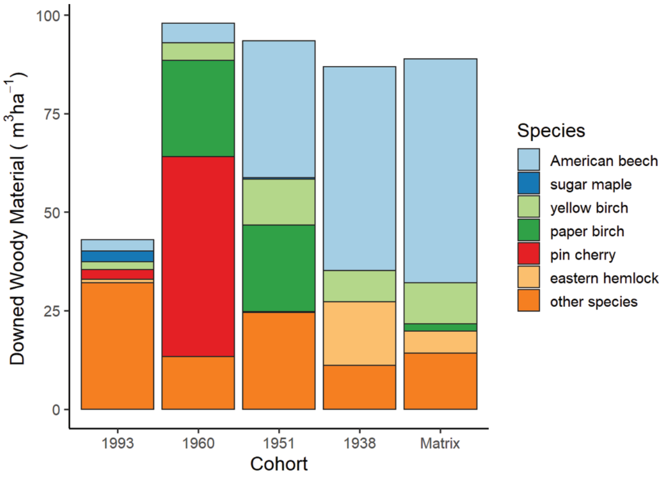
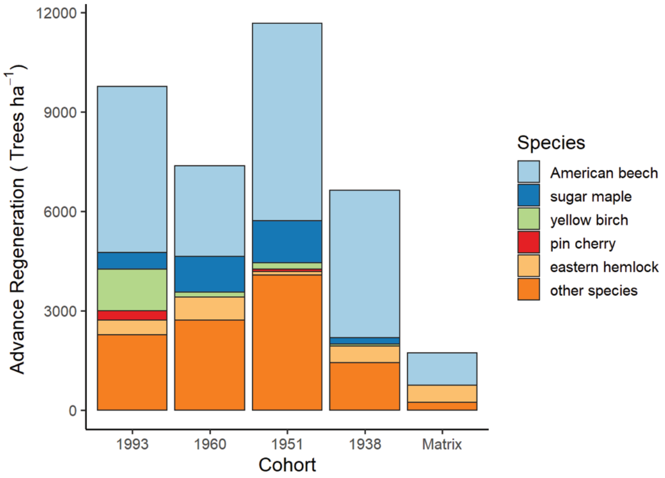


Fig. 8. Density of advance regeneration by species and cohort. Other species most prevalent in each cohort are as follows: matrix and 1938: red spruce and red maple; 1951 and 1960: red maple and white ash; 1993: red maple, white ash, and pin cherry. [Colour online.]



Discussion

Globally, selection systems have long been applied to maintain desirable structural and compositional goals (De Montigny and Smith 2017), but increasingly these systems are used to meet ecologically (Franklin et al. 2002) and socially orientated management objectives (D'Amato et al. 2011). The flexibility in application associated with group selection, relative to single-tree selection, is especially well regarded for achieving contemporary management goals in northern hardwood forests (Lahde et al. 1999). However, the attributes of forests managed with group selection are regularly evaluated at the stand level rather than cohort level (Homyack and Haas 2009). Considering forest evolution under group selection across various spatial scales offers unique insights relative to stand-only assessments. Additionally, the duration of group selection at the BEF is unique. Several long-term studies on group selection exist (e.g., Homyack and Haas 2009), but few cover the same length of treatment as this study or have explored the evolution of stands and individual cohorts over time. This study evaluates 80 years of management, providing a valuable look at the long-term sustainability of group selection for meeting historical and current objectives, particularly in forests containing a recalcitrant beech understory.

Emergent stand properties

Management of forests under group selection revolves around assumptions of sustained yield, retention of desired species, and ample regeneration for future cohorts (Leak and Gottsacker 1985). Findings from this work support our hypotheses that these assumptions can be met with repeated application of group selection cuttings over time. Following 80 years of management, emergent stand structure was classified by a rotated-sigmoid diameter distribution (Table 2). Previous findings from this study reported a reverse-J diameter distribution, although this shape was not confirmed statistically (Leak 1999). The reverse-J distribution has long been the benchmark for uneven-aged silviculture; however, other diameter distributions, including the rotated-sigmoid and increasing-*q*, have been observed in old growth (Goff and West 1975) and managed uneven-aged northern hardwoods (Neuendorff et al. 2007). Diameter distribution shape is driven largely by diameter increment in conjunction with rates of tree removal, whether through harvesting or natural disturbance (O'Hara and Gersonde 2004). The variable shape of these distributions, relative to the balanced reverse-J, likely mimic natural development of forests, particularly a u-shaped trend in mortality rates (Lorimer et al. 2001) and variable diameter increments (Schutz 1997).

An underlying assumption of the reverse-J distribution is the equal allocation of growing space to each cohort in a stand (Nyland et al. 2016). Application of group selection in the areas examined at the BEF was consistent with this assumption and intentionally allocated growing space to each cohort; the negative exponential distribution previously observed likely reflected this (Leak 1999). Deviation from this form in our current assessment may be due to the long time period (25 years) since the last harvest entry, which allowed for increased development and stocking of the small to medium sawtimber size classes. Moreover, not all areas have been treated with group selection in the compartments examined with the stand-level distribution including the influence of unmanaged matrix areas, which were uneven-aged at the onset of this study (Fig. 3). Although the rotated-sigmoid form does not conform to theoretical distributions historically suggested for uneven-aged management, there are ecological and economic advantages to this structure given the higher stocking of larger diameter trees with rotated-sigmoid distributions (Keeton 2006).

As with structural diversity, our findings support the hypothesis that group selection can maintain species diversity over time. At the stand scale, the species with the highest importance values are also the most shade tolerant (Fig. 4), although shade-intolerant species including paper birch and pin cherry are still present throughout the stand. The high importance of eastern hemlock is due to the large portion of the stand in the matrix and the initial practice of retaining advance softwood regeneration in groups. The importance of American beech relative to more desirable and less shade-tolerant species like sugar maple and yellow birch may also be a relic of past management. In earlier cohorts, group openings were smaller on average than openings in more recent cohorts (Table 1). For more shade-intolerant species, regeneration failure is likely unless gaps are large, as smaller openings may not provide the gradient of resource availability (Knapp et al. 2019), primarily light and moisture, from gap center to edge required to recruit a range of tolerances (York et al. 2003). Given that average gap size has increased over the duration of the study, species importance values may shift as younger cohorts transition from sapling to overstory size classes. This theory is supported by the correlations between regeneration stocking and average gap size. For example, the strong positive correlation of yellow birch with gap size and the strong negative correlation of American beech with gap size reflect the differing light requirements of each species (Canham 1988; Falk et al. 2010). Trends in regeneration stocking as gap size increase are expected to further influence future stand composition and structure as trees age.

Regeneration outcomes observed across cohorts may also be a relic of sampling design. The location of plots within the center of each gap left gap edges undersampled, especially when openings were larger in size. Variation in microclimate across gaps has been observed to impact spatial distribution of species (Raymond et al. 2006). These factors likely reflect the positive correlation between stocking of important species and average gap size. Additionally, seedling and sapling growth rates can also vary with distance from gap center, leading to compositional differences over time (Holladay et al. 2006). Changes in regeneration density and overall composition with changing gap size have been observed in multiple studies within the northern hardwood forest type (Bolton and D'Amato 2011; Knapp et al. 2019), as well as in other forest systems (Runguo et al. 1999; Pearson et al. 2003).

At the stand scale, we also observed consistent proportions of desired regeneration (sugar maple and yellow birch) stocking and density relative to American beech based on current conditions and previously published results (Leak and Filip 1977; Leak 1999) (Table 3). Although American beech stocking is nearly 100%, sugar maple and yellow birch regeneration were still present as seedlings and as advance regeneration (Table 3). Retention of these species, especially as advance regeneration, is essential for future management and a key assumption in the application of group selection in northern hardwoods (Leak 1999; Leak et al. 2014). The balance of regeneration from a range of species shade tolerances also more closely mimics the natural dynamics of these forests, which are characterized by a mix of frequent gap scale and less frequent mesoscale disturbances, such as wind storms that generate the range of light and microsite conditions necessary for supporting a diversity of canopy tree species (Hanson and Lorimer 2007).

Cohort properties

Species diversity at the stand scale after repeated group selection was the cumulative effect of distinct species composition within cohorts, which changed with time since harvest (Fig. 4). In the youngest cohort (1993), species importance values reflected early successional conditions with greater abundance of shade-intolerant and mid-tolerant species (pin cherry, paper birch, and yellow birch). As cohorts aged, the importance of shade-tolerant species increased (American beech, eastern hemlock, and sugar maple). These shifting compositional dynamics highlight the longevity and growth strategies of individual species. For example, the changing importance of paper birch over time represents a clear example of cohorts capturing unique aspects of a given species development. There is a marked decrease in the importance of paper birch and a corresponding increase in the volume of paper birch downed woody material between the 1960 and 1951 cohorts (Figs. 4, 7). These results likely reflect the short-lived, early successional nature of paper birch and denote when intermediate and long-lived species become more dominant in the stand (Safford et al. 1990). The developmental strategy of sugar maple is also evident from changing importance values among cohorts. Sugar maple made up little of the 1993 cohort but was a major component of the overstory of the 1951 cohort. This emergence of sugar maple in the stand several decades after harvesting may reflect the long-term development of advance regeneration released by group openings, which after six decades, ultimately begins to ascend into canopy positions with mortality of shorter-lived intolerant species (Hibbs 1983). The shift in dominance towards shade-tolerant species in older cohorts supports our hypothesis that species richness decreases over time due to loss of less tolerant species.

As with species composition and diversity, stand structure reflected the combined effect of different structural conditions within individual cohorts (Fig. 3). The steep initial shape of the overall stand curve is driven by the high density of small stems in the youngest cohort, 1993 (Fig. 3). Similarly, the long tail of the diameter distribution is pulled by the oldest cohorts: the matrix and 1938. McGee et al. (1999) found comparable evolution of overstory structure looking at the changes in diameter distributions among maturing, partially cut, and old-growth northern hardwoods stands in the Adirondack region of New York. The increasing value of H_{Diameter} as cohorts age also demonstrates greater structural diversity with time as was expected (Table 4).

Successional and structural evolution over time

In the context of stand dynamics, uneven-aged management is associated with later stages of stand development, including understory reinitiation and old growth (Oliver and Larson 1996). Nevertheless, the distinct structural and compositional conditions of each cohort suggest earlier developmental stages are also represented throughout the stand. Stem exclusion or the aggradation phase, for example, are more commonly associated with repopulation following stand-replacing disturbances or even-aged regeneration methods (Oliver and Larson 1996); however, the high density of small stems (Fig. 3) and sapling mortality in the 1993 cohort (Fig. 6) are consistent with characteristics of these earlier successional stages.

Regeneration

Differences among cohorts extended to the regeneration layer, with density of advance regeneration substantially lower in the matrix and composed primarily of eastern hemlock and beech, the two most shade-tolerant species in these systems (Fig. 8). Limited regeneration in the matrix is likely due to low light levels created by heavy hemlock dominance (Lorimer et al. 2001), but may also be influenced by high competition for nutrients (Catovsky and Bazzaz 2000). Under group selection, it is assumed a new cohort of desired species will establish at each entry. Overstory species importance values, primarily the presence of sugar maple and yellow birch decades after harvest, support this assumption (Fig. 4). The ability of these species to recruit in northern hardwood forests has been related to changes in litter depth and quality, particularly on sites dominated by American beech. For yellow birch, access to mineral soil is important for regeneration survival (Shields et al. 2007), and these conditions were created by harvesting equipment at the time of group creation. For sugar maple, regeneration occurs on leaf litter, although the seedling radical must be able to reach mineral soil during the moist period of the growing season (Godman et al. 1990). In stands with high populations of beech, litter depths often increase due to the elevated lignin content in leaves relative to other hardwood species leading to the inhibition of regeneration for other species (Dalling and Hubbell 2002). The increase in sugar maple advance regeneration we observed in older cohorts may reflect a change in litter quality over time in groups dominated by species with nutrient-rich foliage, such as pin cherry, white ash, and yellow birch (Leak 2005).

Study limitations

The value of this study lies in the duration of its application; however, limitations do exist and their impact on results needs to be considered. Firstly, the study is not replicated and has no contrasting control, which confines our ability to determine if the outcomes are related to group placement or other underlying environmental variation beyond our control. For example, limited documentation on the timing of harvests prevents us from comparing the effect of weather on stand conditions. Although all harvests occurred in late fall or early winter, variability in precipitation and temperature between harvests may have greatly influenced soil scarification. Scarification, especially in combination with increased group size, is important for establishment and growth of yellow birch (Gauthier et al. 2016). Secondly, group openings varied in size over time so that opening size and age likely confounded to influence structural and compositional outcomes. We sought to recognize the importance of this variability by evaluating the correlation between stocking of advance regeneration and average gap size; however, the influence of gap size on all stages of stand development is complex, and we suspect not fully captured by our study design. Variability in gap size over time is also an issue given our use of a chronosequence approach to evaluate cohort development. Chronosequence analysis is appropriate when temporal changes follow a linear pathway, such as forest succession, specifically species composition and species abundance (Walker et al. 2010). We acknowledge the change in gap size violates an assumption of chronosequence analysis in that the only change is time. Nevertheless, the generally predictable nature of forest succession in northern hardwood forests (Woods 1984; Leak 1991) supports the use of this approach, particularly given that studying changes over time at a fixed location extend beyond the lifespan of any one scientist (Walker et al. 2010). Treatments were also not applied on a consistent cutting cycle, which is an assumption of traditional group selection. The increase in cutting cycle length over time has reflected the increasing complexities associated with receiving approval for harvesting activities on National Forest lands and not a deviation from the original management plan for these areas (W. Leak, personal communication). Collectively, this variation in timing and gap size could also interact with temporal variation in seed availability, climate, and herbivore densities to affect regeneration outcomes. Finally, beech bark disease has been present on the Bartlett Experimental Forest since the late 1930s (Leak 2005); however, the influence of this disease complex on overstory beech mortality was likely greatest during the 1950s and 1960s, influencing levels of American beech recruitment and overstory tree dynamics in these areas. In addition, the high volumes of deadwood observed in the matrix, 1938, and 1951 cohorts were consistent with those observed in other managed northern hardwood forests impacted by beech bark disease (McGee et al. 1999; McGee 2000). Although we did not quantify the impacts of beech bark disease on the areas sampled, it is very probable this disease complex had a positive influence on beech regeneration density and stocking as well as the structural dynamics we documented.

Contemporary objectives and future challenges

At the time of this study's establishment, goals were to maintain a mixture of species and range of size classes, from regeneration to mature overstory trees. It is important to consider these management goals and the current state of the stand in the context of regional conditions and additional management activity. The study area is in a region where white-tailed deer populations are comparatively lower than other parts of northeastern North America and, as such, precautions were not taken to prevent browsing. In regions with elevated deer populations, some direct benefits from gap creation, including increased light availability, may be reduced (Kern et al. 2012), as persistent browsing can arrest succession in these areas (Kern et al. 2012). Additionally, all American beech were felled during later harvests at the BEF, which served to reduce beech composition relative to other studies where beech was not explicitly removed (Leak 1996). In the context of the group selection approaches we examined, focus was primarily on creating and maintaining desirable canopy composition and uneven-aged structure; however, modifications that better integrate structural legacies historically associated with gap disturbances may be necessary to achieve a broader suite of ecological objectives. This includes retention of downed woody material and legacy trees within groups to maintain and increase structural diversity (Bolton and D'Amato 2011). Such within-group retention would need to be coupled with larger group openings to ensure suitable light conditions are still created for less tolerant species (D'Amato et al. 2015). The next harvest within the stand is planned for fall 2021 and will remove portions of the matrix. The matrix is dominated by late successional species, primarily eastern hemlock followed by American beech (Fig. 4). This composition is in line with stand evolution over time given the forest was classified as old growth prior to the first entry in 1937 (Leak and Filip 1977). There are limited markets for either species (Howard et al. 2000; Kochenderfer et al. 2004) as well as low numbers of regeneration (Fig. 8). As such, the location of new groups is unlikely to be driven by capturing overstory trees prior to exceeding economic maturity or releasing pockets of commercially desirable advance regeneration.

Acknowledgements

We thank Ella Chapman for help with field data collection. We also thank Mariko Yamasaki and Chris Costello of the U.S. Forest Service, Northern Research Station, for help locating field sites and for providing additional context for this work. Funding was provided by the University of Vermont Rubenstein School of Environment and Natural Resources and USDA Forest Service Northern Research Station.

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