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Predicted long-term effects of group selection on species composition and stand structure in northern hardwood forests

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ABSTRACT

The group selection method can potentially increase the proportion of shade-intolerant and midtolerant tree species in forests dominated by shade-tolerant species, but previous results have been variable, and concerns have been raised about possible effects on forest fragmentation and forest structure. Limited evidence is available on these issues for forests managed beyond the first cutting cycle. We used CANOPY, an individual-tree forest dynamics model, to assess long-term effects of group selection methods on tree species composition, fragmentation of the mature forest matrix, and sustainability of size distributions in northern hardwoods. Results were also compared to reference treatments that included a no-cut control, single-tree selection, and clearcutting. Model simulations predicted that group selection would increase midtolerant tree abundance compared to single-tree selection and controls, but magnitude of response was highly variable depending on habitat type and harvest design. All conventional single-tree and group selection designs greatly increased small-scale fragmentation of the mature forest matrix. Group or small patch cutting with area control (constant percent of stand area cut in openings in each cutting cycle with no cutting between groups) produced residual stands with 'rings' of mature and large tree crowns in a 'chain-link fence' pattern. All treatments, however, resulted in sustainable populations; size distributions did not deviate substantially from a descending monotonic distribution over the 300-yr period. Results suggest possible tradeoffs between maximizing midtolerant species composition and minimizing fragmentation of the mature forest matrix, and that the potential for increasing the abundance of midtolerant species can be strongly constrained by habitat type.

1. Introduction

Group selection is receiving renewed attention in situations where foresters seek a partial cutting method that can regenerate species of low to moderate shade tolerance, and yet maintain a fairly high proportion of mature forest cover. Long-term studies have demonstrated that single-tree selection is ineffective for the former purpose, as it typically leads to overwhelming dominance by shade-tolerant species (e.g., Tubbs, 1977a; Leak and Sendak, 2002; Neuendorff et al., 2007). Openings larger than 200–400 m^2, on the other hand, can often foster the regeneration of midtolerant and intolerant tree species (McClure and Lee, 1993; Jenkins and Parker, 1998; Dale et al., 1995). In a 60-year study in New England, harvest openings of about 0.2–0.4 ha maintained forest composition comprised of 25–33% midtolerant and intolerant species (Leak and Filip, 1977; Leak, 1999). In mixed forests managed by group selection in the central U.S., openings included more than 50% midtolerant and intolerant species (Dale et al., 1995).

Although group selection has numerous desirable features, concerns have been raised about potential effects on species composition and forest structure if group selection were to be applied on a much larger scale as a partial replacement for clearcutting or shelterwood systems. In many cases, sizable openings alone may not substantially increase the abundance of less tolerant species. Other factors known to constrain recruitment of the less shade-tolerant species include inherent habitat features (soil, microclimate, local flora and fauna), seed source, seedbed conditions, and degree of vegetative competition (e.g., Tubbs, 1969; Kern et al., 2012, 2013; Walters et al., 2016; Willis et al., 2015, 2016). For example, Shields et al. (2007) reported increases in midtolerant yellow birch (*Betula alleghaniensis* Britt.) within group openings in northern hardwood stands compared to single-tree selection, but birch still comprised less than 10% of the cohort developing in the gaps. In southern Appalachian forests, Beckage et al. (2000) found no

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consistent response to creation of multiple-tree gaps for either intolerant or shade-tolerant species. Group selection harvests in some forest types can actually accelerate the replacement of existing midtolerant canopy species with other, more aggressive competitors. In mixed hardwood forests of the central U.S., formerly dominant oaks (*Quercus* spp.) and hickories (*Carya* spp.) are often among the least abundant species in group selection openings, which become dominated by yellow poplar (*Liriodendron tulipifera* L.) and maples (*Acer* spp.) (Jenkins and Parker, 1998; Weigel, 1999).

Group selection may also have negative impacts on 'sensitive' species requiring shady, mature forest environments. For example, eastern hemlock (*Tsuga canadensis* (L.) Carr.) is a shade-tolerant species of special concern in the Great Lakes region because it is currently limited in abundance and difficult to regenerate. Conventional group selection without intentional scarification can result in poor hemlock establishment even with relatively small openings (350–800 m^2) on favorable hemlock habitats (Webster and Lorimer, 2002; Walters et al., 2016). Group selection may also be detrimental to other, less conspicuous flora and fauna adapted to moist microclimates on the forest floor (Harpole and Haas, 1999; Gundale, 2002). Some field experiments, for example, have reported >80% reductions in salamander abundance after group selection, similar to effects of clearcutting (Homyack and Haas, 2009; Hocking et al., 2013).

A related concern is that group selection may cause excessive fragmentation and edge effects in mature forest (Roach, 1974; Gustafson and Crow, 1996; Bigelow and Parks, 2010), potentially magnifying the direct effects of openings on forest interior species. At the stand level, Roach's conceptual diagrams suggest a surprisingly high degree of small-scale fragmentation of the mature forest matrix even when small groups occupy only 20% of the stand area (e.g., after only two cutting cycles). While Roach (1974) focused only on logistical difficulties of marking and keeping track of numerous unmapped groups, aesthetics and wildlife habitat could also be compromised if the forest matrix has been so fragmented that mature trees exist only as small, dispersed clusters. At a broader landscape level, simulations by Gustafson and Crow (1996) demonstrated substantial reduction in interior forest conditions and increased edge with group selection compared to clearcutting. In New England northern hardwoods, negative effects on salamander populations extended 34 m into the forest matrix from the opening margin, suggesting the potential for substantial edge effects with moderate to large group openings (0.1–0.8 ha; Hocking et al., 2013).

While the use of smaller group selection openings might reduce impacts on flora and fauna that prefer mature forest habitat, smaller openings could theoretically lead to irregular size distributions with fluctuating yields under some conditions. If groups are fairly large (e.g., >0.25 ha), a regulated forest with group selection would probably have a sustainable diameter distribution approaching a negative exponential curve (Leak and Filip, 1977; Leak, 1999), similar to that of a regulated even-aged forest (Assmann, 1970, p. 447). But when openings are small, fast-growing pole and mature trees bordering the gaps often close the gaps laterally before sapling recruits can reach the canopy (Hibbs, 1982; Runkle and Yetter, 1987; Cole and Lorimer, 2005). This could potentially inhibit new recruitment and foster dominance by pole and mature trees, creating a quasi-even-aged stand structure (stem exclusion stage of Oliver and Larson, 1996) that deviates from a negative exponential form (Roach, 1974).

A serious limitation in our understanding of group selection effects is that, aside from the 60-yr study by Leak (1999), most field studies have only examined effects after the first cutting cycle. It is therefore difficult to predict long-term effects of group selection from current evidence. Because of funding and time constraints, field studies have also generally only examined the effects of one or a narrow range of opening size, one implementation of group extent (percent of canopy removed in each cutting cycle), and one habitat type. Comparisons of group selection effects have not usually been made with the current prevailing silvicultural systems on the same habitat. The objectives of this study were to assess long-term ramifications of group selection methods with natural regeneration on tree species composition, cohort structure, and size distributions in forests dominated by shade-tolerant species. We evaluated the following specific questions: (1) How do variations in group selection design and habitat differences influence the abundance of midtolerant as well as exposure-sensitive tree species compared to the alternatives of single-tree selection and even-aged management?; (2) Does group selection lead to excessive small-scale fragmentation of the mature forest matrix after many cutting cycles?; and (3) Does group selection with small to moderate opening sizes (200–2000 m^2) lead eventually to irregular or unsustainable size distributions?

A range of group selection alternatives was simulated using CANOPY (v.3), a crown-based, individual-tree model (Choi et al., 2001; Hanson et al., 2011), on two northern hardwood and hemlock-hardwood habitat types of differing productivity and species diversity. Group selection included two designs: combined group/single-tree selection regulated using a residual diameter distribution (Roach, 1974; Miller et al., 1995), and group selection regulated strictly by area control and with no cutting between the groups or thinning of older cohorts (Miller et al., 1995; Leak, 1999). With the latter approach, called 'patch cutting' or 'group/patch selection' by some investigators, an equal amount of the forest matrix is cut in openings in each cutting cycle. An approximate rotation age, useful for making comparisons with even-aged alternatives, can be computed as the inverse of the mean annualized area of openings created (Miller et al., 1995; Leak, 1999). This 'implicit rotation age' involves a simplifying assumption of non-overlap of group openings. In the simulations, group sizes and the proportion of stand cut in group openings per cutting cycle (hereafter 'group extent') were systematically varied. Single-tree selection, clearcutting, and untreated controls were also simulated for comparative purposes and to provide insights into the implications of shifting management of specific tracts from the existing silvicultural system to group selection.

2. Methods

2.1. Model description

CANOPY is a spatially explicit, individual-tree model designed to simulate the long-term response of tree saplings and mature trees to natural or harvest-created openings (Choi et al., 2001; Hanson et al., 2011). The model simulates the gap-capture process in forest openings by projecting the height growth of saplings in a gap, as well as the height growth and lateral crown growth of mature trees bordering the gap. Crown radial growth is predicted in four cardinal directions for each tree, with the most rapid growth typically in the direction facing a gap (Choi et al., 2001). Sapling height growth is also influenced by gap size, which is monitored annually. Successful gap capture occurs if a sapling or pole tree can reach canopy height before becoming overtopped by the crowns of mature gap-border trees.

The model assesses competition level to predict several processes, including sapling recruitment, tree growth (height, diameter, and crown radius), and mortality. Plot-level competition is evaluated using northern hardwood stocking charts (Tubbs, 1977b), in which plot basal area is compared to average or maximum observed levels in the region for stands with the same mean diameter at breast height (DBH), similar conceptually to self-thinning diagrams (Drew and Flewelling, 1977; Westoby, 1984). In CANOPY, a stand is divided