

Canopy gap dynamics of second-growth red spruce-northern hardwood stands in West Virginia

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ABSTRACT

Forest restoration requires an understanding of the natural disturbance regime of the target community and estimates of the historic range of variability of ecosystem components (composition, structure, and disturbance processes). Management prescriptions that support specific restoration activities should be consistent with these parameters. In this study, we describe gap-phase dynamics of even-aged, second-growth red spruce-northern hardwood stands in West Virginia that have been significantly degraded following early Twentieth Century harvesting and wildfire. In the current stage of stand development, gaps tended to be small, with mean canopy gap and extended canopy gap sizes of 53.4 m² and 199.3 m², respectively, and a canopy turnover rate of 1.4% year⁻¹. The majority of gaps resulted from the death of one or two trees. American beech snags were the most frequent gap maker, partially due to the elevated presence of beech-bark disease in the study area. Gaps ranged in age from 1 to 28 years, had a mean of 13 years, and were unimodal in distribution. We projected red spruce to be the eventual gap filler in approximately 40% of the gaps. However, we estimated that most average-sized gaps will close within 15–20 years before red spruce canopy ascension is projected (30–60 years). Accordingly, many understory red spruce will require more than one overhead release – an observation verified by the tree-ring record and consistent with red spruce life history characteristics. Based on our observations, silvicultural prescriptions that include overhead release treatments such as thinning from above or small gap creation through selection harvesting could be an appropriate activity to foster red spruce restoration in the central Appalachians.

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1. Introduction

Restoring degraded forest ecosystems has become a major focus of applied forest research in the United States. For example, substantial resources have been committed to restoring bottomland hardwood and longleaf pine (*Pinus palustris* Mill.)-wiregrass (*Aristida* spp.) systems in the southern United States (Stanturf et al., 2001; Brockway et al., 2005), and ponderosa pine (*Pinus ponderosa* C. Lawson) forests in the western United States (Lynch et al., 2000) that have been reduced in extent or compositional quality. Currently, there are a number of ongoing projects in the Central Hardwood Region examining the efficacy of fire as a tool to restore upland oak (*Quercus*) communities (Brose et al., 2001; Nowacki et al., 2009). At the landscape level, successful restora-

tion requires management strategies guided by realistic estimates of the historic range of variability of ecosystem dynamics and, in particular, the disturbance regime of the restoration target community (Engstrom et al., 1999; Harvey et al., 2002). At the stand level, restoration should include the selection of specific management activities (e.g., regeneration harvesting, thinning and release treatments, and planting) that are consistent with the outcomes of natural disturbances and stand development processes (Seymour et al., 2002; Franklin et al., 2007).

In this study, we describe canopy gap dynamics of second growth, red spruce (*Picea rubens* Sarg) – northern hardwood forests in the Allegheny Mountain portion of the central Appalachians of east-central West Virginia. Most of these communities are artifacts of widespread cutting and subsequent fire that occurred between 1880 and 1920. These disturbances produced a homogeneous landscape where even-aged northern hardwoods largely replaced structurally complex, multi-aged forests that formerly were dominated by red spruce. After approximately 100 years, extant stands are in the late stem exclusion or early understory

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reinitiation stage of development, with red spruce largely relegated to understory canopy positions (Rentch et al., 2007).

On public land, interest in restoration of red spruce forest communities in West Virginia has been driven by three concerns. First, these forests provide habitat for threatened or endangered species such as the Cheat Mountain salamander (*Plethodon nettingi* Green) and the recently de-listed Virginia Northern flying squirrel (*Glaucomys sabrinus fuscus* Shaw) (Menzel et al., 2006a; Ford et al., 2010), as well as other globally rare fungal, lichen, plant and animal associates (Selva, 1994; Byers et al., 2010). Second, red spruce, along with eastern hemlock (*Tsuga canadensis* L. Carr) provides an evergreen canopy critical for maintaining temperatures and water quality of cold water fisheries in high-elevation, headwater streams (Martin and Petty, 2009). Finally, concern about the impacts of climate change on existing and future habitat has provided impetus for forest restoration. Although some vegetation models (e.g., Prasad et al., 2007) suggest that climate change may significantly reduce current red spruce distribution, restoration may also mitigate some of the impacts of climate change by increasing biodiversity, forest connectivity, and ecosystem resilience (SER, 2009).

Prior to European settlement, Hopkins (1899) estimated that 600,000 ha of mixed hardwood-coniferous forest existed in the region where red spruce comprised 50% of the overstory, in association with northern hardwood species such as yellow birch (*Betula alleghaniensis* Britton), sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), black cherry (*Prunus serotina* Ehrh.), and eastern hemlock. The loss of seed trees and seed-bed desiccation following harvest, destructive wildfires, and wind and water erosion proved lethal to red spruce retention, reestablishment, or competitiveness, producing a landscape largely dominated by hardwood species (Murphy, 1917; Korstian, 1937; Minckler, 1940, 1945; Allard and Leonard, 1952; Clarkson, 1964; Pielke, 1981; Pyle and Schafale, 1988). Today, less than 10,000 ha of red spruce-dominated forests remain in West Virginia (Griffith and Widmann, 2003). Although much of the historic habitat does contain understory red spruce, it is largely devoid of a significant spruce overstory component. The Monongahela National Forest (MNF), the largest owner of this forest type in the region, recently revised its Land Management Plan to include active and passive restoration projects on >60,000 ha (USDA, 2006). Statewide, approximately 224,000 ha could support red spruce, singly or in mixed forest conditions (Menzel et al., 2006b).

Although our understanding of the disturbance dynamics of the former (pre-European) red spruce-northern hardwood system in the central Appalachians is limited, some elements of the natural disturbance regime have been broadly described. Although rare, stand initiating disturbances such as large fires and blowdowns have been noted in the historical record from the region (Hopkins, 1899; Brooks, 1910; Rollins, 2005). Historically, canopy dynamics were principally driven by small, single or multiple-tree mortality events caused by wind, ice, snow, and lightning strikes, resulting in gap-phase regeneration (White et al., 1993). The prevailing wet and humid conditions at high elevations greatly subdued fire occurrence (White and Cogbill, 1992; Thomas-Van Gundy et al., 2007) — so much so, that these forests were noted to retard the spread of fires starting at lower elevations (Korstian, 1937). Insects and disease also played an important role in presettlement times. Hopkins (1891, 1899) documented extensive red spruce mortality from outbreaks of the spruce bark beetle (*Dendroctonus rufipennis* Kirby) and an unknown pine beetle in the 1880s and 1890s in mature stands. At present, many high-elevation forests are infected by beech-bark disease and the hemlock woolly adelgid (Morin et al., 2005). Although neither of these mortality agents affects red spruce directly, host tree species are very abundant regionally and their

mortality drastically impacts forest canopy dynamics and species turnover.

Canopy gap dynamics have been described for old-growth red spruce stands in North Carolina, New Hampshire, and Maine (White et al., 1985; Foster and Reiners, 1986; Fraver and White, 2005b, respectively), but to date there have been no comparable studies in the central Appalachian region. More importantly, none of this research has considered gap dynamics of secondary forests where composition and structure are drastically different from their pre-harvest condition. The primary purpose of our study was to describe the canopy gap disturbance regime of principally even-aged, second-growth mixed red spruce-hardwood forests in West Virginia. This research has been part of a larger effort in the region to a) describe stand dynamics and regeneration patterns in this forest type, b) use quantitative modeling to simulate the effectiveness of silvicultural treatments to enhance long-term overstory recruitment of red spruce, and c) field test the effectiveness of release treatments to enhance height growth of mid-story red spruce (see Schuler et al., 2002; USDA Forest Service, 2006; Rentch et al., 2007). Herein, we combine gap transect and dendrochronological data to address three questions:

- (1) What are the current patterns of canopy disturbance in this heavily altered forest type, including canopy gap formation rate and percentage of the forest occupied by gaps, as well as average size, shape, and age;
- (2) What are the most common agents of canopy gap formation, and what form does canopy mortality commonly take (e.g., uproot, snap, or snag); and
- (3) What are the most common gap fillers, and how successful are under- and mid-story red spruce in capturing canopy gaps before lateral closure from above.

We believe answers to these questions are necessary to fully understand the current ecological status of a drastically altered system where red spruce is now substantially underrepresented. It will also inform resource managers about the current successional trajectory of these forests, and will provide an ecological framework for the design and implementation of restorative silvicultural techniques to increase the extent of red spruce and improve the habitat for rare associates dependent on this ecosystem.

2. Study area and field methods

Regionally, red spruce and spruce-northern hardwood mixes occur along higher ridges and plateaus (>900 m) in the Allegheny Mountain subsection of the Appalachian Plateau Physiographic Province in east-central West Virginia and small portion of extreme western Virginia (Fenneman, 1939). Mountains are capped by Pennsylvanian sandstone and shale; soils are frigid silt or sandy loam soils that are shallow, stony, strongly acid and relatively infertile (Losche and Beverage, 1967; USDA Forest Service, 2006). Red spruce site indices (base age 50 years) ranged from 13.0 m to 19.7 m depending on elevation, landform, and soil type (Flegal, 1999). Climate is continental, with frequent fog, high annual precipitation, and the possibility of freezing temperatures any month of the year. Average January minimum and July maximum temperatures are -10.3°C and 21.4°C , respectively, and annual precipitation is 152 cm, with more than 400 cm of snowfall annually (SRCC, 2010).

We used 2003 digital color SAMB orthophotography (WV GIS Technical Center, 2006) to identify suitable study areas across and adjacent to the Monongahela National Forest (Fig. 1). Ten stands were selected that contained red spruce either in the overstory, understory, or both strata. All stands occurred within the MNF

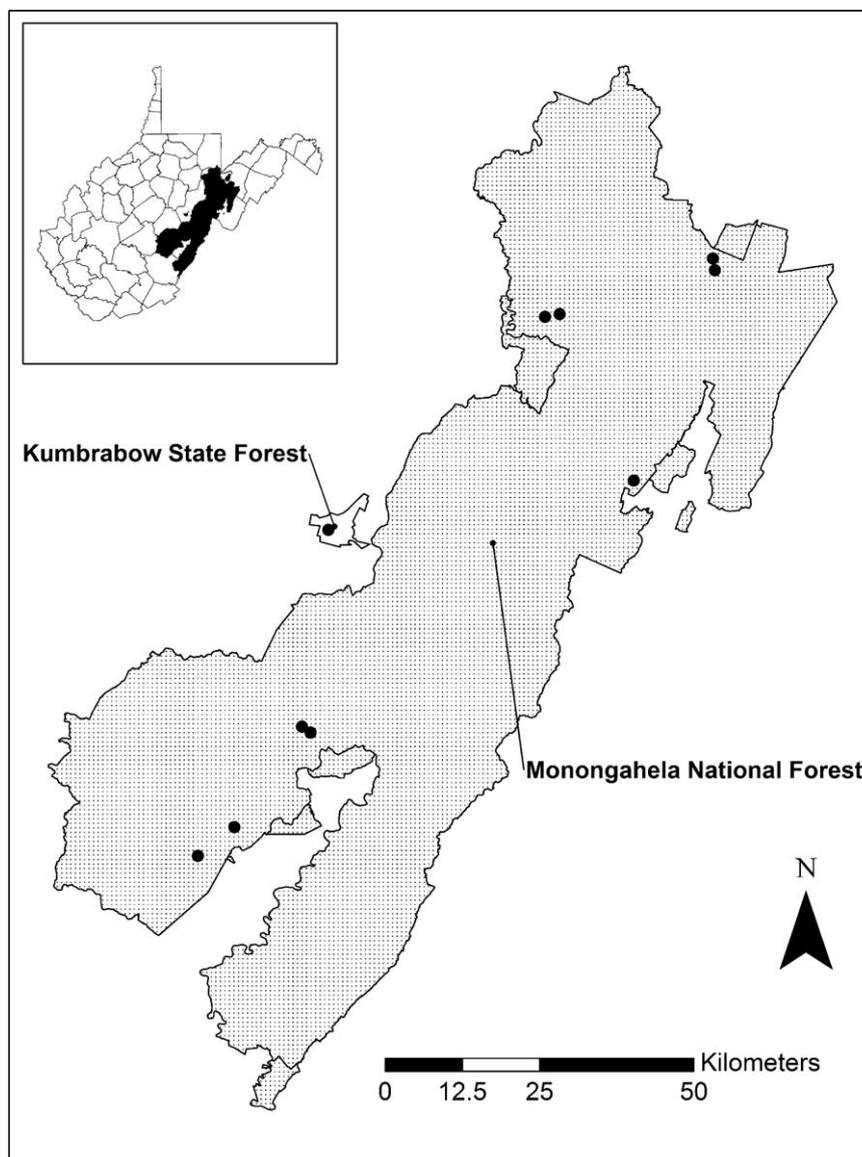


Fig. 1. Map of study area and 10 study stands in the Allegheny Mountains of east-central West Virginia.

except for the Rich Mountain stand that was located in Kumbrabow State Forest.

We sampled canopy gaps using the line-intercept method (Runkle, 1992) along one transect per stand. Transects were established from a randomly selected point and paralleled the contour of the topography within each stand. We defined canopy gaps as a space in the canopy produced by the death of at least one overstory tree where active recruitment of new individuals into the overstory was occurring (Watt, 1947). Gaps were formed either by standing snags (a dead tree from which the leaves and most of the branches have fallen), snaps (downed trees with the bole completely broken somewhere between the ground line and the base of the live crown), or uprooted trees (downed trees with at least some of the root-ball attached). When a line transect intersected a gap, we recorded the following data: 1) distance along the transect intercepted by the canopy gap, 2) canopy gap width and length (defined by the dripline of crowns of gap-border trees), 3) width and length of the extended canopy gap as defined by gap-border tree boles, 4) gap maker(s) species and diameter at breast height

(dbh, 1.4 m), 5) mode of gap origin (snag, snap, or uproot), 6) probable gap filler(s) species, dbh, and height, and 7) the species and dbh of gap-border trees whose crowns encircled the gap. In addition, we cored 2–4 trees at each gap to identify release dates and canopy gap age, as well as 2–4 additional trees along each transect to estimate stand age. Altogether, we increment cored 106 trees. We used cores from 68 trees to identify canopy gap formation dates (including 12 saplings). One gap occurred during sampling season, so no trees were cored. Eighteen non-gap overstory trees were used to identify stand age. Twenty cores were unusable.

We characterized stand composition and structure using the point-centered quarter method (Smith, 1996). At every 33 m along transects, we measured the distance from a point to the closest overstory tree in each of four cardinal directions (quarters). At each point, we identified trees by species, measured tree dbh, and distance of tree to the point. We used these data to calculate species importance values (IV) by averaging relative abundance, relative basal area, and relative frequency (max. IV = 100) using the technique outlined in Smith (1996).

Table 1
Species importance values and summary stand data from point-quarter sampling for 10 stands in the Allegheny Mountains of east-central West Virginia. (IV = Rel. density + Rel. basal area + Rel. freq)/3, max = 100). "Other" includes balsam fir (*Abies balsamea* L.(Mill.)), sugar maple, black birch, mountain magnolia (*Magnolia fraseri* Walt.), cucumber tree, bird cherry (*Prunus avium* L.) and mountain ash (*Sorbus americana* Marsh.) Stands sampled in 2006 and 2007.

Site	Red maple	Red spruce	Yellow birch	Black cherry	Am. beech	Eastern hemlock	Other	TPHa	BA/Ha	Stand origin
Briery Mtn. (BM)	3.6	4.4	17.9	25.9	34.5	0	13.7	566	36	1915
Cabin Mtn. 1 (CM1)	40.7	22.2	27.1	4.3	0	3.1	2.6	506	21	1920
Cabin Mtn. 2 (CM2)	26.3	32.6	29.8	4.4	0	0	6.9	697	20	1920
Kennison Mtn. (KM)	17.3	58.2	12.9	3.6	3.4	2.3	2.4	682	56	1924
Rich Mtn. (RM)	34.1	0	6.1	27.7	4.2	0	27.9	679	63	1926
Red Spruce Knob (RSK)	21.2	37.6	28.3	1.5	7.5	4	0	682	54	1918
Stuart Knob 1 (SK1)	59.2	0	6.5	13.9	6.3	3.1	11.1	356	39	1923
Stuart Knob 2 (SK2)	35.9	18.9	21.5	12.5	2.1	9.2	0	487	48	1915
Spruce Knob (SPK)	27.0	2.3	15.5	11.5	13.0	0	30.7	469	51	1917
Tea Creek Mtn. (TCM)	36.6	10.6	18.8	18	10	0	6.2	588	29	1920
Average	30.2	18.7	18.4	12.3	8.1	2.2	10.1	571	42	1920

3. Data analysis

We calculated canopy gap and extended canopy gap area by fitting width and length dimensions to the formula for an ellipse. We calculated percent of land in canopy gaps by dividing the total transect distance in gaps by the total transect distance and then multiplying by 100. We used ANOVA (PROC GLM, SAS 2002, ver. 9.1) to compare mean canopy gap and extended canopy gap sizes among stands as well as the diameters of overstory trees, gap makers, and gap-border trees. We used Fisher's Exact Test (PROC FREQ, SAS 2002, ver. 9.1) to evaluate the species distribution of gap makers.

We determined canopy gap age using a variety of techniques. For very recent gaps (formed within the last growing season), we checked leaf and bud conditions of gap makers. For older gaps, we applied dendrochronological methods to identify full release dates of gap fillers and/or identify partial release dates of gap-border trees. Sapling gap-fillers were cored approximately 0.2 m from ground surface, whereas overstory codominants were cored at breast height (1.4 m). We extracted increment cores parallel to topographic contours to avoid tension or compression wood, and prepared sample cores using standard dendrochronological techniques as outlined by Stokes and Smiley (1968). We cross-dated each tree-ring series and annual rings were measured under a dissecting microscope to the nearest 0.001 mm interfaced conjunction with J2X software (VoorTech Consulting 2000). We validated tree-ring dating using COFECHA (Grissino-Mayer, 2001), using 50-year segments lagged successively by 25 years.

We used a variety of dendroecological procedures to derive canopy disturbance dates based on tree type (gap-filler vs. gap-border tree). We identified releases using the percent growth change technique (%GC) with a 25% growth change threshold for overstory gap-border trees (Nowacki and Abrams, 1997) and a 100% threshold for sapling gap-fillers (Lorimer and Frelich, 1989). Because of concerns that the %GC technique may be overly sensitive at low growth rates (i.e., accepting false positives of suppressed saplings) and overly stringent at higher growth rates (i.e., producing false negatives), we also employed the absolute-increase method (AI) proposed by Fraver and White (2005a). In this method, release events occur when the absolute difference of running 10-year means exceeded a predetermined species-specific threshold. The advantage of this method is that it provides a scaling factor that automatically adjusts the percent-increase threshold to the growth rate immediately prior to the disturbance (Fraver and White, 2005b). We used predetermined absolute-increase thresholds by Fraver and White (2005a), that were 0.52 mm for red maple (*Acer rubrum* L.) and sugar maple, 0.58 mm for red spruce, and 0.67 mm for yellow birch. Both the %GC and AI techniques could

not be used for gaps younger than 10 years as the post-disturbance time interval was not long enough to compare sequential 10 year means. Accordingly, we used a simple visual inspection of radial growth rates to identify likely release dates. For those gap-filling saplings that had above-average growth (i.e., $\geq 1.0 \text{ mm year}^{-1}$) with no evidence of suppression, we designated the initial ring-year as the release date. Finally, we calculated annual canopy turnover rate (gap formation rate) by summing the total distance along transects in canopy gaps and dividing that by the total transect distance, and then dividing that by the maximum gap age of the study.

4. Results

4.1. Stand composition and structure

The examined stands originated between 1915 and 1926 (Table 1) and are currently in the late stem exclusion or early understory reinitiation stages of stand development (Fig. 2, Oliver and Larson, 1996). Overstories generally consisted of a single, even-aged cohort of trees consistent with clearcut harvesting, although remnant trees from the preceding stand were occasionally present. Red maple was the most important tree in 6 of the stands, red spruce in 3 stands, and American beech in a single stand (Table 1). Other northern hardwood species typical of the region such as sugar maple, black cherry, and yellow birch were frequent associates. Although red spruce either did not occur or was a very minor overstory component in four stands, it was nevertheless present in the mid- and understory throughout all stands surveyed.

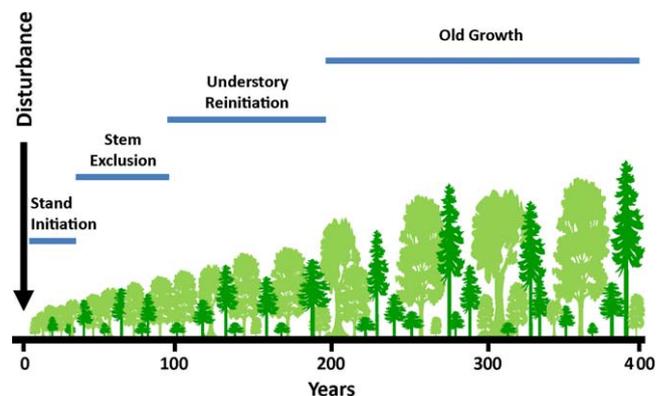


Fig. 2. Proposed timeline of forest stand development of anthropogenically altered red spruce-northern hardwood stands in the Allegheny Mountains of east-central West Virginia.

Table 2

Physical characteristics of 39 canopy gaps and extended canopy gaps for 10 stands in the Allegheny Mountains of east-central West Virginia. Means for canopy gap and extended canopy gap size refer to mean of all values from all stands (see Table 1 for key to stand abbreviations). Stands sampled in 2006 and 2007.

Metric	BM	CM1	CM2	KM	RM	RSK	SK1	SK2	SPK	TCM	AVE.
# canopy gaps	1	5	3	5	4	5	3	3	7	1	3.7
% canopy gaps	1.8	10.8	3.4	8.5	5.1	2.3	3.4	3.9	6.9	0.7	4.7
% extended gaps	3.3	17.3	7.9	16.0	16.5	5.1	8.8	14.4	18.9	2.1	11.0
Mean canopy gap (m ²)	43	127	33	26	16	12	31	20	36	30	53.4
Mean ext. canopy gap (m ²)	143	297	137	132	163	78	192	199	178	137	199.3
Transect length (m)	462	500	450	495	345	660	500	300	500	528	474

Overall, stands were relatively uniform in species composition. Average Sørensen percent similarity among paired samples was 77% and no values were <50%. All stands were well stocked, with tree densities ranging from 356 to 697 trees/ha and basal areas ranging from 20 to 63 m² ha⁻¹ (Table 1).

4.2. Gap size and frequency

Thirty-nine canopy gaps occurred along the total 4.74 km of transects sampled. Averaged across all stands, gaps occupied 4.7% of the canopy, whereas extended canopy gaps occupied 11.0% (Table 2). Gaps primarily were elliptical in shape; the ratios of the long and short diameters were 1.3 and 1.7 for canopy and extended gaps, respectively. Mean canopy and extended canopy gap areas were 53.4 ± 71.1 m² and 199.3 ± 127.8 m², respectively. The size distribution of canopy gaps was strongly skewed to the smallest classes, with approximately 70% of the gaps being ≤100 m² (Fig. 3). The extended canopy gap-size distribution was normal, excluding the large size-class outlier. The smallest canopy gap was 6.2 m², formed by a 22 cm (dbh) yellow birch snag; the largest gap was 276.4 m², formed by six American beech snags. There were no statistically significant differences in mean canopy gap or extended canopy gap sizes among the 10 stands ($p=0.682$ and $p=0.440$, respectively).

4.3. Gap makers and gap fillers

Sixty-five percent of the canopy gaps resulted from the death of one or two trees. American beech was the most frequent gap maker, accounting for 41% of individual tree mortality events and 21% of the gaps (Fig. 4). This was largely the result of beech-bark disease along one transect at Spruce Knob where six of the seven gaps were created, on average, by five American beech snags. Overall, the most common type of mortality was snag (72%), followed by snags (15%) and uprooting (13%). Mean gap maker dbh was 27.2 ± 12.2 cm (range 10.8–77.5 cm) and there were no significant differences in gap maker tree dbh with respect to species ($p=0.26$).

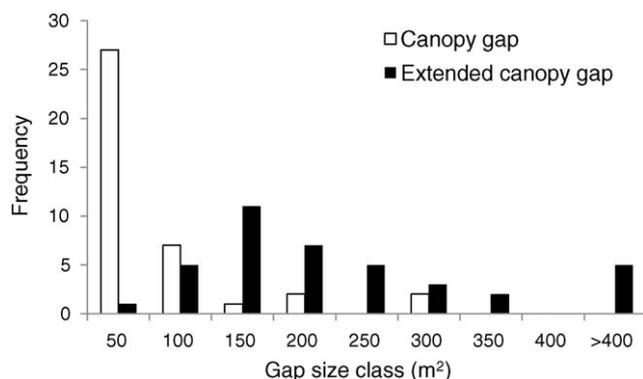


Fig. 3. Frequency of canopy gap (CG) and extended canopy gap (ECG) sizes for 10 stands in the Allegheny Mountains of east-central West Virginia. Stands sampled in 2006 and 2007.

With the exception of American beech, species as a factor was not helpful in predicting what tree would be a gap maker (Fishers Exact Test, $p=0.228$). Other common gap makers were yellow birch (33%) and red maple (16%), in proportions that were the opposite of their average overstory importance (Table 1). Tree size (dbh) was also not a good predictor of mortality. There was no significant difference between the mean dbh of gap makers and non-gap overstory trees (28.3 ± 12.2 cm, range 6.2–79.9 cm) inventoried using point-quarter sampling ($p=0.429$). Because of the abundance of red spruce saplings, this species projected to be the eventual gap filler in 15 of 39 gaps (Fig. 4). Other common gap fillers were American beech, yellow birch and red maple.

4.4. Gap age and gap formation rate

Thirty-three of 39 canopy gaps were successfully aged based on 62 tree-ring chronologies using at least one of the four methods previously described. Because six of the gaps were the result of beech-bark disease, multiple-snag gaps probably reflect more than one mortality event. In such cases, we used the most recent date as the release year. Release dates of eight gaps were identified by visual inspection of 24 red spruce gap-filling chronologies, either by the presence of recent abrupt growth increases or by high initial growth rates. There was close agreement between the %GC and AI techniques, with 39 and 42 gap-border trees showing partial canopy release using these two methods, respectively, and in 30 instances the two methods agreed exactly.

Mean gap age was 12.9 ± 7.3 years. The oldest gap was 30 years old, and the youngest gap was estimated to be 1-year old based on the presence of fresh leaves and buds on the gap maker. Based on an inspection of the gap age distribution, the disturbance regime seemed to be in flux rather than in equilibrium. The oldest gaps occurred most infrequently, as expected through gap disappearance, however, 11–15-year old gaps were more abundant than either the 1–5 or 6–10-year old gaps (Fig. 5). Based on the total distance of canopy gaps along all transects, we estimate a canopy turnover rate of approximately 1.4% year⁻¹.

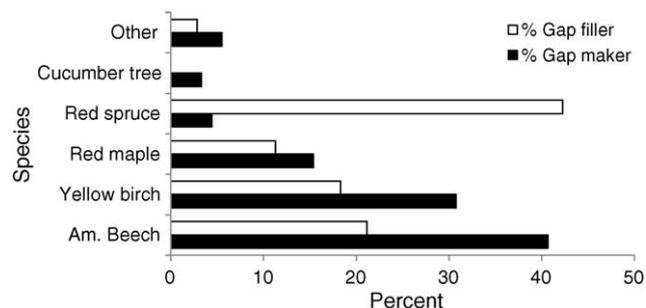


Fig. 4. Percent frequency of gap makers and gap fillers by species in 39 canopy gaps for 10 stands in the Allegheny Mountains of east-central West Virginia. "Other" includes sugar maple, black birch, black cherry, chestnut oak, American basswood, and eastern hemlock. Stands sampled in 2006 and 2007.

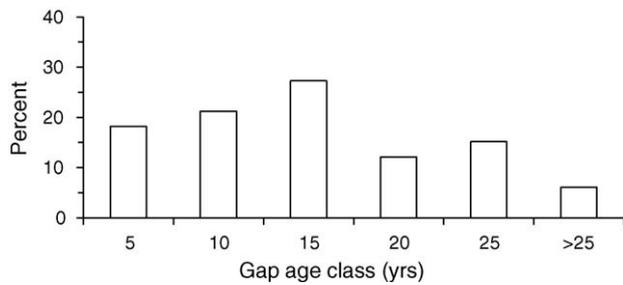


Fig. 5. Distribution of gap ages by 5-year age classes for 10 stands in the Allegheny Mountains of east-central West Virginia. Stands sampled in 2006 and 2007.

5. Discussion

Ecosystems are a product of the interactions of biota, climate, edaphic conditions, and disturbance processes. Over long periods, species best suited to the prevailing conditions eventually succeed and dominate (Denslow, 1980). Historically, red spruce was one such species at high elevations in the Appalachians. Here, the cool moist climate, shallow acidic soils, and principally wind-based disturbance regime greatly favored red spruce (White and Cogbill, 1992). Recognizing long-established biotic–abiotic relations, silviculturists seek to emulate the natural disturbance regime in order to successfully regenerate not only the tree(s) of interest but the entire community of species regardless of life-form (Seymour et al., 2002). Operating outside of the natural disturbance regime often has negative effects at the stand, landscape and regional scales (Engstrom et al., 1999), as was the case with the widespread cutting and burning of red spruce in the late 1800s and early 1900s in both the central and southern Appalachians (Korstian, 1937; Minckler, 1940, 1945; Allard and Leonard, 1952; Clarkson, 1964; Pielke, 1981; Pyle and Schafale, 1988; Hayes et al., 2007). The severity of these human-based disturbances had no natural analogue; hence it led to the extensive exhaustion of the red spruce resource, loss of site productivity, local extirpation of species such as Cheat Mountain salamander (Dillard et al., 2008; Pauley, 2008), and reduced heterogeneity of stand structure. These disturbances greatly benefitted early successional and/or hardwood species at the expense of shade-tolerant red spruce (Korstian, 1937; Clarkson, 1964) and led to the ubiquity of mono-canopied, even-aged forests seen today. It was from this highly modified forested landscape that our gap data was derived. As such, the dataset essentially represents a single point in time in forest stand development and needs to be interpreted accordingly.

5.1. Gap size and frequency

In southern Appalachian red spruce–Fraser fir (*Abies fraseri* Pursh.) stands, White et al. (1985) estimated an average gap size of 66 m², an average gap age of 33 years, and a canopy turnover rate of 0.6–0.9% year⁻¹. Fraver and White (2005b) found similar mean gap sizes and canopy turnover rates (66 m², and 1.01% year⁻¹) in red spruce in northern Maine, even though these forests were subject to periodic outbreaks of spruce budworm where 18–54% of the percent of canopy area was lost. Although both of these studies examined old-growth forests, mean values for gap size, frequency, and turnover rates were comparable to findings of our study, and indeed, from many other temperate, mesic forests in eastern North America. Runkle (1985) argued that because of the vulnerability of larger and older trees, forest disturbance rates, and thus maximum tree age, seemed to be constrained by a small range of possible values. In fact, he found

that average rates of forest disturbance showed little variation among forest types, even when wide differences in vegetation and types of disturbances were present. He concluded, absent differences in average disturbance rates, different disturbance regimes were more likely to be distinguished by differences in the distribution of disturbances in space and time, as well as their severity.

Although our mean and median canopy gap sizes were comparable to other studies of mixed hardwood–conifer forest types, only 2 of 39 canopy gaps were larger than 200 m², considerably less frequent than found by others (White et al., 1985; Foster and Reiners, 1986; Kneeshaw and Bergeron, 1998; Worrall et al., 2005). A myriad of biotic (tree species, size, and age) and abiotic (soil depth, slope percent, landscape position, aspect) factors affect canopy gap size, however we suggest that the relatively young age and stage of development of our stands are largely responsible for the absence of larger gaps (Lohmander and Helles, 1987).

As trees age, they become taller, larger canopied, and the ratio of above-ground to below-ground biomass increases, such that the tree is subject not only to greater drag and wind stress, but the anchoring ability of the roots becomes proportionately less (Coutts and Grace, 1995). These stresses, plus an increase in internal defects, make older and larger trees increasingly susceptible to windthrow (Nowacki and Kramer, 1998). In old-growth forests, crown sizes and tree spacing are greater than in stands in the stem exclusion or understory reinitiation stages, often yielding larger gaps that remain open longer (Oliver and Larson, 1996). Moreover, the greater frequency of large-canopied trees in old-growth forests augments the formation of large, multiple-tree gaps through tree-to-tree impact (domino effect). This explains, in part, why Kneeshaw and Bergeron (1998) found increasing gap area and faster canopy turnover and species replacement rates with stand age in eastern boreal Canada.

Forest canopy gaps are dynamic in that they are created, sometimes expand, sometimes combine with others, and eventually disappear, all of which can occur simultaneously at the stand or landscape level (Ott and Juday, 2002). Large gaps are often the result of two or more discrete canopy gap disturbance events. Re-sampling gaps in old-growth mixed deciduous–conifer montane stands in North Carolina, Runkle and Yetter (1987) found that in 42% of the gaps sampled in 1976, at least one gap-border tree had died or was dying after 5 years, and in 13% of the gaps, a new gap occurred near enough to influence gap closure in the first gap. Worrall et al. (2005) found this gap expansion process to occur more frequently than new gap initiation. Repeat disturbance at a single location is likely as a result of canopy tree crown asymmetry (Young and Hubbell, 1991), as well as stochastic processes related to simple probability and canopy tree geometry (Runkle and Yetter, 1987). As hardwood gap-border trees grow and laterally close gaps, crowns become increasingly asymmetrical. Crown asymmetry may not result in higher mortality rates, however, it probably does increase the likelihood that windblown or snapped border trees will fall and expand an existing gap. On average, the relatively small gaps we surveyed were surrounded by 8.5 ± 2.1 border trees, so the probability was high that at least one of those trees could be subject to a mortality event prior to gap closure.

We found 12 gaps whose release record suggested the occurrence of multiple disturbances, based on the tree-ring chronologies of gap-border trees. Repeat events occurred, on average, every 5.1 ± 3.2 years. One larger gap on Spruce Knob indicated three distinct mortality events. Repeat disturbances are not unexpected when disease epidemics such as beech-bark disease are the disturbance agent. Aside from direct mortality attributed to the disease, indirect mortality may arise from increased susceptibility of diseased trees to windthrow and ice storm damage (Latty, 2005).

5.2. Gap closure rate

Although red spruce was predicted to be the gap filler in 15 of 39 cases, gap capture will depend on its initial height and growth rate (relative to other competitors), gap size, and lateral growth rates of gap-border crowns. Estimates by Korstian (1937) and Carmean et al. (1989) project red spruce height growth rates of 23–28 cm year⁻¹ depending on site index. At these growth rates, if the height of the bottom of the overstory is 12 m, approximately 31 years of growth would be required for a 3 m red spruce sapling to capture a gap. The red spruce growth model of Moores et al. (2004) estimated that this time period would require 42 years in 50% full light. To reach 20 m, a reasonable estimate of overstory height of high-elevation sites in this region, the time interval increases to 60 and 90 years for the two light regimes, respectively.

Gaps also will close from lateral growth of the crowns of gap-border trees. However, lateral closure can be problematic for red spruce in these stands because the competing overstory is almost exclusively deciduous hardwoods that unlike conifers, display weaker apical control and strongly decurrent crown shapes (Oliver and Larson, 1996). Assuming hardwood lateral growth rates of 18–50 cm year⁻¹ (see Runkle and Yetter, 1987) lateral closure of an average-sized canopy gap would occur as early as 9–20 years; for gaps of 100 m², closure would occur in 12–29 years. However, this projection assumes a constant branch extension rate (Webster and Lorimer, 2005). Using repeat hemispheric photography, Valverde and Silvertown (1997) determined that canopy openings in European hardwood forests decreased in size by approximately 21% year⁻¹. Using this rate, average-sized gaps (i.e., 50 m²) may close in 13 years, while larger (≥ 100 m²) may require 16 years.

Considering the relatively fast rate of lateral extension of hardwood border trees, most red spruce saplings will require more than one release event to ascend into the overstory. Fortunately, red spruce is well-adapted to this environment as the species is exceedingly shade tolerant (Blum, 1990), and can respond to release following as much as 100 years of suppression (Seymour, 1992). Rentch et al. (2007) reported that 40% of understory red spruce saplings in West Virginia showed evidence of major releases (%GC $\geq 100\%$), and that 6% experienced two or more releases. In both North Carolina and Maine, more than 70% of successful overstory red spruce required at least one major release to reach the overstory, and more than 20% required two major releases (Wu et al., 1999; Fraver and White, 2005b).

5.3. Tree mortality and gap origin

Different types of gap makers and modes of tree mortality have different impacts on forest dynamics (Krasny and Whitmore, 1992; Battles and Fahey, 2000). Trees that die standing release growing space gradually, resulting in minimal disruption to the forest floor and damage to the understory. This mode of tree death greatly favors advanced regeneration, although the slow release of resources (especially light) may delay the onset of canopy ascension. In contrast, snaps and uprooted trees increase light availability instantaneously, but often result in mechanical damage to the forest understory. These modes of tree death can, in turn, foster the establishment and growth of a new cohort of seedlings. The effects of different modes of tree mortality on red spruce differ based on its pre-disturbance understory status. Where red spruce advanced regeneration exists, gap formation that includes minimal understory damage is most advantageous. Where red spruce regeneration is limited or non-existent, gap creation that disturbs the forest floor and/or damages existing hardwood regeneration would help provide avenues for red spruce establishment.

Our results on gap origin differ from that of other studies within the eastern United States. Wind disturbance was cited as the most common agent of tree mortality of old-growth red spruce-Fraser fir stands in North Carolina (White et al., 1985) and red spruce-balsam fir stands in New Hampshire (Foster and Reiners, 1986; Worrall et al., 2005). Similar results were reported for southern Appalachian cove-hardwood forests (Runkle, 1985) and second-growth hardwoods in Tennessee (Hart and Grissino-Mayer, 2009) and West Virginia (Himes, 2009). In contrast, 72% of the gap makers in our study were standing snags. American beech was the most common snag, largely due to gaps where as many as 10 individuals succumbed to beech-bark disease (similar to Krasny and Whitmore, 1992). Snags, however, were the most common form of tree mortality among other species as well. For instance, 75% of yellow birch gap makers were snags. Cucumber tree (*Magnolia acuminata* L.), basswood (*Tilia americana* L.), red maple, eastern hemlock, and black birch (*Betula lenta* L.) were all more often standing snags than wind-related snaps or uproots. The absence of a stronger trend in obviously wind-related mortality is curious because, with the exception of American beech, none of the other snag gap-makers showed evidence of acute disease or pest infestation that would account for the number of standing dead trees.

The preponderance of snags in our study may be merely the reflection of stand development stage (Taylor et al., 2007). During the stem exclusion stage, trees die primarily as a result of density-dependent mortality (i.e., self-thinning), as more vigorous stems outcompete less vigorous ones. This competition is reflected first in crown differentiation, with more competitive trees occupying the upper canopy as dominant or codominant stems and less competitive stems increasingly relegated to intermediate and overtopped crown classes. Inferior canopy positions and crown sizes are eventually reflected in lowered rates of diameter growth, reduced vigor, and eventual death, unless very shade tolerant. Mortality due to this allogenic process may account for the relatively large number of snags in this study. Snaps and uprooting will undoubtedly increase as these stands age, consistent with the modes of tree death and canopy dynamics of the understory reinitiation and old-growth stages seen elsewhere.

6. Management implications

It is noteworthy that red spruce was the most common gap filler even though the main gap makers were American beech, yellow birch, and red maple. This suggests a shift in species composition is occurring, albeit slowly, from northern hardwood dominance to a forest with a much larger red spruce component (see Nowacki et al., 2010). This is encouraging news for those land management agencies and conservation organizations in the region that are actively engaged in red spruce restoration. However, it is also clear from our results that most canopy gaps are small and are likely to close by lateral expansion of mostly northern hardwood trees before overstory ascension. Moreover, our results and the results of others (White et al., 1985; Fraver and White, 2005b) indicate that only about 5% of the forest area is within a gap environment at any one time. As such, opportunities for natural red spruce release at any given location are limited.

To accelerate the red spruce recovery process, we believe a series of management actions is feasible. Both pre-commercial and commercial thinning are possible and should focus on a range of gap sizes, but smaller gaps that persist for about 10–20 years should predominate. Smaller gap sizes will retain moister seed beds and be more resistant to windthrow than larger openings (Westveld, 1953), and will discourage aggressive shade-intolerant hardwood competition from overwhelming existing understory red spruce in the gap environment. Larger gaps (i.e., group selection) should only

be used where red spruce forms a nearly continuous subcanopy. Depending on the size of the opening, forest managers developing red spruce restoration plans should anticipate the potential need for several releases before understory red spruce will reach the main canopy. As an additional bonus, thinning from above or a crop tree release approach may provide sufficient revenue from harvesting commercial species to pay for pre-commercial operations in other areas less suitable for commercial thinning. Uneven-age management in the form of single-tree selection may also be an option for restoring degraded red spruce forests. Because red spruce is extremely shade tolerant, single-tree selection would provide great flexibility in controlling residual stocking, tree quality, and establishing a cutting cycle that meets both ecological and economic objectives. More intensive measures, such as understory herbiciding and planting, may be needed for those forests lacking adequate red spruce regeneration. Specific guidelines with residual stand structure recommendations are beyond the scope of this paper and have not been tested experimentally in these central Appalachian forest stands. However, given the paucity of experimental evidence and potentially changing environmental conditions, we believe our study provides a foundation that forest managers could use to develop adaptive forest management techniques for restoration objectives.

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