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Seedling recruitment and stand regeneration in spruce-fir forests of the Great Smoky Mountains[1,2]

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ABSTRACT

NICHOLAS, N. S., S. M. ZEDAKER (Department of Forestry, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061), C. EAGAR (Northeastern Forest Experiment Station, USDA Forest Service, Durham, New Hampshire 03824), AND F. T. BONNER (Forestry Sciences Laboratory, USDA Forest Service, Starkville, Mississippi 39759). Seedling recruitment and stand regeneration in spruce-fir forests of the Great Smoky Mountains. Bull. Torrey Bot. Club 119: 289–299. 1992.—Seedfall and seedling recruitment was assessed in spruce-fir forests of the Great Smoky Mountains (Tennessee and North Carolina) from 1985 to 1990. A permanent system of 66 plots was measured including overstory, understory, and seedling strata with seedtraps located at a third of the plots. Fraser fir (*Abies fraseri* (Pursh) Poir.) seed production was highest in 1987 when almost two and a half million seeds per hectare were collected at the highest elevations (1980+ m). In other collection years fir production ranged from 300,000 to 500,000 seeds/ha, with the exception of 1990 (complete seed failure). Red spruce (*Picea rubens* Sarg.) seed production was highest at lower elevations. The majority of fir (88–100%) and spruce (54–100%) seeds were empty. Spruce seed viability was highest in 1987 and increased with decreasing elevation (18–41%) while fir seed viability in that year was lower (6–9%). Spruce and hardwood germinal (<1 year) and seedling (1 year to 1.37 m) densities tended to decrease with increasing elevation while fir germinal counts increased at higher elevations. No fir germinals were found in 1989 or 1990. Spruce seedling and understory densities were greatest at 1675 m elevation. Stem densities (seedlings, understory, and overstory) tended to decrease with increasing size with the exception of red spruce at 1525 and 1980 m elevation classes where understory densities were less than overstory densities.

Key words: red spruce decline, balsam woolly adelgid, Fraser fir.

Southern Appalachian spruce-fir forests have experienced serious perturbation in the last century. Commercial logging and associated fires of the early 1900's reduced the southern Appalachian spruce-fir to less than a tenth of its former expanse in West Virginia, Virginia, North Carolina, and Tennessee (Korstian 1937). Currently, these forests are being severely impacted by the balsam woolly adelgid (*Adelges piceae* Ratz.), first detected in the southern Appalachians in the late 1950's (Speers 1958). Mature Fraser fir (*Abies fraseri* (Pursh) Poir.), a southern mountain endemic, is highly susceptible to attack by the exotic insect with death occurring in two to nine years. Furthermore, dendroecological evidence suggests a red spruce (*Picea rubens* Sarg.) growth decline in the southern Appalachians both in the past twenty years and the early 1900's (Cogbill 1977; Adams *et al.* 1985; McLaughlin *et al.* 1987) as well as canopy crown deterioration over the

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past five years (Zedaker *et al.* 1989; Nicholas and Zedaker 1990).

The vast majority of the remaining southern Appalachian spruce-fir (74 percent) is found in the Great Smoky Mountains (Dull *et al.* 1988) where only 20 percent of the forest type was previously logged (Pyle and Schafale 1988). Even without logging, stand structure and composition have been altered after adelgid infestation, and further change is expected. Recent disturbances have raised concern for the continued health and existence of the forest and have prompted a long term monitoring of the ecosystem. Perturbation from wind-throw, debris slides, and ice/snow damage to these high elevation systems is normal and may be of limited long-term consequence as long as adequate regeneration is taking place. However, the impacts from site degradation from adelgid infestation, climate change and possible atmospheric deposition are still unknown. Some preliminary studies (Witter and Ragenovich 1986; Busing and Clebsch 1987) indicate that accelerated mortality rates and changing stand age structure may result in some shifts in species composition. Regeneration patterns need to be quantified before assessment can be made of the potential for or possibility of stand replacement. The intent of this paper is to describe existing regeneration, including seedfall and seedling composition along an elevational gradient, at permanent monitoring plots in spruce-fir stands located in the Great Smoky Mountains, and compare regeneration patterns to current overstory densities.

Methods. In 1985 sixty-six stratified, randomly-located 20 × 20 m permanent plots were established at the Great Smoky Mountains in Tennessee and North Carolina (from Newfound Gap to Clingman's Dome) as part of the National Acid Precipitation Assessment Programs (NAPAP) Forest Response Program to monitor current spruce-fir forest vigor and long-term dynamics. Stratification factors included elevation (four classes from 1525 to 1980+ m), exposure to prevailing winds (exposed versus protected), and topography type (ridge/slope/draw) with three replicates per strata combination wherever possible.

Overstory (stems with diameter at breast height [DBH] $\geq$5.0 cm) stratum measurements included DBH, inspection for crown condition, and damage/injury symptomology (signs of disease or damage to stem) by species on every tree on each plot. All qualitative observations were made by at least two technicians for each tree. The understory (DBH $<$5.0 cm and height $\geq$1.37 m tall) and seedling (woody species with height $<$1.37 m) strata were sampled in nested subplots within the 400 m^2 overstory plot. Three 2 × 8 m subplots were selected at random and permanently marked for understory data collection. All understory woody stems were recorded by species and measured for basal diameter (15 cm above ground from the uphill side of the stem) to the nearest mm. Four 1 × 1 m sub-subplots were permanently located in each understory subplot and all seedlings were counted by species and recorded in one of five age-size classes (Class 1: $<$1 year, Class 2: 1–4 years, Class 3: 4 years to 0.25 m tall, Class 4: 0.25–1.0 m, and Class 5: 1.0–1.37 m). After plot establishment, seedling sub-subplots were remeasured annually through 1990.

Three seed traps (0.5 × 0.5 m), made of polypropylene and medium density mesh polyethylene and framed with 0.5 inch (1.26 cm) PVC pipe, were set up at one randomly selected plot for every elevation/exposure/topography combination. Traps were randomly located outside, within 10 m, of the plot. All litter found in or on the traps was collected from late November through December starting in 1986 and continued through 1990; however, some traps were destroyed by small and large mammals. Litter was air-dried and sorted to separate seeds of arborescent species. Seeds were counted by species and sent to the Forestry Sciences Laboratory at Starkville, Mississippi for germination testing. A maximum of 50 seeds per species per trap was tested, and seeds were scored as viable (contained an embryo that was capable of germination), empty (seed coat that contained no embryo), or dead (embryo that was no longer viable). Test procedures followed the prescriptions of the Association of Official Seed Analysts (1988).

Analysis of variance (ANOVA) and the Duncan multiple range test was used to test for differences among selected class variables (elevation, species, year) (SAS Institute 1985). Percentage data were tested for normality to determine if an arcsine transformation was necessary. In order to determine the relationship between seedling densities and overstory conditions, linear regression equations were fitted for spruce and fir regeneration. The dependent variable was regeneration density summing seedling classes 2–5, omitting stems less than a year old. Independent overstory variables were considered separately, in combination, and as interactions including: spruce, fir and/or total stand live basal

Table 1. Seedfall density (and next year germinal counts in parentheses) at four elevations in the Great Smoky Mountains for 1986–1990.

		Year[a]				
		1986	1987	1988	1989	1990[c]
Elev.[b] m	Species	seeds/ha (next year seedlings/ha)				
1525	Spruce	466,665 (2685)	35,343,331 (158,512)	1,161,664 (3241)	968,333 (5000)	60,000
	Fir	10,000 (0)	3333 (46)	0 (0)	3333 (0)	0
	Hardwoods	1,446,663 (72,682)	10,346,664 (114,579)	711,665 (38,193)	13,394,990 (130,661)	426,666
1675	Spruce	1,249,997 (8287)	8,580,000 (189,020)	226,666 (3241)	2,783,996 (19,499)	88,889
	Fir	0 (46)	960,000 (417)	3333 (0)	5333 (0)	0
	Hardwoods	2,236,661 (46,285)	10,360,000 (182,122)	270,000 (35,230)	11,446,639 (243,990)	17,778
1830	Spruce	385,332 (2037)	1358,330 (71,432)	217,777 (1343)	1,797,330 (1667)	30,000
	Fir	306,666 (93)	533,332 (1389)	13,333 (0)	5333 (0)	0
	Hardwoods	96,000 (3194)	1,074,997 (15,972)	34,444 (4676)	10,450,642 (54,998)	20,000
1980	Spruce	0 (833)	1,743,333 (16,249)	404,999 (139)	95,000 (208)	10,000
	Fir	306,666 (1805)	2413,328 (10,277)	288,333 (0)	534,999 (1250)	0
	Hardwoods	44,444 (556)	341,666 (4583)	31,667 (1042)	73,333 (1667)	286,666

[a] Significant differences ($P < 0.05$) were found among years for hardwoods seedfall density and for spruce and hardwood germinals.

[b] No significant differences ($P < 0.05$) were found among elevation classes for seedfall or germinal density of any of the species.

[c] No counts were made of 1991 germinals.

area; spruce, fir, and/or total dead basal area; spruce, fir, and/or total stand density; elevation, and average stand age of dominants and codominants. Data were also examined to determine if partitioning by elevation class would improve the models' fit.

Results. SEEDFALL. During the five year period from 1986 through 1990, seed crops were greatest in 1987 (Table 1), with the exception of large counts of hardwoods (mostly yellow birch (*Betula lutea* Michaux f.) in 1989. Spruce and fir seed production increased between 1986 and 1987, decreased between 1987 and 1988, increased between 1988 and 1989, and decreased in 1990 to the lowest levels found during the study. Hardwood species (primarily yellow birch, maples, mountain-ash (*Sorbus america* Marshall), and fire cherry (*Prunus pensylvanica* L.) seed production followed a similar pattern as spruce and fir except that seed production levels in 1990 were not as low as conifer levels.

In 1986 spruce seed viability varied between 3 and 10 percent (Table 2). In 1987 seed viability varied along an elevation gradient, decreasing with increasing elevation. In contrast to the 1987 crop, spruce seed viability in 1988 was quite low (0–3%). In the fourth year (1989) of sampling (Tables 1–2) both viability and production increased. No viable spruce seeds were found in 1990.

In 1986 the only viable fir seed was found at the higher elevation classes (1830 and 1980 m) with 12 percent viability (Table 2), while in 1987 fir viability ranged between 6 to 9 percent (excluding the 1525 m sample where only one seed was tested). Very few fir seeds were collected in 1988 and 1989 (Table 1), and of those no viable seeds were found (Table 2). No fir seeds were found in 1990.

Table 2. Seedfall viability at four elevations in the Great Smoky Mountains for 1986–1990 (number of seeds tested in parentheses).

		Year[a]							
		1986				1987			
Elev.[b] m	Spp.	Viable	Empty	Dead	(N)	Viable	Empty	Dead	(N)
			%				%		
1525	Spruce	5	88	7	(130)	41	54	5	(399)
	Fir	0	100	0	(1)	100	0	0	(1)
	Hardwoods	38	62	0	(258)	39	49	12	(466)
1675	Spruce	10	89	1	(290)	26	66	8	(100)
	Fir	—	—	—	(—)	6	88	6	(48)
	Hardwoods	11	88	1	(262)	20	68	12	(97)
1830	Spruce	3	96	1	(141)	23	70	7	(359)
	Fir	12	88	0	(50)	9	90	1	(156)
	Hardwoods	4	96	0	(27)	14	77	9	(224)
1980	Spruce	—	—	—	(—)	18	78	4	(251)
	Fir	12	88	0	(50)	6	91	3	(344)
	Hardwoods	0	100	0	(1)	76	20	4	(25)

[a] Significant differences ($P < 0.05$) were found among years for spruce and hardwood seed viability.

[b] No significant differences ($P < 0.05$) were found among elevation classes for any of the species.

In 1986 hardwood species seed viability was greatest at the lowest elevation (1525 m) (Table 2). During the five year study hardwood seed viability was greatest in 1987; 31 percent of all seeds sampled were viable. In 1988 seed viability ranged from 0 to 11 percent but viability increased in 1989. In 1990 the only viable seeds were found at the lowest elevation.

SEEDLING REGENERATION. Spruce and hardwood germinal (<1 year) densities tended to peak at 1675 m and then decrease with increasing elevation while fir germinal counts increased at higher elevations (Table 1). Germination success (the number of first year seedlings as a fraction of the number of viable seeds of the year before) varied among years and species. Between 5 to 28 percent of viable spruce seeds germinated and lived until the survey. Higher germination success rates for spruce did not follow high seed production years. Fir germinals were found only during the first two years of this study and at the highest elevations, and averaged 3 percent germination success from viable seed. Germination success for viable hardwood seed ranged from 6 to 95 percent and, like spruce, higher germination rates did not follow high seed production years.

Highly significant differences ($P < .001$) for seedlings (1 year to 1.37 m tall) among elevation classes were found for spruce and fir (Table 3). Both spruce and hardwood seedling numbers tended to decrease as elevation increased while fir seedling densities showed an opposite trend. As found for germinal counts, spruce and hardwoods densities were greatest at the 1675 m elevation class. Low densities of fir of all age-size classes were found at 1525 m elevation. Stem densities for a species within an elevation class tended to decrease with increasing size. However, at all elevations, current red spruce understory (1.37 m tall to 5.0 cm dbh) densities were statistically similar (according to the Duncan test) or less than overstory densities. Analysis of species composition of seedlings, understory, and overstory densities indicated that, for spruce, at all elevations percentages of understory densities were less than percentages of overstory densities. In contrast, hardwood species made up a greater proportion of understory stems than found in the overstory.

PREDICTIVE EQUATIONS. A series of linear and nonlinear regression models were examined for suitability of seedling density prediction. Regression analysis detected no meaningful trends for fir regeneration patterns. Model fitting success for red spruce regeneration ($R^2 = .526$, adjusted $R^2 = .481$, $P < .001$) relied on significant ($P < .01$) overstory live basal area and elevation terms:

$$\text{Seedlings (stems/ha)} = -85{,}561 + 642 * \text{Live Basal Area (m}^2\text{/ha)} + 33.3 * \text{Elevation (m)}.$$

Examination of the differences between predict-

Table 2. Extended.

Year											
1988				1989				1990			
Viable	Empty	Dead		Viable	Empty	Dead		Viable	Empty	Dead	
	%		(N)		%		(N)		%		(N)
3	88	9	(213)	5	93	2	(179)	0	100	0	(9)
–	–	–	(–)	0	100	0	(1)	–	–	–	(–)
8	87	5	(203)	26	72	2	(417)	23	59	17	(64)
2	89	9	(56)	23	72	5	(374)	0	100	0	(20)
0	100	0	(1)	0	100	0	(2)	–	–	–	(–)
7	90	3	(60)	34	64	2	(352)	0	100	0	(–)
0	93	7	(43)	5	91	4	(395)	0	100	0	(8)
0	100	0	(2)	0	100	0	(2)	–	–	–	(–)
0	100	0	(6)	12	86	2	(615)	0	100	0	(3)
1	93	6	(108)	4	92	4	(25)	0	100	0	(3)
0	100	0	(57)	0	99	1	(139)	–	–	–	(–)
11	89	0	(9)	11	89	0	(19)	0	75	25	(40)

ed and observed regeneration counts showed a tendency of the model to overestimate high seedling densities. Data were also examined to determine if separate equations for each elevation class would be more appropriate. Division of the data resulted in much poorer models.

Discussion. Species distribution in undisturbed southern Appalachian high elevation forests tends to follow an elevation gradient: spruce forest from 1370 to 1675 m, spruce-fir from 1675 to 1890 m, and fir forest above 1890 m. On lower or drier slopes, red spruce may share dominance with yellow birch and birch may dominate at moister draw sites. At the higher elevations, Fraser fir is often the sole dominant, and mountain-ash may be the only other canopy tree present (Whittaker 1956).

Balsam woolly adelgid has infested most of the fir in the Smokies (Nicholas and Zedaker 1990). Salivary substances secreted by the insect diffuse into the xylem and disrupt translocation. Impaired water and nutrient flow to the crown eventually results in tree death (Puritch and Johnson 1971). Heavy stem infestation causes death quite rapidly, often within a few years of initial attack. Other deleterious effects of infestation can include increased susceptibility to *Armillaria* root rot and impaired reproductive function (Fedde 1973; Hay *et al.* 1978).

In order to maintain Fraser fir on the Appalachian peaks in the continued presence of the balsam woolly adelgid, fir seedlings and saplings must survive to seed bearing age and produce viable seed. Seed bearing of overstory or open grown *Abies* trees usually begins at 20–30 years with larger seed crops occurring at 2–4 year intervals. Seed production may be reduced by adverse climatic conditions, squirrels, or birds and typically large numbers of mature fir seed are empty (USDA Forest Service 1974).

Fir seed production was highest in 1987 with estimates of almost two and a half million seeds per hectare at the highest elevation. Seed production in other collection years was minimal except at the highest elevation with production ranging from 300,000 to 500,000 seeds/ha. The majority (88 to 100 percent) of fir seeds were empty. Average germination capacity of *Abies* seed has been reported to be low, often between 20–50 percent of filled seeds (USDA Forest Service 1974). However, we found germination capacity of filled seeds (viable and dead seeds) for all five collection years to be 79 percent.

The possibility of a red spruce decline has also prompted concern for the capability of spruce to produce viable seed. Overstory spruce usually begin seed bearing at 30–40 years of age, depending on canopy position, with larger seed crops occurring at 3–8 year intervals (USDA Forest Service 1974). Like fir, spruce seed production was highest in 1987 with the largest estimates of the crop at lower elevations. Seed production in other collection years was substantially less. Like fir the majority of spruce seeds were empty. For all spruce seeds tested over a five year period, 80 percent were empty. Agmata and Bonner (1988) suggest that low seed yield (filled seeds per cone) for red spruce may be normal for high elevation stands. While the USDA Forest Service (1974)

Table 3. Seedling (1 year to height ≥1.37 m), understory (DBH <5.0 cm and height >1.37 m), and overstory (DBH ≥5.0 cm) density (stems/ha) five year means stratified by elevation of red spruce, Fraser fir, and all hardwoods in the Great Smoky Mountains, Tennessee and North Carolina (percentage of stem densities by species for each elevation in parentheses).

Elevation[a] m	Species	1–4 yr	4 yr–0.25 m	0.25–1.0 m	1.0–1.37 m	Understory	Overstory
		stems/ha					
		(%)					
1525	Spruce	35,897	20,519	1926	65	278	503
		(56)	(81)	(18)	(4)	(4)	(38)
	Fir	56	1602	815	28	23	10
		(–)	(6)	(8)	(2)	(0)	(1)
	Hdwds	28,277	3287	8000	1509	6029	817
		(44)	(13)	(74)	(94)	(96)	(61)
1675	Spruce	44,998	39,119	4889	463	590	356
		(61)	(77)	(24)	(21)	(14)	(58)
	Fir	2213	5768	4148	389	660	67
		(3)	(11)	(20)	(17)	(15)	(11)
	Hdwds	26,573	6241	11,509	1324	3101	187
		(36)	(12)	(56)	(61)	(71)	(31)
1830	Spruce	26,721	13,898	1055	222	405	267
		(62)	(46)	(7)	(11)	(12)	(42)
	Fir	8944	10,689	3852	343	706	189
		(21)	(36)	(26)	(18)	(21)	(32)
	Hdwds	7518	5352	9814	1370	2303	176
		(17)	(18)	(67)	(71)	(67)	(28)
1980	Spruce	4500	1250	125	28	35	158
		(23)	(11)	(2)	(2)	(1)	(16)
	Fir	9388	8236	2889	611	1232	773
		(48)	(70)	(48)	(44)	(41)	(77)
	Hdwds	5611	2306	3042	736	1718	79
		(29)	(19)	(50)	(54)	(58)	(7)

[a] Significant differences ($P < 0.05$) were found among elevation classes for spruce, fir, and hardwood stem densities. Highly significant differences ($P < 0.001$) were found among elevation classes for spruce and fir seedling densities.

reported an average red spruce germination capacity for filled seeds of 62 percent, our study found an 82 percent average germination capacity for filled seed.

Actual germination and subsequent seedling survival is critical. Pauley (1989) and Pauley and Clebsch (1990) studied patterns of fir regeneration in a Great Smoky Mountains stand (1760–1830 m elevation) on Mt. Collins in 1988 after the impact of the adelgid. They found an average fir seedling (1 year to 1.37 m tall) density of 33,000 stems/ha compared to our value of 23,828 stems/ha and an average spruce seedling density of 106,000 stems compared to our value of 41,896 stems/ha at that elevation (Table 3). White et al. (1985) studied regeneration patterns on Mt. Collins (1750–1800 m elevation) in 1984, comparing relative densities under canopy trees, in gaps, and within the forest excluding gaps. The majority of fir seedlings were found to be ≤.25 m tall by Pauley and Clebsch (87%), White et al. (89%) and our study (82%, Table 3). However, the Pauley and Clebsch study did not find any germinal fir seedlings in 1988 while our study did find an average density of 1,389 stems/ha at a comparable elevation that year (Table 1). One reason may be that our study was far more geographically dispersed and our actual number of seedling sub-plots was ten times larger.

The possible role of elevation needs to be considered in germination success and seedling survival. Overall germination rates (germinal density/seedfall density × 100) were greatest at 1675 m elevation for both spruce (4.8%) and hardwoods (1.3%) while the highest elevations had the best rate (0.3%) for fir (Figure 1). In contrast, elevation was a source of little variation in stem density distributions (with the exception of spruce at 1525 m) (Figure 2). Both Table 3 and Figure 2 provide stark evidence that large spruce seedling densities (.25–1.37 m tall) are a fraction of the number of small seedlings regardless the elevation.

After the death of mature fir by the adelgid,

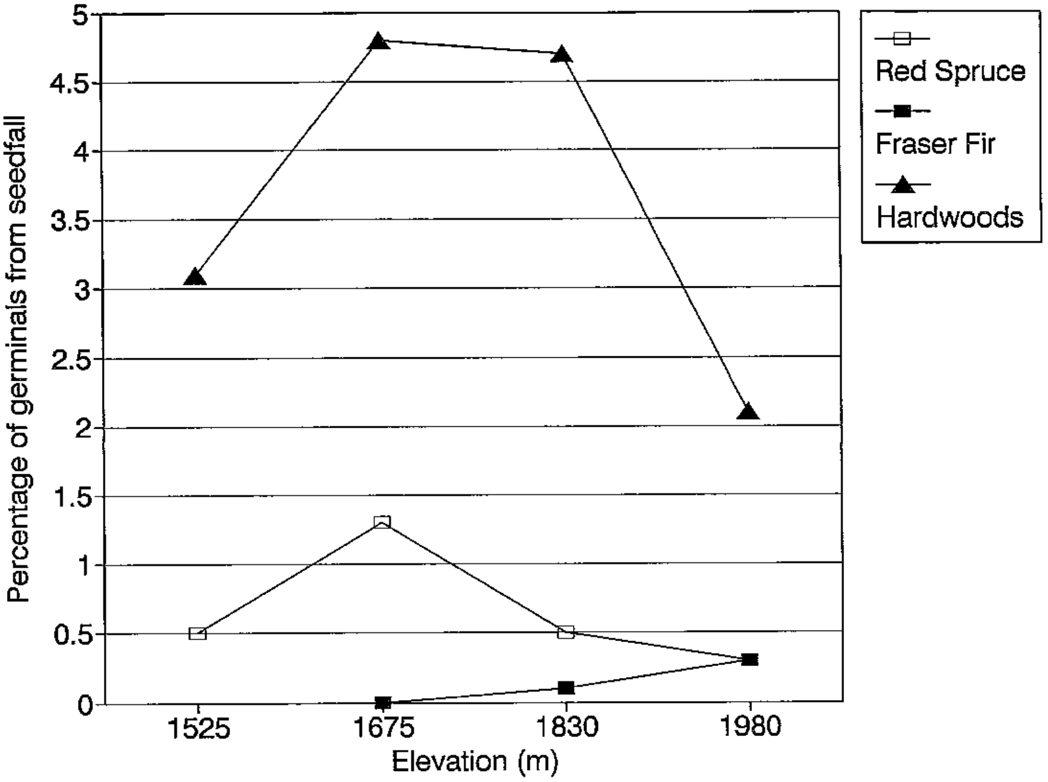

Fig. 1. Percent of overall germination (germinal density/seedfall density) for red spruce, Fraser fir, and hardwoods at four elevations in the Great Smoky Mountains.

vegetation changes have been reported to include a large increase in *Rubus canadensis* L. densities, which may impact woody species seedling survival. Boner (1979) reported a ten-fold increase in *Rubus* densities ten years after canopy opening in the Smokies. Pauley and Clebsch (1990) found low fir densities in areas of high *Rubus* densities and suggested that *Rubus* appears to interfere with the establishment and survival of Fraser fir. Sampling in areas infested by the adelgid, Boner (1979) determined fir seedling (≥2.5 cm dbh) densities increased and spruce seedling densities decreased with the number of years since fir canopy opening (data collected in 1974). Witter and Ragenovich (1986) and Witter (1988) sampled seedlings (≤244 cm) on permanent plots at Mt. Mitchell (120 km east of the Great Smoky Mountains), where the adelgid infestation occurred much earlier than in the Smokies, and found that fir seedling densities decreased between 1966 and 1985 while spruce and hardwood seedlings increased between 1966 and 1978 but stabilized between 1978 and 1985. Our data also showed higher fir seedling densities at higher elevations (at or above 1830 m). Interestingly, our study had higher spruce, fir, and hardwood seedling counts than the Witter and Ragenovich studies for all applicable elevations (Table 3). One reason may be that most (if not all) of the Witter and Ragenovich sampling sites were in second growth stands with average age ranging from 50–100 years while our stands in the Smokies averaged 150–250 years (age data from Zedaker et al. 1988). Stand dynamics may vary with stand age and disturbance history (Nicholas and Zedaker 1989) and seedling densities may vary accordingly.

The understory stratum provides data on the intermediate stage between seedlings and canopy trees, but there is little information available on the southern Appalachian spruce-fir understory to provide comparisons to our study. In a study examining differences between high elevation (≥1830 m) areas in the Smokies and the Black Mountains, as yet undisturbed by the adelgid, and those that were infested 16–20 years prior, DeSelm and Boner (1984) found an increase in subsaplings (.6 m tall to 2.5 cm dbh) of 450 to

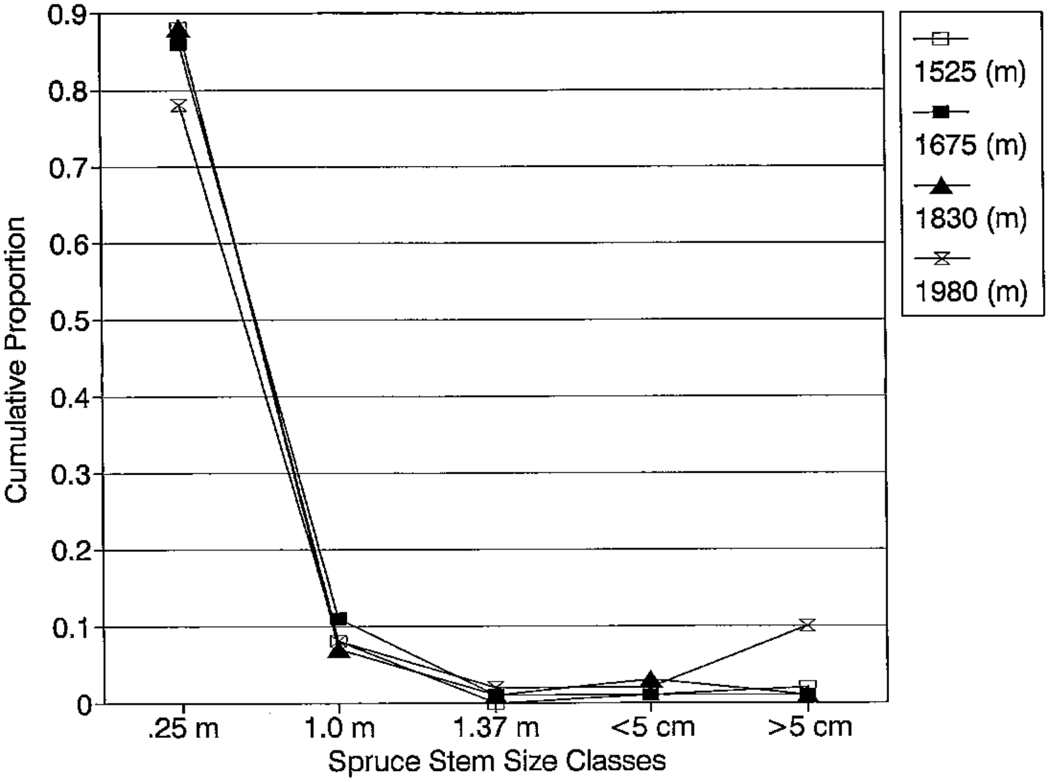

Fig. 2a. Cumulative size class (4 year to .25 m tall, .25–1.0 m, 1.0–1.37 m, 1.37 m–4.9 cm dbh, 5.0 + cm dbh) distributions for red spruce at four elevations in the Great Smoky Mountains.

2525 stems/ha with an increase of both spruce and fir densities. They also measured a decrease in saplings (2.5 to 12.4 cm dbh) of 49 to 34 stems/ha with a decrease in fir densities. When we merged our study's largest seedling (1.0–1.37 m) class and understory (1.37 m tall to 5.0 cm dbh) category together for comparable elevations, we found much higher average densities (4855 stems/ha, Table 3) than did DeSelm and Boner. White *et al.* (1985) considered tree replacement patterns in an old-growth spruce-fir stand in the Smokies using direct observation of the gap capture process; however, their analysis was done prior to any substantial adelgid impact to the forest. Using an assumption that sapling mortality was constant for spruce, fir, and birch, their advanced regeneration data led to the prediction that fir would increase in canopy importance. But the authors cautioned that fir was also found to have a shorter canopy residence time and higher turnover rate than the other two species.

Some comparison of Smokies spruce-fir densities might be made to several northeastern studies. Leak and Graber (1976) examined stem density distribution in ten northern hardwood stands (which included some red spruce and balsam fir (*Abies balsamea* (L.) Mill.) in New Hampshire. Comparisons were made to very similar size class densities found in our 18 low elevation (1525 m) plots. Leak and Graber reported an average germinal count of 53,000 stems/ha (compared to our 131,400), a seedling count of 261,500 stems/ha (compared to our 101,981), an understory count of 12,100 stems/ha (compared to our 6,330) and an average overstory count of 900 stems/ha (compared to our 1,330) (Tables 1 and 3). Calculation of a seedling to overstory stem ratio for the Leak and Graber data gave a figure that was more than three times higher than for our low elevation data (291 versus 77).

In another study, Foster and Reiners (1983) sampled stem density in four old-growth fir-spruce stands at Crawford Notch, New Hampshire (elevation 825–1020 m) which we compared to our 12 plots at 1980 m elevation. They found live stem density for trees greater than 5 cm dbh was 1125 stems/ha with 66 percent in fir and 21 percent in spruce while our plots av-

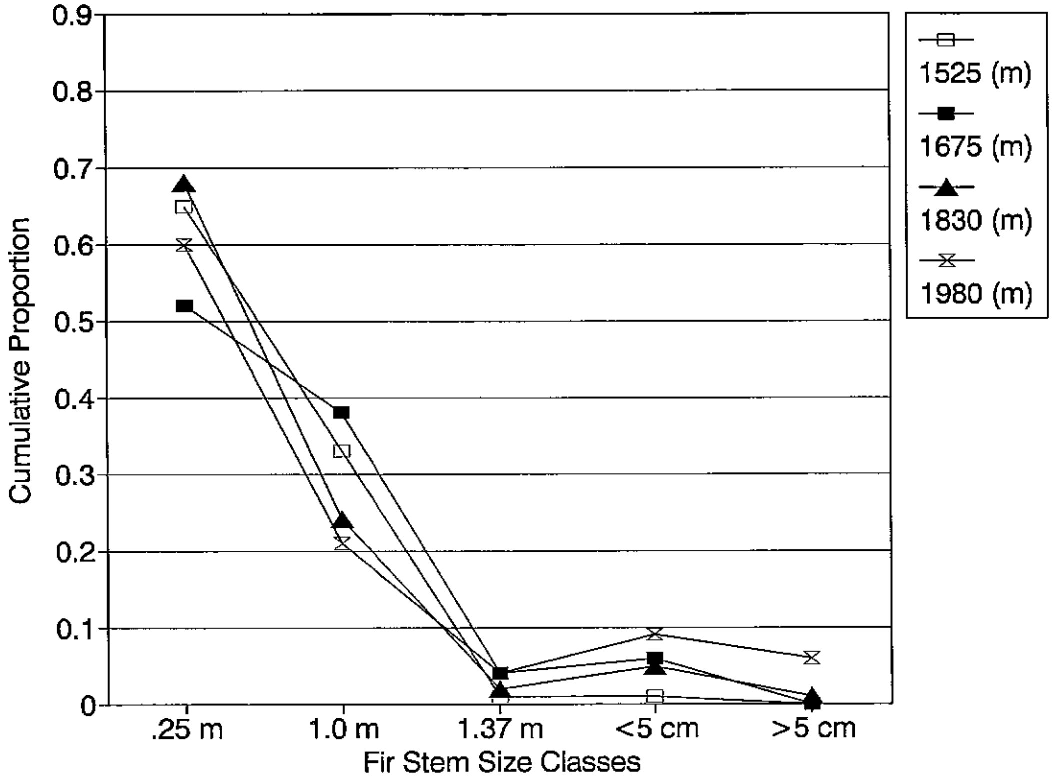

Fig. 2b. Cumulative size class (4 year to .25 m tall, .25--1.0 m, 1.0–1.37 m, 1.37 m–4.9 cm dbh, 5.0 + cm dbh) distributions for Fraser fir at four elevations in the Great Smoky Mountains.

eraged 1010 stems/ha with 76 percent in fir and 16 percent in spruce (Table 3). Foster and Reiners also reported 623 stems/ha for all stems 1.0 m tall to 4.9 cm dbh (compared to our 4360) and a density of 28,125 stems/ha for seedlings 0.2–1.0 m tall (compared to our 6056 for seedlings 0.25–1.0 m tall). Calculation of a seedling to overstory stem ratio for the Foster and Reiners data was four times higher than we found for our high elevation data (25 versus 6). Survivorship and growth patterns may differ between northeastern and southeastern spruce-fir seedlings and saplings, both the Leak and Graber (1976) and Foster and Reiners (1983) studies show a much higher seedling count than our study.

Figure 2 for both spruce and fir shows a type of concave survivorship curve similar to an inverted J-shaped curve (Leak 1965). Understory red spruce only has 22 to 165 percent the stem density of overstory spruce, which may be an artifact of stem size classes. Slight deviations from the inverse J shape do not lead to straightforward inferences regarding population trends if possible mitigating factors are present (Peart *et al.* 1992). Red spruce is shade tolerant and capable of remaining in the understory at least sixty years. Regeneration occurs sporadically. Therefore, present demographic trends may bear little relation to those that produced the present population structure. However, the question still remains if present and future trends can create the current stand structure and composition.

Seedling mortality rates would provide some indication of future rates of entry into the understory and overstory. We were unable to track individual seedlings but instead monitored densities on the same subplots over time. Comparison of seedling (excluding germinals) densities in Year 1 (1985) to Year 5 (1989) found that for all but class 2 (1–4 year) spruce and fir (not hardwoods) seedlings there have been stable or increasing densities at all elevations. Small spruce and fir seedling densities started dropping in 1987 and continued through 1989. Two reasons for the decrease may be the low germination rates (which may or may not be normal) of the 1987 seed crop and the summer drought conditions of 1986 through 1988 (Mohnen 1992).

What quantity of seedlings constitutes adequate regeneration for stabilized spruce-fir community dynamics is unknown. While we can quantify production and current stem densities, replacement rates are needed to account for temporal trends, as well as consideration of stochastic events such as droughts or catastrophic storms. Adequacy of current numbers of fir regeneration can only be considered in terms of the survivorship rates of these seedlings for continued fir at the high peaks. In some areas of the Smokies where the overstory has been devastated by the balsam woolly adelgid, understory fir are approaching a life stage that can support adelgid populations. Eagar (1984) suggests a scenario where initial infestation is followed by limited recovery and then regeneration infestation. In this scenario fir regeneration survives long enough to produce viable seed. However, Busing and Clebsch (1987) simulated balsam woolly adelgid infestation in an old-growth spruce-fir stand using a canopy gap model and found that a spruce-dominated forest with low total stand density was predicted.

Because of possible growth decline and observed crown deterioration, current seed production and seedling recruitment of red spruce as well as Fraser fir may be crucial for southern Appalachian spruce-fir stand dynamics. Spruce seed production and smaller seedling classes may or may not be ample; however overstory densities are close to or less than the understory strata. Understory densities for both spruce and fir are dependent on a number of periodic factors: seed production which appears to be intermittent in this system, adequate seed viability which may not be coincident with higher production years, germination which is a small fraction of viable seeds, and survivorship of germinals and seedlings which appears to follow a steep inverted J-shaped curve.

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