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Structure and Dynamics in a Virgin Northern Hardwood-Spruce-Fir Forest—The Bowl, New Hampshire

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Abstract

A phytosociological investigation was conducted in a virgin northern hardwood-spruce-fir forest in the lower elevations of the Bowl in the White Mountains of New Hampshire to determine the structure and dynamics of relatively small units of the forest. There is no evidence that the composition of the present forest has been influenced by human activity or fire, though portions of the present community demonstrate the effects of catastrophic damage caused by a severe hurricane in 1815. Forty-five 20- by 30-m plots ranging in elevation from 586 to 920 m were studied. Tree densities ranged from 685 to 3,851 stems/ha, basal areas from 22.0 to 60.5 m^2/ha, and shrub-seedling densities from 0.15×10^5 to 2.27×10^5 stems/ha. Bray and Curtis ordination was used to position the plots on the X and Y axes of a vegetational mosaic. The primary differentiating species were *Picea rubens* and *Acer saccharum* on the X axis and *Betula alleghaniensis* and *Fagus grandifolia* on the Y axis. The ordination was divided into seven subjectively defined plot clusters based primarily on the size-class distributions of four major tree species found in each plot. Cluster A represents a high-elevation, stable *Picea/Abies* unit. Cluster B represents a lower elevation, edaphically controlled *Picea/Abies-Fagus grandifolia-Betula alleghaniensis* unit which is projected to develop into a *Picea/Abies-Fagus grandifolia* unit. Clusters C to G represent stages in a successional sequence initiated by a catastrophic blowdown. The sequence is postulated to start with a *Betula alleghaniensis* Reproduction-Sapling unit, none of which was observed in the present forests of the Bowl. This stage develops into an All-Sized Immature *Betula alleghaniensis* unit (Cluster C) followed by a Mature *Betula alleghaniensis*/Sapling *Acer saccharum-Fagus grandifolia* unit (Cluster D). Then, depending on tree density, will follow a Mature *Fagus grandifolia*/Residual Decadent *Betula alleghaniensis* unit (Cluster E) or a Mixed *Acer saccharum-Fagus grandifolia*/Residual Decadent *Betula alleghaniensis* unit (Cluster F). Cluster F develops into a Decadent *Acer saccharum/ Fagus grandifolia* unit (Cluster G). This and the unit represented by Cluster E could develop into a Hypothetical Decadent *Fagus grandifolia/Acer saccharum* unit.

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Introduction

The Bowl is a 607-ha tract located in the White Mountain National Forest near Wonalancet, New Hampshire (Fig. 1). The Bowl Research Natural Area is a 206-ha segment of this watershed. This forest is unusual in that it has not been subjected to significant man-caused disturbance nor recent disturbances of natural origin (Leak 1973, 1974; Lyon and Reiners 1971; Martin 1975, 1977). The major objective of this study was to prepare a conceptual model describing the structure, successional patterns, and, when applicable, the steady-state dynamics of small units within this undisturbed northern hardwood ecosystem. There is a paucity of sites suitable for developing such a model because nearly all of these ecosystems in New England have a history of extensive logging, agricultural development, forest fires, or hurricanes. This has forced workers to develop models of climax communities through projections of stand development based on studies of early and midsuccessional stages (Henry and Swan 1974; Oliver and Stephens 1977) or by preparing reconstructions of primal forest communities using historical records (Lorimer 1977; Siccama 1971). Additionally, only recently has the significance of the patchy nature of mature steady-state ecosystems, e.g., the "shifting-mosaic steady state" of Bormann and Likens (1979), been widely recognized.

The failure to adequately weight this concept and recognize that a particular stand of trees, though it may appear homogeneous in composition may include many smaller vegetational units, has led to a tendency to combine the information collected from small samples or plots into generalized descriptions of the stand as a whole (Bormann and Buell 1964; Leak 1973; Martin 1977). Although useful from a forest-products viewpoint, these studies fail to deal adequately with the dynamic nature of the steady-state forest, exemplified by the variety of vegetational units making up the stand.

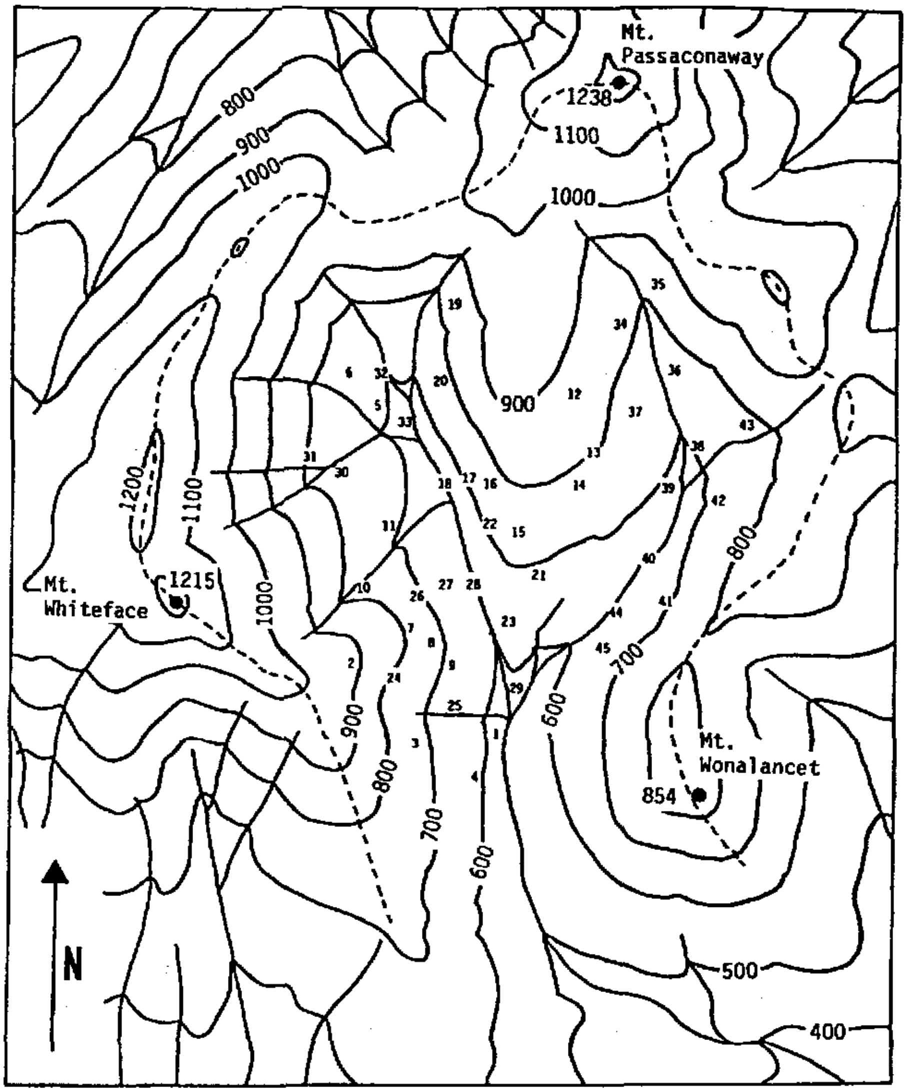

Figure 1.—Location of sample plots within the Bowl. Contours and elevations (in meters) were derived from the U. S. Geological Survey Mt. Chocorua quadrangle.

Study Area

A cirquelike geomorphological structure, the Bowl is located at Lat. 43° 56', Long. 71° 23' in the township of Waterville Valley, New Hampshire (Fig. 1). The bedrock is primarily of the Passaconaway syenite formation but with small areas of Littleton slate and Conway granite (Billings 1956). The glacial till of the Bowl was derived from Conway granite, coming from the bedrock in the Passaconaway Valley lying just northwest of the study area.

Soils of the Canaan, Lyman, Berkshire, Whitman, Peru, and Herman series are found in the Bowl[1] (Martin 1975). They are complex and variable and much of the area exhibits disturbed soils with buried horizons caused by windthrown trees. Hummocks and hollows are frequent. Except in isolated pockets, all of the soils of the Bowl are well-drained, sandy loam, spodosols with humus layers up to 6 cm thick. Work on similar soils at the nearby (16 km to the northeast) Bartlett Experimental Forest indicates that these soils are acidic, with pH ranging from 3.5 to 5.5. The cation-exchange capacities of the mineral subsoils tend to be low because of their low clay content. As a result, the major plant nutrients generally are severely limiting to plant growth (Hoyle 1973; Martin 1975).

The climate of the Bowl is similar to that of the Bartlett Experimental Forest, for which the following description is given. An average annual precipitation of about 127 cm is distributed fairly evenly throughout the year. About one-third of the moisture is in the form of snow. As much as 150 to 180 cm of snow accumulates on the ground by the latter part of winter and remains until midspring. Average monthly temperatures range from -10° to -13°C in January to nearly 21°C in July. Temperature extremes range from about -37°C to the mid 30's. The growing season is slightly more than 100 days (Filip and Little 1971).

According to Braun (1950), the Bowl is a part of the hemlock-white pine northern hardwood region which extends from Nova Scotia to Minnesota. The Bowl would be classed as spruce-hardwoods of the New England Section of the Northern Appalachian Highland Division. Bormann et al. (1970) reviewed the literature pertinent to the vegetation at Hubbard Brook Experimental Forest at West Thornton, New Hampshire. This area lies about 27 km due west of the Bowl. It has roughly the same elevation and similar physiognomy.

Historical accounts of the Bowl (Harkness 1958) indicate that little of this area has been disturbed by logging activity. Around 1888, a steam-powered lumber mill operated in the eastern sector of the Bowl. This mill operated for about 2 years and sawed only coniferous species (Martin 1975). Surveys of the lower reaches of the Bowl Research Natural Area (Leak 1973, 1974) indicate that the forest has developed naturally with no evidence of past logging operations. According to Lyon and Reiners (1971), "the Natural Area seems not to have been cut, as indicated by the large size of the hardwoods and red spruce as well as the absence of old logging roads." Working primarily in the hardwood forests below an elevation of 915 m, Martin (1975, 1977) found no significant differences between the basal areas of the trees of the Natural Area and the remainder of the Bowl. During this study, no cut stumps and few trees of sprout origin were observed in the study area. Therefore, although the upper reaches of the eastern section of the Bowl may have supported some logging in the late 1800's, the entire western watershed and the lower hardwood areas of the eastern watershed remain essentially undisturbed by man.

Although Harkness (1958) maintained that the vegetation of the Bowl had been "immune to hurricane," there is abundant evidence that the trees of the area are subject to heavy windthrow, with older red spruce (*Picea rubens* Sarg.) especially vulnerable. "Pit and mound" or "hummock and hollow" soil-surface types and "tipover mounds" are found throughout the Bowl. Severe hurricanes passed by the general vicinity of the Bowl in 1635, 1815, 1821, 1938, and possibly 1400 (Perley 1891; Channing 1939; Tannehill 1939; Dunn and Miller 1960; Jorgenson 1977). Only the hurricane of 1815, classified by Dunn and Miller (1960) as "extreme" (maximum winds greater than 136 mph), could have had a severe effect on the forests of the Bowl. However, this disturbance would not have been apparent to an untrained observer (such as Harkness) looking at the area about 150 years after the event. The hurricane of September 1938, also classed as "extreme" by Dunn and Miller, usually is considered one of the most severe and damaging storms ever to strike New England, though the center passed at least 100 miles to the west of the Bowl (Tannehill 1939). Had the vegetation in the Bowl been seriously damaged, Harkness would have been able to observe the resultant destruction. In addition to hurricanes, powerful local storms for which there are few permanent records are common in the area (Kilbourne 1916).

I found no evidence that fire influenced the development of vegetation in this area. None of the trees bear fire scars, there is no charcoal in the soil, and none of the tree species present would be classified as "fire followers." Harkness (1958) stressed that in the memory of the local populace, forest fires had never been observed in the Bowl. The magnitude of disease and insect influences is unknown, though W. B. Leak (USDA For. Serv. pers. commun.) believes that some of the larger specimens of beech (*Fagus grandifolia* Ehrh.) may have been seriously affected in the late 1940's and early 1950's by attacks of the scale-*Nectria* complex.

Methods

General Approach

Forty-five 20- by 30-m plots oriented parallel to the contour were established in the lower elevations of the Bowl (Fig. 2). Plots were distributed evenly throughout the study area and

[1]Winkelaar, P. 1969. Soil classification of the Bowl Natural Area. Unpublished report. On file at USDA Forest Service, Laconia, New Hampshire.

on the basis of visual assessment were required to have structural, floristic, and habitat homogeneity. An attempt was made to include the range of forest types found in the Bowl. For example, although eastern hemlock, *Tsuga canadensis* (L.) Carr., is considered rare in the Bowl (Leak 1973; Martin 1977), five plots were established in vegetational units containing this species (Table 1). Therefore, the choice of sample sites must not be considered as random and the results should not be considered as a quantitatively accurate reflection of the structure of the forests of the Bowl taken in its entirety. The data are consistent with the objective of preparing a conceptual model of forest development based on the range and variety of the vegetation structure as observed in relatively small (20 by 30 m) units of the forest.

Field Procedures

Living trees more than 2.5 cm d.b.h. were measured and the diameter and species recorded. Woody vegetation less than 2.5 cm d.b.h. was sampled by counting stems in each of twelve 1- by 1-m quadrats located regularly within the plot. Hereafter, vegetation sampled in this manner is referred to as shrub-seedling. For each plot, elevation, average slope inclination, and aspect were measured. Plots ranged in elevation from 585 to 920 m, and had slope inclinations from 4 to 65 degrees. Elevation and slope were positively correlated ($r = 0.390$, $p < 0.01$). Aspect ranged from NE to NNW.

Importance values were calculated for tree and shrub-seedling classes by different methods according to the kinds of data taken. The importance value for each tree-size species was the sum of its relative density, basal area, and frequency (in percent). Hence, the sum of all importance values of trees in a single plot was 300. The importance value for each species of shrub-seedling size in a plot was the sum of its relative density and its relative frequency (in percent). Therefore, the sum of all importance values for shrub-seedling size species in any one plot was 200 (Table 1). Only the importance values of the tree-size species were used in the ordination analysis.

Numerical Analysis

The ordination technique used followed that developed by Bray and Curtis (1957) and described by Gemborys (1974). In this case, however, only two axes were extracted from the data. Selecting suitable end stands for a third or Z axis was extremely difficult due to the similarity of the plots, which was caused by the relative uniformity of habitat within the Bowl and its relatively advanced successional status. The appropriate X and Y coordinates for each plot are given in Table 1. Figure 1 is the plot ordination constructed from these values.

The mean weighted X axis location for each species was calculated according to the following formula:

mean weighted X axis location of a species =

$$\frac{\Sigma\,(\text{importance value of a species in a plot})\,(\text{X axis location of plot})}{\Sigma\,(\text{all importance values of the species})}$$

Similarly, mean weighted Y locations were calculated for each species (Table 1).

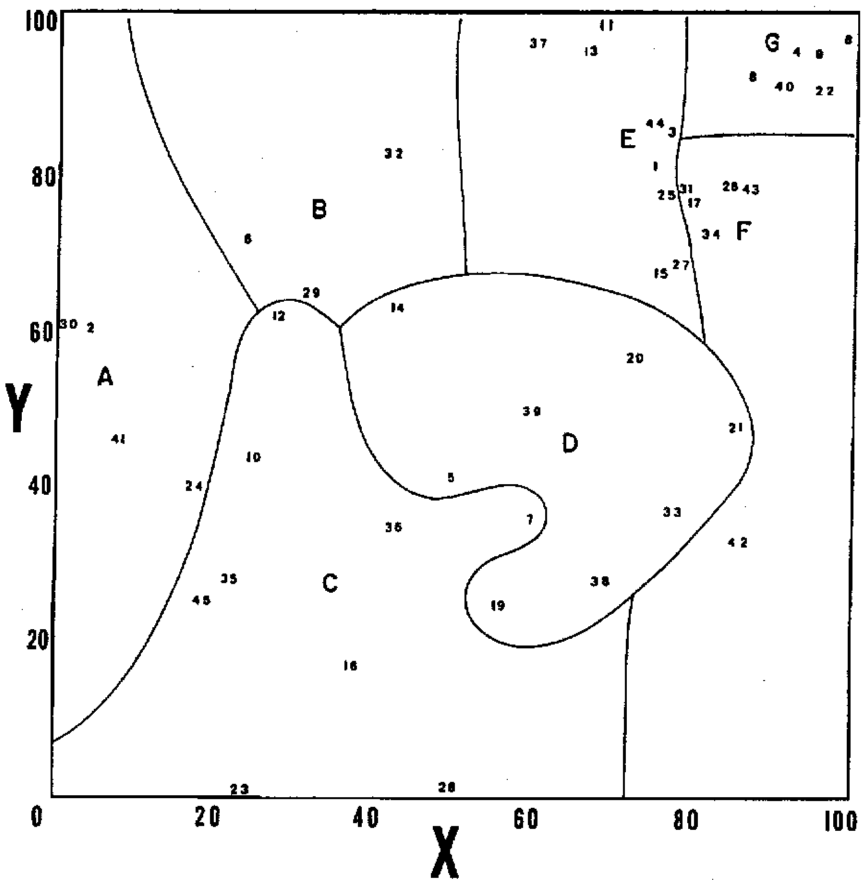

Figure 2.—Positions of the 45 plots on the X and Y ordination axes. The plot clusters, (A to G) are delineated on the ordination.

Table 1.—Species importance values and midpoint coordinates for tree and shrub-seedling layers; stand coordinates; basal area and density of the tree layer; and density of the shrub-seedling layer (maximum importance values in plots underlined, revealing the leading dominant species)

Species, stand coordinate, basal area, or density	Stand number																					
	30	2	41	24	45	35	6	23	10	12	29	16	32	36	14	5	28	19	7	39	37	13
X coordinate of stand	0	3	8	18	19	22	24	24	25	28	32	38	42	43	43	50	50	56	60	60	60	67
Y coordinate of stand	61	61	46	40	25	28	72	0	44	62	65	17	83	35	63	41	1	25	36	50	97	96
Tree layer																						
Red maple	17			6																		
Eastern hemlock	30				63			23			7		9									
Paper birch			71		12			12														
American mountain-ash	16					9				10				5		12						
Red spruce	150	211	198	169	89	53	112	50	85	23	89	35	72	20	62	38	36	8	27	64	25	17
Balsam fir	49	58	8	31	23	33	48	32	42	27	34	52	36	34	34	9		10	6		25	6
Pin cherry						25				70				10							24	
Mountain paper birch	13						23		11	42					5			35	5			
Mountain maple							5	29	18	15	24		13		4	6	41	18	19		5	
Yellow birch	24	31	23	49	86	147	33	128	62	75	39	141	43	143	93	98	140	101	95	82	60	62
Striped maple				12	8	33	32	16	48	34	53	24	41	47	23	67	35	64	62	31	61	51
American beech							48		14	4	49	31	86	32	78	42	25		36	83	102	164
Sugar maple				32	20			11	20		5	16		9		28	23	64	52	39		
Basal area (m²/ha)	47.9	33.3	51.1	39.6	36.2	26.2	43.6	25.2	42.0	29.8	36.7	27.5	52.5	29.1	35.2	31.4	33.1	27.3	27.8	52.8	26.3	31.6
Density (#stems > 2.5 cm d.b.h./na)	3851	3050	1887	1584	2338	2371	2117	1234	1417	3483	1750	1467	2866	1787	2050	1300	1534	1300	1582	1837	1687	2033
Shrub-seedling layer																						
Eastern hemlock	22																					
Pin cherry									10													
Balsam fir	7	38	42	26	29	65				78		11		22	30	6		5			13	11
Red spruce	63		78	38	86	71	28	9	30	28	36	11	65	34	14		13	11		7	22	6
American mountain-ash		25				8			5	5												
Yellow birch	7	137	45	53		8	78		43	37					8	64		11	62			33
Red maple							11															
Striped maple	73		27	66	59		56		10	18	13	61	39	56	97	54	13	5		50	34	61
Mountain maple				10		32	11	103	7	23	26	72	16	40	6	38	52	92	62	7	15	18
Wild sarsaparilla				7	26				10		10					12		7				
Hobblebush	20					8	17	46	66	10	83		23	20		6	97	21	60	25	6	
American beech			7								32	36	34	10	30	8	13			45	94	56
Fly honeysuckle																						
Sugar maple						8		43	18			11	23	17	33	12	11	47	16	65	15	15
Red berried elder	7																					
Witherod																						
Density (#stems < 2.5 cm d.b.h x 10⁵/ha)	0.35	2.07	0.39	0.31	0.15	0.23	0.31	0.39	0.51	0.88	0.28	0.23	0.18	0.31	0.45	0.42	0.48	0.55	0.37	0.30	0.39	0.64

Table 1.—(Continued)

Stand number																							Species Midpoint	
11	38	20	1	44	25	15	3	27	33	31	17	34	26	43	42	21	18	40	4	9	22	8		
69	69	73	75	75	76	76	76	78	78	79	80	82	85	86	86	86	87	91	93	95	96	100		
100	28	57	81	87	78	68	87	69	37	79	77	73	79	79	33	48	93	92	96	91	91	98	X	Y
																							5	56
																							18	35
			9												10								23	41
																							25	48
19	22		29	17	9	24	14	17	6	15	21	16	6	7	8		8		10				30	53
10		4					1		8		6			17									31	52
												6											36	60
		23																					39	52
		14						21	14	14													48	41
32	129	66	32	30	65	74	21	46	99	33	64	54	64	17	47	105	27	23	10	12	12		53	48
107	35	66	18	46	17	43	39	38	19	76		40	44	20	32			17		11		13	60	42
116	65	47	156	174	184	106	196	128	66	87	92	83	106	68	27	92	143	130	129	132	93	106	74	77
17	49	81	56	34	25	53	30	49	87	74	117	100	79	171	177	103	122	129	151	145	195	181	81	71
28.7	33.5	25.1	36.3	33.1	32.9	27.0	60.5	28.1	48.2	32.9	40.5	29.5	22.0	42.3	25.3	35.2	51.4	34.4	33.6	40.2	35.2	27.2		
1167	2371	1883	1167	2138	1134	1700	1450	1517	1350	1683	1200	1836	1367	1202	952	1134	1500	1369	899	900	1134	684		
																							0	61
																							25	44
												12			8	5	5						28	50
5	28	60		24	5	6				4		6					5		3	5			34	72
					5																		36	50
97							4			6	27				5								46	62
			8																				46	76
17	23	45		53	8	8	69	41	31	22	28	63	24	13	17	6	8	4	22	14	7	11	52	62
10	15		8					24	65	11		24	36		29		25					19	54	40
										16	4	8	18	6	11		13						58	56
26	67		126	39	6		12	64	24	57	16	18	41	64	29		27	57	4	5		11	63	58
17	28	22	59	28	42	62	21	31	29	29		30	5	31	8	74	24	52	39	32	40	15	73	73
										6													79	79
29	39	70		56	133	124	51	38	70	49	125	40	76	81	94	125	91	87	96	145	153	128	79	73
								44												47		15	82	87
														6									96	79
0.76	0.18	0.37	0.59	0.31	1.20	0.65	1.23	0.38	0.62	0.68	1.16	0.49	0.73	0.48	0.86	1.10	0.62	0.77	1.54	2.27	0.98	1.22		

Results

Of the 18 woody species encountered, 3 were observed only in the tree layer, 5 only in the shrub-seedling layer, and 10 in both layers. The species in the tree layer with the highest importance value was designated the "leading dominant" for the plot. Four species were leading dominants in at least one plot (Table 2). Of these, beech was the most common leading dominant (15 plots), followed by yellow birch (*Betula alleghaniensis* Brit.) (13 plots), sugar maple (*Acer saccharum* Marsh.) (9 plots), and red spruce (8 plots). Although they may not have achieved leading dominant status in a particular plot, beech, yellow birch, sugar maple, red spruce, striped maple (*Acer pensylvanicum* L.), balsam fir, *Abies balsamea* (L.) Mill., and mountain maple (*Acer spicatum* Lam.) often ranked high in importance in the plot. The average number of tree species in a plot was 5.9 with a range of 3 to 9. The density of trees larger than 2.5 cm d.b.h. ranged from 684 to 3,851 stems/ha. Basal area ranged from 22.0 to 60.5 m^2/ha.

Within the shrub-seedling layer, sugar maple was the most common leading species (17 plots), followed by striped maple and hobblebush (*Viburnum alnifolium* Marsh.) (7 plots each); red spruce, yellow birch, and mountain maple (4 plots each); and balsam fir and beech (1 plot each). The average number of shrub-seedling species in a plot was 5.9 with a range of 3 to 9. The density of stems ranged from 15,000 to 227,000/ha. This compares with 474,000, 245,625, and 80,523 seedlings/ha for the lower, middle, and upper elevations, respectively, for watershed 6 at Hubbard Brook (Bormann et al. 1970). However, it should be noted that the seedling layer exhibits little numerical stability from year to year due to the erratic nature of seed production (Forcier 1975; Bormann and Buell 1964).

Plots 30 and 8 were selected as end plots for the X axis because they had the lowest coefficient of similarity [c = 2w/(a+b), where a = the sum of importance values of all species in one stand, b = a similar sum for a second stand, and w = the sum of the lesser values for only those species common to the two stands], based on the importance values of the tree species, of all plot combinations. Stand 30 is located in the northwest section of the Bowl at an elevation of 760 m. It has a northeasterly aspect of 46 degrees (most northerly of all plots) and a slope of 56 degrees. The leading dominant is red spruce and there are significant numbers of balsam fir, yellow birch, eastern hemlock, and red maple (*Acer rubrum* L.). Striped maple, red spruce, and eastern hemlock are important shrub-seedling layer constituents. The plot has a tree density of 3,851 stems/ha (highest of all plots) and a basal area of 47.9 m^2/ha. The shrub-seedling layer has a density of 35,000 stems/ha. Sapling-size red spruce and balsam fir are common and the plot contains a single eastern hemlock that is 59 cm d.b.h. Although eastern hemlock is not represented in the sapling classes, it is well represented in the shrub-seedling layer. The plot is above average in species diversity with seven recorded in the tree layer and seven in the shrub-seedling layer. Mosses are common on the ground surface.

Plot 8 is located in the southern section of the Bowl at an elevation of 725 m. It has an east-southeasterly aspect of 121 degrees and a slope of 51 degrees. The leading dominant is sugar maple; the only other tree-size species present are beech and striped maple. Sugar maple is the most important shrub-seedling layer component, with no other constituent exceeding an importance value of 19. The plot has a tree density of 685 stems/ha (lowest of all plots) and a basal area of 27.2 m^2/ha. The shrub-seedling layer has a density of 122,000 stems/ha. This plot has a relatively open appearance, sugar maple having a wide distribution of size classes and a shrub-seeding density of 97,000 stems/ha. Tree-layer diversity is lowest of all plots and the shrub-seedling layer is average in this respect. Not only are plots 30 and 8 dissimilar with respect to the relative importance of

Table 2.—Level of importance of tree species based on the number of times each was ranked in the top eight in importance in a given plot

Species	Level of Importance								Importance value range
	1	2	3	4	5	6	7	8	
American beech	15	10	4	5	1	—	1	—	196-0
Yellow birch	13	8	16	7	—	—	—	—	147-0
Sugar maple	9	7	9	1	4	2	1	1	195-0
Red spruce	8	3	4	8	10	4	2	—	211-0
Striped maple		11	5	13	6	1	1	—	107-0
Balsam fir		2	4	4	4	4	3	1	58-0
Mountain maple		1	—	1	3	6	4	1	41-0
Paper birch		1	—	—	1	2	1	—	71-0
Pin cherry		1	—	—	1	2	—	—	70-0
Eastern hemlock			2	—	1	—	2	—	63-0
Mountain paper birch			1	1	1	2	1	2	42-0
Red maple					2	—	—	—	17-0
American mountain-ash						3	—	2	16-0

the tree species they contain, they are at the opposite ends of a tree-density gradient. Plot 30 also has the most northerly aspect of all plots.

Plots 28 and 37 were selected as end plots for the Y axis. These plots were dissimilar (1 - c) but close together on the X axis. Plot 28 had the highest e value and was used as the first reference stand on the Y axis. The value of e is calculated by: $e^2 = Da^2 - X^2$ where Da is the dissimilarity of plot 28 to plot 30 and X is the location of plot 28 on the X axis. The plot on the other end of the Y axis was determined by the plot least similar to plot 28, plot 37. Plot 28 is located in the south-central part of the Bowl near one of the major drainageways. It has an elevation of 622 m, a slope of 32 degrees, and an easterly aspect of 96 degrees. The leading dominant is yellow birch; red spruce, mountain maple, striped maple, beech, and sugar maple are important associate species. The shrub-seeding layer has a density of 48,000 stems/ha. Species diversity is about average for both layers. Yellow birch is well represented in the various size classes. The shrub-seedling layer is closed due to the abundance of hobblebush. Mosses, ferns, and *Lycopodium* sp. were common on the ground surface. Although this plot is steeply sloped and is elevated 20 to 30 m above a nearby stream, implying a relatively dry site, it is quite wet due to its position near the base of the east side of the Bowl.

Plot 37 is located in the north-central section of the Bowl at an elevation of 762 m. It has an east-southeasterly aspect of 121 degrees and a slope of 33 degrees. The leading dominant is beech, with striped maple and yellow birch also common. The most important shrub-seedling species is beech, with balsam fir, red spruce, striped maple, mountain maple, hobblebush, and sugar maple also present. The plot has a tree density of 1,687 stems/ha and a basal area of 26.3 m^2/a. The density of the shrub-seedling layer is 39,000 stems/ha. The plot is characterized by the presence of frequent hummocks or tip-over mounds, though none are of recent origin. Pin cherry (*Prunus pensylvanica*, L.f.), is represented by stems 13 to 15 cm d.b.h., and there are numerous beech saplings of root sprout origin. Diversity in both tree and shrub-seedling layer is above average.

It is apparent that the X axis separates the plots dominated by red spruce and sugar maple with a reciprocal or inverse relationship along this axis (Fig. 3), that is, as the importance value of one species increases along the axis, the other decreases. There is a similar relationship between yellow birch and beech along the Y axis. There is clumping (at high X, high Y values) of plots dominated by sugar maple or beech because these two species and others occurring with them often are highly associated. Low X, low Y plots do not show this clumping. A Pearson correlation test was applied among the plot locations of the two axes. Locations along X and Y axes were positively correlated ($r = .518$, $p < 0.01$). Therefore, it was probable that the Y axis repeated in part information previously revealed in the X axis. However, this repetition was not sufficient to justify discarding the Y axis

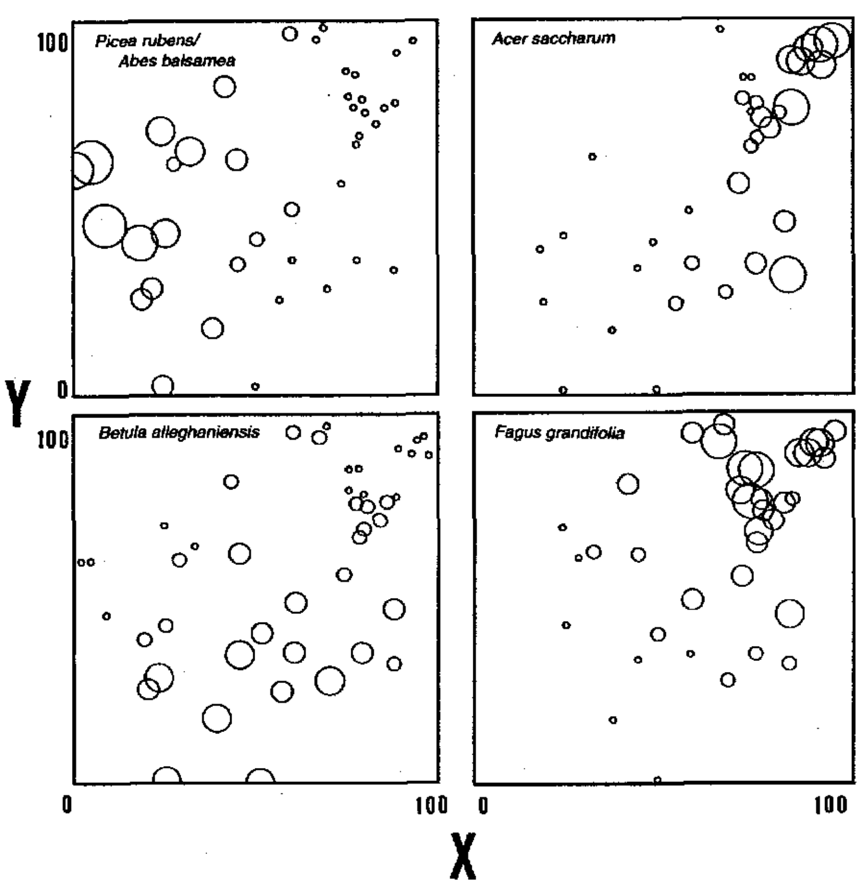

Figure 3.—Distribution patterns of tree layer for *Picea rubens* and *Abies balsamea, Acer saccharum, Betula alleghaniensis,* and *Fagus grandifolia* within the ordination. The six circle sizes represent importance values of 1-40, 41-80, 81-120, 121-160, 161-200, and 201+, respectively.

because of the pattern of distribution of leading dominant (Fig. 3) and shrub-seedling species (Fig. 4) within the vegetational mosaic, and because of the correlations between the X axis location of a plot and the tree (tree density in number/ha = $2611 - 15.48X$, $r = -0.659$, $p < 0.01$) and shrub-seedling (shrub-seedling density in number/ha = $1.026 - 0.03195X + 0.0003586X^2$, $R^2 = 0.421$, $p < 0.01$) densities, and the correlation between the Y axis plot locations and shrub-seedling densities (shrub-seedling density in number/ha = $0.1933 + 0.007422Y$, $r = 0.435$, $p < 0.01$). Although the X and Y axes are correlated, they each reveal information not present in the other.

The distributions within the vegetational mosaic of shrub-seedling importance values (Fig. 4) should be considered independent estimates of the validity of the ordination since it was constructed solely from the importance values of the tree-layer species and did not include data on the shrub-seedling layer. Striped maple, mountain maple, wild sarsaparilla (*Aralia nudicaulis* L.), and hobblebush show noda or peaks in density in the vegetational mosaic. Red spruce, sugar maple, yellow birch, and beech also show patterns in the distribution of shrub-seedling density. However, these patterns, which are similar to their corresponding tree-layer components, may be the result of the proximity of a suitable seed supply. There is an inverse relationship in the density distributions of mountain maple and striped maple. Mountain maple predominates in yellow birch-dominated plots where striped maple is not as important. However, striped maple is more important in plots dominated by beech and sugar maple. Yellow birch seedlings are important in the plots dominated by red spruce but are relatively unimportant in plots with yellow birch as the leading dominant. Hobblebush shows a tendency toward high density in the plots dominated by beech and sugar maple.

Another indicator of the validity of the tree layer, importance value-based ordination is whether a characteristic independent of importance value is correlated with the X or Y axis. In this case, the total density of the tree and the shrub-seedling layers in each plot showed a high correlation ($r = -0.659$, $p < 0.01$ and $r = 0.649$ $p < 0.01$, respectively) with the X axis. The density of the shrub-seedling layer was highly correlated with the Y axis ($r = .435$, $p < 0.01$). Basal area, slope, and elevation showed no significant correlations with the X or the Y axis. In general, low X, low Y plots tend to have a sparse shrub-seedling component; high X, high Y plots have dense shrub-seedling layers. Low X plots tend to have many small trees and high X plots have fewer but larger trees.

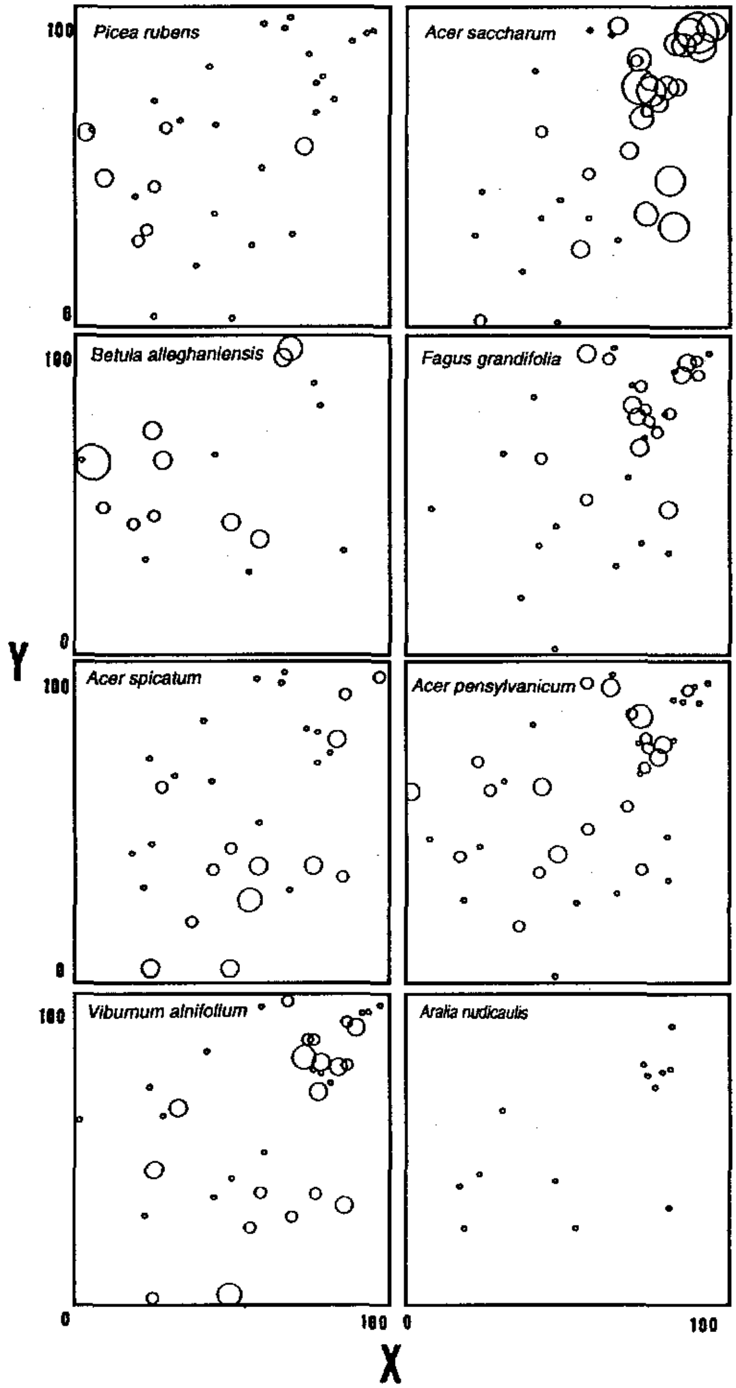

Figure 4.—Distribution patterns of shrub-seedling layer *Picea rubens* and *Abies balsamea, Acer saccharum, Betula alleghaniensis, Fagus grandifolia, Acer spicatum, Acer Pensylvanicum, Viburnum alnifolium,* and *Aralia nudicaulis* within the ordination. The seven circle sizes represent densities of 1,000-5,000, 6,000-10,000, 11,000-25,000, 26,000-50,000, 51,000-100,000, 101,000-200,000, and 201,000+ stems/ha, respectively.

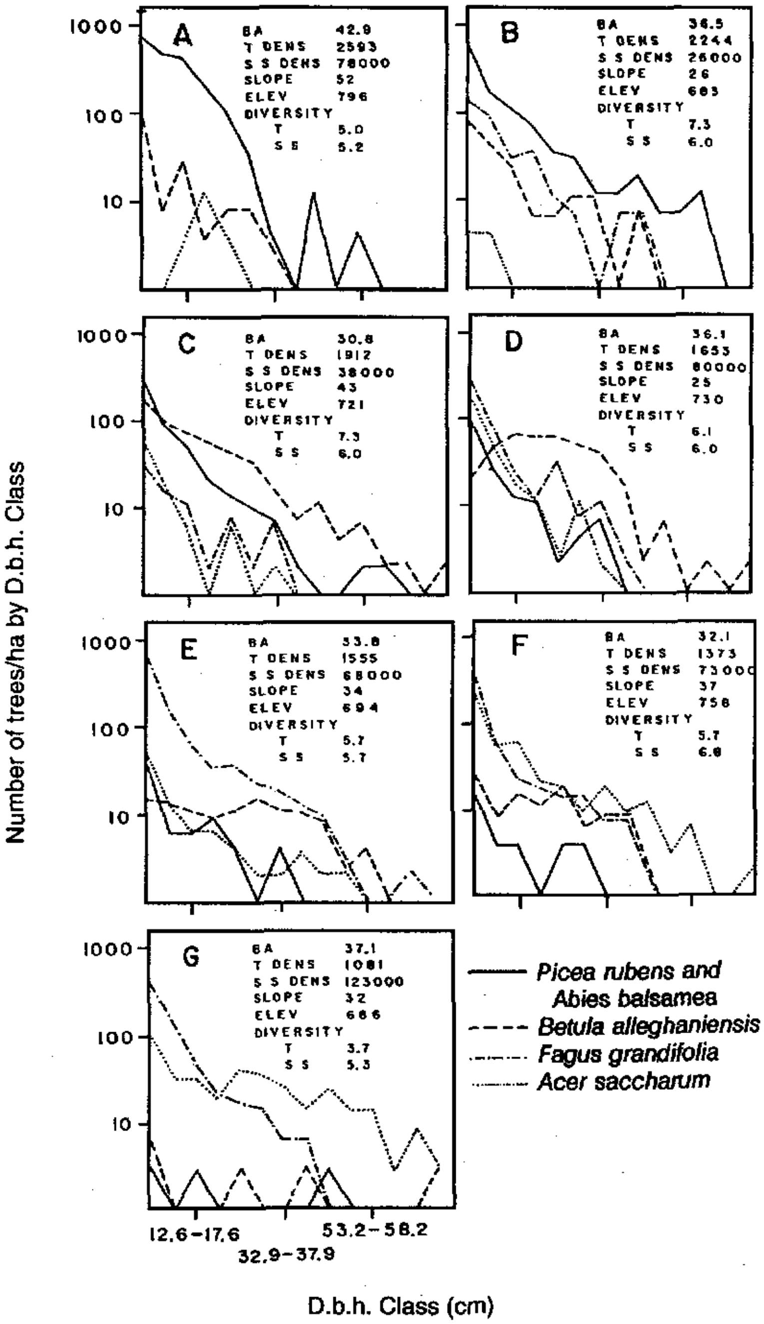

Figure 5.—Stand curves for species in the seven defined plot clusters in the Bowl. Numbers of stems, on a logarithmic scale, are indicated on the ordinate for 10-cm d.b.h. classes on the abscissa. *Picea rubens* and *Abies balsamea* combined, and *Betula alleghaniensis, Fagus grandifolia,* and *Acer saccharum* are plotted. BA = basal area in m^2/ha; T DENS = number of tree-layer stems (greater than 2.5 cm d.b.h.) per ha; S S DENS = number of shrub-seedling layer stems (less than 2.5 cm d.b.h.) per ha; SLOPE = slope across plot in degrees; ELEV = elevation of plot above sea level (in m); DIVERSITY-T = number of tree-layer species per plot; DIVERSITY-S S = number of shrub-seedling layer species per plot. Values are means for each of the plot clusters.

Discussion

Although the ordination represents a continuum philosophy, it is useful to divide the vegetational continuum into a mosaic of groups or clusters of plots with similar characteristics. Of course, many criteria can be used in the construction of such a classification. As I was interested in community dynamics as they revealed forest history and predicted the future composition of the forest, I used the distribution of stems by size class of the leading dominants as a differentiating criterion. Because of their ecological similarities, red spruce and balsam fir were combined for this analysis. After studying the diameter distributions of leading dominant species in all plots, and taking into consideration the locations of these plots within the ordination, I was able to isolate seven groups or clusters. Plots in each cluster had similar diameter distributions of leading dominant species and were near each other in the ordination (Fig. 2). This figure also contains a listing of the means of some habitat and measured vegetational attributes of each of these clusters. Stand curves for each of the leading dominant species in each of the clusters were generated by determining the average density by 10-cm size class for plots in each cluster (Fig. 5).

Cluster A consists of four plots (30, 2, 41, 24) dominated by red spruce and balsam fir, with lesser but consistent amounts of yellow birch. Beech and sugar maple are absent from most of these plots. There is little mountain maple, beech, sugar maple, or hobblebush in the shrub-seedling layer, but red spruce, balsam fir, and yellow birch are common. These plots show a high tree density and low shrub-seedling and tree diversity, and are found on steep slopes (average: 55 degrees) at high elevations (average: 795 m). These elevations apparently are too great for significant amounts of beech or sugar maple to develop (Bormann et al. 1970; Leak and Graber 1974), so the structure of domination by spruce-fir will be maintained.

Cluster B consists of three plots (6, 29, 32) dominated by red spruce and balsam fir, with significant amounts of yellow birch and beech. Cluster B differs from Cluster A in that: 1) beech is important in the tree layer of B and not in A; 2) balsam fir and yellow birch are present in the shrub-seedling layer of A but not in B; 3) mountain maple and hobblebush are important in the shrub-seedling layer of B but not in A; 4) basal area, tree and shrub-seedling density, slope (average: 26 degrees), and elevation (average: 680 m) are lower in B than in A; and 5) tree and shrub-seedling diversities are higher in B than in A.

These might be considered low-elevation spruce-fir plots but with an admixture of beech and yellow birch. They will trend toward spruce-fir-beech composition as the intolerant yellow birch fades from importance due to death of older individuals and declining reproduction. Field notes indicate the presence of various species of mosses, ferns, and club mosses, characteristic of a relatively wet environment. This suggests that the spruce-fir dominance is under strong edaphic control, unlike the elevation-dominated environmental complex which sustains the spruce-fir plots of Cluster A. Because this cluster is at a lower elevation, beech is not excluded. Also, beech is able to tolerate wet soils, whereas sugar maple, which might be expected in these lower elevation plots, is sensitive to this condition and probably is excluded from Cluster B plots as a result (Fowells 1965).

Cluster C plots have yellow birch as the leading dominant; this species is strongly represented in the smaller size classes. This cluster contains nine plots (45, 35, 23, 10, 12, 16, 36, 28, 7) and occupies a low X, low Y position in the ordination. Spruce-fir and to a lesser extent beech and sugar maple are associates in this cluster. Beech becomes more important with increasing Y values of plots. Red spruce, sugar maple, striped maple, and mountain maple are important shrub-seedling species while yellow birch is seldom found in this stratum. Plots in this cluster are characterized by their relatively low basal area and high species diversity in the tree layer. Cluster C plots illustrate a relatively immature type which has only recently closed its canopy sufficiently to prevent the establishment of yellow birch. The basal area of 30.8 m^2/ha is the lowest of all clusters, indicating that this successional type is still accumulating biomass. On the basis of age-diameter regressions for yellow birch developed by Leak (1985) from a stand located in the southwest sector of the Bowl, the ages of trees that are 55 and 35 cm d.b.h. are approximately 172 and 111 years, respectively, at the top of root swell. Therefore, these trees originated in openings created in the late 1700's and early 1800's. As the plots in this cluster age and the yellow birch die out, beech and sugar maple will increase in importance.

Cluster D plots also are dominated by yellow birch. They differ significantly from Cluster C plots in that the yellow birch has weak representation in the smaller size classes. This cluster consists of eight plots (14, 5, 19, 7, 39, 38, 20, 33, 21). Beech and sugar maple are more important in the tree layer of D than in C. Sugar maple, beech, striped maple, and mountain maple are important in the shrub-seedling layer. Cluster D represents a further development of Cluster C type plots. Basal area is higher in D than C (36.1 vs. 30.8 m^2/ha and tree density is lower (1,653 vs. 1,912 stems/ha). This higher basal area results from the maturation of the yellow birch and the growth of the beech-maple component. This increase in basal area occurs despite a decline in the importance of red spruce and balsam fir. Cluster D has fewer but larger trees than C and, probably as a result of a more open canopy, has more stems in the shrub-seedling layer (0.80×10^5 vs. 0.38×10^5/ha). There is a decline in diversity of trees from C to D (7.3 to 6.1 species per plot).

That Cluster D plots have been free from disturbance longer than the C plots is indicated by the greater number of larger size beech and sugar maple stems and the smaller number of small size yellow birch in D vs. C plots. (Fig. 5D). D plots had an earlier canopy closing and subsequent depression of yellow birch reproduction. It is reasonable to postulate that the micro-successional development of Cluster D plots began in the late 1700's, while Cluster C plots developed sometime before the mid-1800's. The extreme hurricane of 1815 may have initiated these Cluster D areas dominated by yellow birch by creating blowdown patches within the Bowl. Another intense but local storm in 1826 (Kilbourne 1916) may have been the initiating factor in the development of the C plots. These two events probably are too close together to be reflected in the size-class diagrams. In any case, 1815 is a reasonable date for the initiation of D plots; 1826 may be an appropriate date for the origin of C plots.

Cluster E consists of nine plots (37, 12, 11, 44, 1, 3, 25, 15, 27) in which beech typically is the leading dominant, and sugar maple, red spruce, balsam fir, and yellow birch are absent or of little importance. Striped maple, hobblebush, beech, and sugar maple are important shrub-seedling components, and mountain maple is of less importance in this layer. Currently, sugar maple, yellow birch, red spruce, and balsam fir have not been successful in entering the sapling size classes, so beech likely will increase in dominance in these plots.

Cluster F consists of six plots (31, 17, 34, 26, 42, 43) dominated by beech or sugar maple; sugar maple is strongly represented in all size classes. This differs from Cluster E, where sugar maple is weakly represented in the smaller size classes. Red spruce, balsam fir, and yellow birch are not important contributors to Cluster F plots. Plot 42 has an unexpectedly low Y value and may appear to be more closely allied to Cluster D than to F. However, this is a peculiarity created by the ordination technique used. Plot 42 has an extremely high importance value for sugar maple (177), a low value for beech (27), and a medium value for yellow birch (47) (Table 1). As a result, this plot has a lower Y value (more similar to yellow birch than to beech-dominated plots) than its sugar maple component would lead one to expect. This plot clearly is not dominated by yellow birch, and with sugar maple's domination and representation in all size classes is logically located in Cluster F.

Within Cluster F, red spruce, balsam fir, and mountain maple are nearly absent and yellow birch is rare in the shrub-seedling layer. Striped maple, sugar maple, hobblebush, and beech are important in the shrub-seedling layers. Wild sarsaparilla (*Aralia nudicaulis* L.), though never showing a high density in any plot, is present in each of the F plots. Those plots differ little from those of Cluster E with respect to their shrub-seedling layers except for the greater importance of sugar maple in F. The tree layer in Cluster F is slightly less dense (1,373 vs. 1,555 stems/ha) and somewhat more diverse in the shrub-seedling component 6.8 vs. 5.7 species/plot). With time, yellow birch will decline in importance and these plots will shift toward dominance by sugar maple or beech depending on the relative success of maple/beech seedlings in reaching sapling size. Currently, sugar maple is more dense in the shrub-seedling layer than beech (.38 x 10^5 vs. 0.06 x 10^5 stems/ha), though beech has a higher survival rate in this size classification (Forcier 1975). In the 2.5- to 7.5-cm size class, beech outnumbers sugar maple by 333 to 274 stems/ha. Perhaps this indicates a trend toward dominance by beech.

Cluster G consists of six plots (18, 40, 4, 9, 22, 8) in which sugar maple is the leading dominant or has a high importance value. The high importance values of sugar maple are primarily derived from its high relative dominance values. In fact, it has a low relative density in these plots. Cluster F plots are characterized by relatively few small but many large sugar maples, high densities of beech in the smaller size classes, and the virtual absence of red spruce, balsam fir, and yellow birch (24 trees/ha total). There are few balsam fir, red spruce, yellow birch, mountain maple, or wild sarsaparilla plants in the shrub-seedling layer. Hobblebush and beech are important and sugar maple shrub-seedlings reach maximum density (0.96 x 10^5 stems/ha) in this cluster. Although not differentiated in the data, most of the sugar maple are small seedlings. Cluster G plots show a fairly high basal area (37.1 m^2/ha), a low tree density (1,081 trees/ha), a high shrub-seedling density (1.23 x 10^5 stems/ha), and an extremely low tree-layer diversity (3.7 species/plot).

That the vegetation in these plots has developed free from disturbance for a long time is indicated by the paucity of yellow birch. Although the seedling density of sugar maple is high due to the large number of seed-producing trees present, few individuals seem to achieve sapling size. However, beech, with fewer seedlings, produces 4.2 times as many trees in the 2.5- to 7.5-cm size class. The size distributions of sugar maple and beech indicate a declining importance of the former and a rising importance of the latter as large, old sugar maple trees die out.

Figure 6 represents a scheme describing the developmental relationships between the subjectively defined plot clusters. This scheme is based on the current and projected future age/diameter structure of the important tree species. Yellow birch is a key species as it is used to indicate the amount of time that has elapsed since the last major wind-related disturbance. Yellow birch generally is rated as intermediate in tolerance and according to Fowells (1965) is "well represented in many climax types of northern forests (but) tends to give way with age to more tolerant species." Graham (1941) stated that yellow birch apparently does not become established as well in the thick leaf mold and deep shade of the forest as on exposed soil or recent burns. Zillgitt and Eyre (1945) said that yellow birch is a good seeder but develops best where the humus is scarified or disturbed, and that reproduction is most successful when the opening made in the stand is about 1/10 acre (0.04 ha) in size. According to Stearns (1951), yellow birch is found in higher numbers due to widespread windfall or fire, or both. In addition to the 0.04-ha opening, it is important to remember that an exposed, scarified, or disturbed soil is required for the establishment of yellow birch seedlings. This can occur only by the uprooting of large trees. Although much has been written about gap-phase micro-successions in climax stands (Forcier 1975; Oliver and Stephens 1977), there is no indication that this mechanism plays a significant role in the forest of the Bowl. If it did, D, E, F, and G clusters should show significantly higher numbers of yellow birch stems in the 2.5- to 17.6-cm classes. As it is, D, E, and F clusters show density diameter curves that are inadequate to maintain current overstory densities of yellow birch, and cluster G shows an almost complete absence of this species in all size classes.

Although there is continued mortality of canopy trees, much of this mortality does not result in the disturbance of the ground surface required by yellow birch. Dead trees usually are not uprooted but tend to rot near the base and then break. This does create a canopy opening but the beneficial results of the increased light are bestowed not on newly germinated yellow birch seedlings but on individual understory beech and sugar maple.

No areas were observed that contained only yellow birch in the predominantly reproduction or sapling-size classes. Only one plot of beech contained stems of these size classes in the Bowl. That plot contained 2 m^2/ha of basal area (Martin 1975). In his study, Martin used circular 100-m^2 (0.01-ha) plots, so this plot may not have been representative of an extensive area. Working in the southeast section of the Bowl, Leak (1974) used eighteen 0.1-ha plots to sample the larger trees in this stand, and presented age-structure diagrams similar to those of Cluster D. Since his data are a composite of the 18 plots, it is not possible to determine whether units composed of small yellow birch were present. However, in a subsequent personal communication, Leak indicated that no young yellow birch were found in his study area. Therefore, since the present forest of the Bowl certainly has almost no stands of young yellow birch and we know that areas of at least 0.04 ha are required for the establishment of this species, we must postulate the occurrence of a catastrophic disturbance which destroyed patches of the existing forest and reinitiated a successional cycle. There being no past history of fire in the Bowl, the agent probably was a severe windstorm.

Red spruce might be considered another, though somewhat less reliable, indicator of the time elapsed since disturbance. Leak (1973) indicated that the age distributions of spruce, fir, and yellow birch in the southeast corner of the Bowl are typical of declining populations. Bormann et al. (1970) maintained that due to the small energy reserves of the seeds and slow growth of seedlings, establishment of red spruce on the floor of a hardwood forest is difficult because of the often droughty nature of the organic horizons and mechanical crushing by hardwood litter. However, red spruce

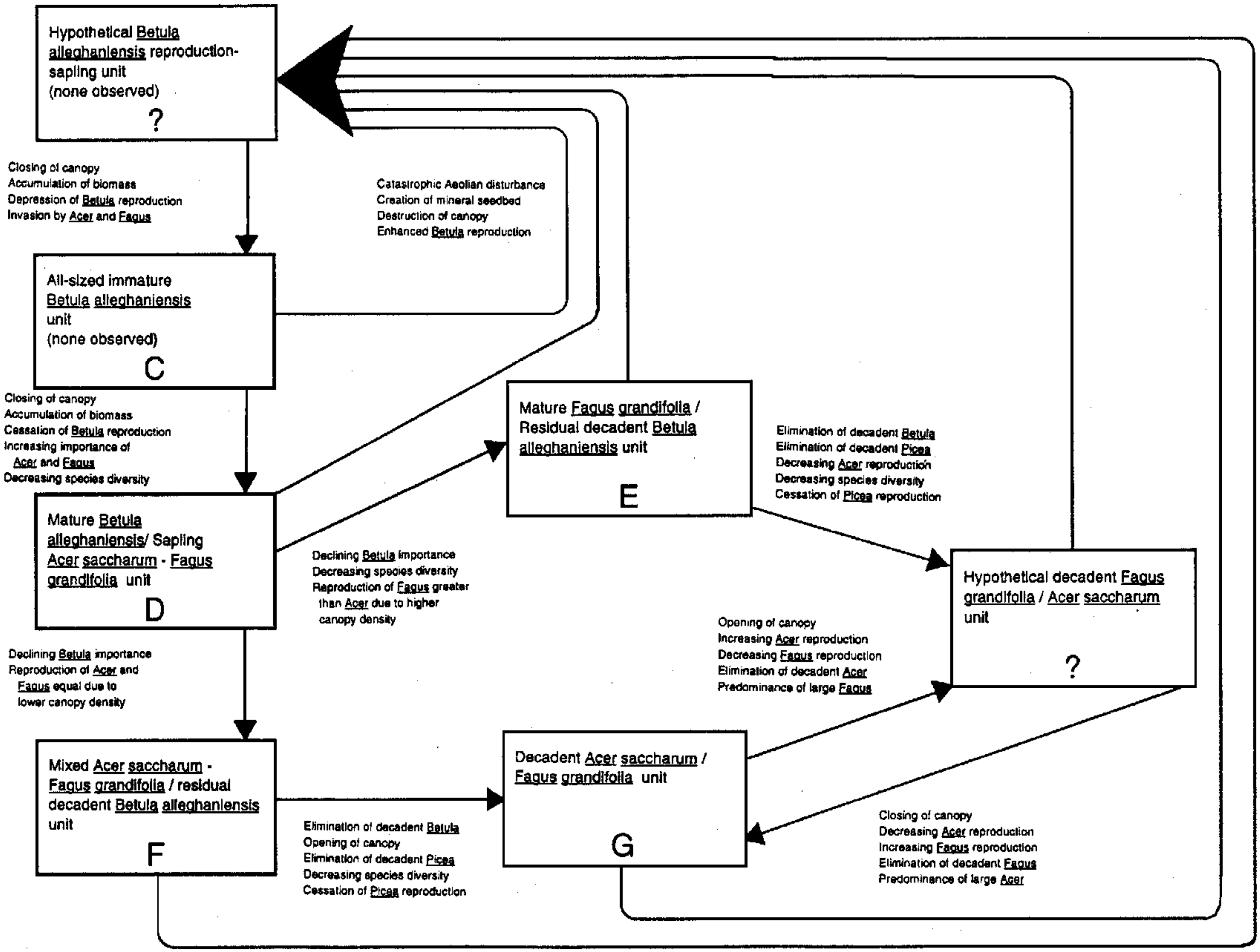

Figure 6.—Proposed scheme, based on the community ordination and consideration of stand curves, illustrating successional relationships within northern hardwood forests of the Bowl.

seedlings are shade tolerant, have exceptional longevity, and can respond to release (Fowells 1965). Therefore, we would expect both shrub-seedlings and adult trees to decrease in number as the forest ages. As indicated in Table 2, this is the case with respect to shrub-seedling importance values and the number of large red spruce trees (Figs. 5C-G).

The presence of yellow birch or red spruce in plots at low elevations (Cluster A) or under weak edaphic control (Cluster B) indicates that these units had been subject to some type of catastrophic windstorm in the past. Conversely, the absence of these species implies that a long period has elapsed since disturbance. For trees in the southwest corner of the Bowl, Leak (1985) found a 55-cm (diameter just above root swell) yellow birch that was approximately 170 years old, and a red spruce of the same diameter that was about 230 years old. Since trees of this size of these species occur frequently in Cluster C, D, E, and F units, but not in G type units, we can assume that the latter have been free from disturbance for at least 200 and probably 400 years, assuming an additional 200 years for the yellow birch and red spruce saplings in C units to mature and then drop out of the forest.

The divergence in the successional train at Cluster D seems to depend on the ability of sugar maple vis-a-vis beech to become established in stands with different overstory densities, with the resultant variation in light intensity at ground level. According to Fowells (1965), "Beech may be more tolerant than sugar maple under field conditions." So units with higher densities, those that will eventually develop into E units, would have more beech reproduction and less sugar maple. On the other hand, the less dense D units would have a more balanced species structure. This relationship also would hold in later units. When overstory density declines, sugar maple reproduction would be favored. When overstory density increased, beech reproduction would increase. For example, in Cluster G units, tree density is low (1,081 stems/ha) and sugar maple shrub-seedling density is maximal (9.6×10^4). In the previous stage (Cluster F), tree density was 1,373 stems/ha and the shrub-seedling density of sugar maple was 3.8×10^4/ha. This stage (Cluster F) generated the preponderance of beech over sugar maple saplings evident in Cluster G (Fig. 5G).

Working in the forests of the Catskill Mountains, McIntosh (1972) found that "stands dominated by beech had proportionately less beech in the smaller size classes and saplings, whereas sugar maple and hemlock increase in the smaller size classes and saplings....suggesting that sugar maple and hemlock are invading the beech stands." He also found that "old growth sugar maple stands show an increase in the proportion of yellow birch in the larger size classes and an increase in the proportion of beech in the medium size classes, which suggests an inverse relation between beech and sugar maple." Working with treefall gaps in a beech-sugar maple forest in Ohio, Runkle (1984) concluded that "beech and sugar maple show a tendency to alternate canopy dominance on a given site, with each species doing relatively better in gaps formed by the other." Thus, it is possible to envision a terminal successional stage that oscillates between a "Decadent *Acer saccharum/Fagus grandifolia* unit" and a "Decadent *Fagus grandifolia/Acer saccharum* unit." These forms would have a decadent overstory of one species, a vigorous and dense understory of the other species, and a shrub-seedling layer dominated by the same species that dominates the overstory.

Alternatively, both the "Mature *Fagus grandifolia*/Residual Decadent *Betula alleghaniensis* unit" and the "Decadent *Acer saccharum/Fagus grandifolia* unit" may develop into nearly pure self-maintaining beech units. This would agree with the findings of Siccama (1971) that in the presettlement forests of northern Vermont, beech made up 40 percent of the forest composition, whereas it is now only 10 percent as abundant as it was originally. It is well known that disturbance leads to a decline in beech reproduction (Fowells 1965). However, it has not been demonstrated that freedom from disturbance favors reproduction in this species. It does seem apparent that few if any of these units have reached an equilibrium situation and may never do so. None of the size/diameter diagrams (Figs. 5C-G) demonstrate curves that would be representative of stable, self-maintaining communities. Clusters C to F contain species that cannot persist in undisturbed situations, and Cluster G represents a group wherein beech is increasing and sugar maple is declining (Meyer and Stevenson 1943; Whittaker 1956; Bormann et al. 1970; Leak 1975). Although some species in some clusters follow the reverse J-shaped or negative exponential curve, none of the clusters show both this and the absence of successional species. In addition, none of the clusters have achieved numerical stability with respect to tree density. Even within Cluster G, tree densities range from 684 to 1,500 stems/ha.

The decline in tree layer-species diversity along the successional sequence results from a gradual removal of balsam fir, mountain maple, red spruce, striped maple, and yellow birch from the community. Although each of these species can persist in undisturbed forests for extended periods, each requires occasional openings for the germination and establishment of new seedlings or the release of suppressed individuals. If such openings are not created, these species cannot persist indefinitely in the community. Shrub-seedling diversity does not show a similar trend because as some species drop out, others are added. For example, while balsam fir, red spruce, yellow birch, and mountain maple decline in presence and importance along the successional sequence, wild sarsaparilla, hobblebush, beech, and American mountain-ash successfully invade the community.

In conclusion, on the basis of direct observation of long undisturbed stands, I have hypothesized a successional scheme for northern hardwood forests that includes a consideration of the dynamics of mature steady-state communities. Although the earlier successional stages are not found in the Bowl, their existence is well documented by other workers. The Bowl is small relative to the overall extent of northern hardwoods, but the principles outlined here should be applicable to a wider area.

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A phytosociological study was conducted in a virgin northern hardwood-spruce-fir forest in the Bowl in the White Mountains of New Hampshire. There is no evidence of fire or human disturbance but hurricane winds were significant in the past. Bray and Curtis ordination was used to develop an XY vegetational mosaic. Differentiating species were *Picea rubens* and *Acer saccharum* on the X axis and *Betula alleghaniensis* and *Fagus grandifolia* on the Y axis. This ordination was divided into seven plot clusters based on size-class distributions of major tree species. Clusters represent stages in a successional sequence, with final stages oscillating between *Fagus* and *Acer* dominated communities.

Keywords: Virgin forest, Bowl Research Natural Area, ordination, succession

Headquarters of the Northeastern Forest Experiment Station is in Radnor, Pennsylvania. Field laboratories are maintained at:

Amherst, Massachusetts, in cooperation with the University of Massachusetts

Burlington, Vermont, in cooperation with the University of Vermont

Delaware, Ohio

Durham, New Hampshire, in cooperation with the University of New Hampshire

Hamden, Connecticut, in cooperation with Yale University

Morgantown, West Virginia, in cooperation with West Virginia University

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