10. Forest Communities and Patterns

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The vegetation of the Coweeta Basin is traditionally included in the oak–chestnut association (Braun 1972). However, since chestnut (*Castanea dentata*) has been lost as a dominant due to the chestnut blight, the area is probably more correctly classified as belonging to the oak–hickory association. The plant communities in the basin are typically diverse for the southern Appalachians and are distributed in a reasonably predictable mosaic over the highly varied topography in relation to moisture gradients (Day and Monk 1974). The composition and structure of many of these communities are apparently still changing and are dynamic. The predominant species composition is a mix of deciduous oaks with a commonly abundant evergreen undergrowth of *Rhododendron maximum* and mountain laurel (*Kalmia latifolia*). (Species authority throughout this paper follows Radford et al. (1964).)

Community composition has been affected by human disturbances (Chapter 2). The Coweeta Basin was occupied by the Cherokee Indians prior to 1842. Between 1842 and 1900 the main disturbances were light semiannual burning and grazing. Between 1900 and 1923 logging operations occurred over the entire basin, but cutting was heaviest on the lower slopes, valleys, and accessible coves. Since 1924, no major human disturbance such as burning, grazing, or logging has occurred within the basin except for restricted U.S. Forest Service experimental studies.

General Distribution Patterns of Plant Communities

Permanent quadrats were used to study the broad-scale vegetation patterns and changes over time in forest communities at Coweeta. During 1934 and 1935, 997 0.081 ha (0.2

acre) quadrats were established along 13 parallel transects spanning the Coweeta Basin. Trees >1.3 cm (0.5 inches) DBH were tallied by species in 2.5 cm (1 inch) DBH classes. During 1969 to 1973, the 403 permanent quadrats which occurred on control watersheds, undisturbed since 1934, were reinventoried in the same way (W. T. Swank, 1969, unpublished). Percent slope, aspect, elevation, and slope position (ridge, upper slope, middle slope, lower slope, and cove) were also recorded for each plot.

The permanent quadrats were plotted on axes of elevation and topographic position. Using this direct gradient analysis approach, variations in vegetation composition associated with changes in the environmental axes could be determined. Figure 10.1 outlines the position of four major community types on the landscape. The topographic position axis runs from mesic coves to slopes to dry ridges. Within each of these, slope aspects are arranged in order of most mesic (NE) to most xeric (SW), so the axis corresponds roughly to a topographic moisture gradient. The major community types recognized are:

1. Northern Hardwoods: This forest type occurs at higher elevations, mostly above 4000 ft on slopes and in coves. It is dominated by a variety of species including yellow birch (*Betula lutea*), basswood (*Tilia heterophylla*), buckeye (*Aesculus octan-*

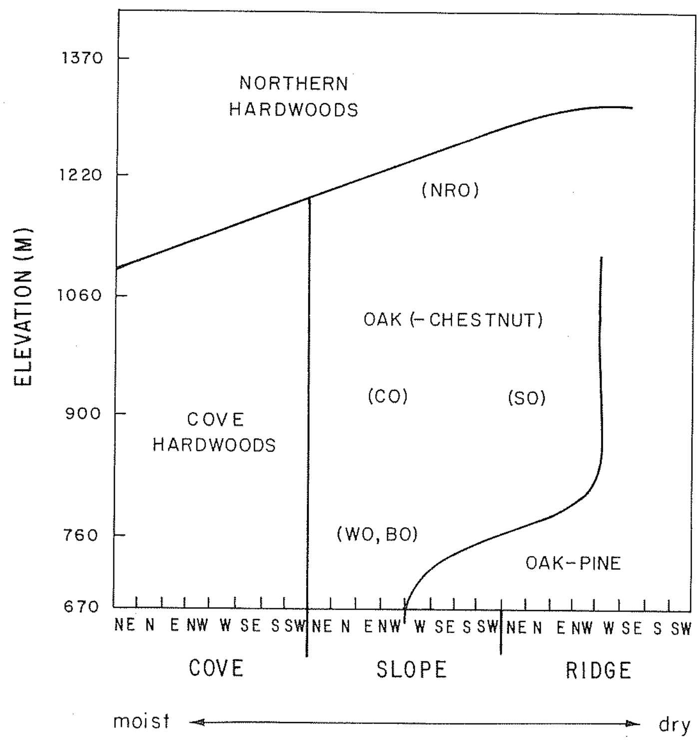

Figure 10.1. Major forest types at Coweeta and their locations. BO, Black Oak; CO, Chestnut Oak; NRO, Northern Red Oak; SO, Scarlet Oak; WO, White Oak.

dra), northern red oak (*Quercus rubra*), yellow poplar (*Liriodendron tulipifera*), and black cherry (*Prunus serotina*).

2. Cove Hardwoods: Occurring in mesic coves and blending into the Northern Hardwoods at higher elevations is the heterogeneous Cove Hardwoods type. Yellow poplar and hemlock (*Tsuga canadensis*) are among the many dominants, which also include red maple (*Acer rubrum*), northern red oak, hickory (*Carya* spp.), black birch (*Betula lenta*), and formerly chestnut.
3. Oak (–Chestnut): Widely distributed over the slopes of the Coweeta Basin are forests dominated by oak, and formerly by chestnut before the chestnut blight. Chestnut oak (*Quercus prinus*) is the most widespread and important oak species in the Coweeta Basin. Its importance is perhaps greatest at middle elevations on slopes with mesic aspects. Scarlet oak (*Q. coccinea*) increases in importance on drier slopes and ridges. At higher elevations above 1070 m, northern red oak increases in importance, while at lower elevations below 820 m, white oak (*Q. alba*) and black oak (*Q. velutina*) are important species. Besides oaks, red maple and hickories are also significant components.
4. Oak–Pine: This community type is found on the ridges and drier slopes at low elevations. Pitch pine (*Pinus rigida*) and scarlet oak predominate here, along with chestnut oak.

Community Change

Prior to the introduction of the chestnut blight fungus [*Endothia parasitica* (Murr.) P.], the American chestnut was the dominant tree species over much of the Coweeta Basin. At the time of the first survey of the permanent quadrats in 1934 and 1935, chestnut was still present but dying from the blight. As shown in Table 10.1, the relative basal area of chestnut in 1934 to 1935 in the various forest types ranged from 46% on mesic slopes in the Oak (–Chestnut) type to 16% on the drier slopes and ridges of the Oak–Pine type.

In order to determine the replacement patterns for chestnut in these various forest types, basal areas and importance values for each species were compared at the time of the blight (1934 to 1935) and 35 years later (1969 to 1973). Table 10.1 shows the major changes in relative basal area over the period. Changes in importance value were similar and are not shown.

In most cases, the species which exhibited the greatest increases in relative basal area were those which were already codominants at the time of the blight, with at least 5% basal area. These included various species of oaks in the Oak (–Chestnut) type, scarlet oak in the Oak–Pine type, northern red oak in the Northern Hardwoods type, and yellow poplar and hemlock in the Cove Hardwoods (Table 10.1).

The death of chestnut by blight was a gradual process. First a few small limbs succumbed, then larger limbs, and eventually the whole tree in a process that took 2 to 10 years (Woods and Shanks 1959). Gaps in forest canopies may be filled in by (a) expansion of the crowns of adjacent codominant trees, (b) growth of advanced reproduction seedlings, and (c) new establishment of seedlings by germination. The first process may explain in part why the relative basal area of codominant species increased so much. Other studies have demonstrated increases in tree ring widths following the

Table 10.1. Changes in Relative Dominance in Response to Chestnut Blight from 1934–35 to 1969–73

Northern Hardwoods		Cove Hardwoods		Oak–Chestnut NE,N,E,NW,W		Oak–Chestnut SE,S,SW ridges		Oak–Chestnut <2700 ft		Oak–Pine	
Species	Change in % Basal Area	Species	Change in % Basal Area	Species	Change in % Basal Area	Species	Change in % Basal Area	Species	Change in % Basal Area	Species	Change in % Basal Area
CN	−36.7	CN	−37.6	CN	−46.1	CN	−33.9	CN	−34.5	CN	−15.7
YB	+9.9	YP	+9.8	CO	+13.4	CO	+9.2	SO	+8.2	SO	+5.7
NRO	+9.3	HE	+5.5	RM	+7.4	RM	+4.0	CO	+5.7	RM	+3.5
YP	+7.7	BB	+4.3	NRO	+5.3	YP	+3.9	WO	+4.9	SW	+3.2
CH	+5.7			SW	+3.0			BO	+4.8		
								RM	+3.3		
								SW	+3.3		

Only species with >3% increase in relative basal area are included. BB, black birch; BO, black oak; CO, chestnut oak; HE, hemlock; NRO, northern red oak; RM, red maple; SO, scarlet oak; SW, sourwood; WO, white oak; YB, yellow birch; YP, yellow poplar. Circled species were codominants in 1934–35, comprising >5% of the basal area.

death of an adjacent chestnut tree (Nelson 1955; Woods and Shanks 1959). However, almost every species which showed a significant increase in basal area also showed a significant increase in density. Therefore, seed germination and/or release of advance regeneration seedlings must also have contributed to this rise. This is not unexpected, because codominant species would have an advantage due to the already established advance regeneration seedlings and an available seed source.

In addition to the increased basal area and density of already codominant species, several other species increased significantly in importance. Yellow birch, yellow poplar, and red maple were among the most notable in the different forest types. All of these species are characterized by copious production of relatively small wind-borne seeds and rather rapid growth in openings. Thus, while the slow opening of gaps by dying chestnuts primarily allowed an increase in codominant species, more opportunistic species were also able to take advantage of the gaps.

Age structures for nine tree species (Spring 1973; Iglich 1975; Monk and Day 1984) collectively show periods of increased recruitment about 80 years ago and again 40 to 60 years ago. The first recruitment period coincides with early logging, while the second recruitment period begins in the logging period prior to chestnut blight introduction. Since the second period of recruitment includes the effects of both logging and chestnut blight damage, the relative importance of the two disturbances cannot be separated.

The data from 1934 to 1935 and 1969 to 1973 surveys of the permanent quadrats were also used to assess changes in tree regeneration over the time period and to evaluate the impact of *Rhododendron maximum* on these changes (Phillips and Murdy 1984). Plots in two subgroups of the Oak (–Chestnut) type on slopes were selected for the study: those between 884 to 975 m dominated by chestnut oak, and mixed oak stands between 701 to 792 m where white oak, black oak, and scarlet oak predominated. These in turn were subdivided into high density rhododendron (HR; at least 15% rhododendron basal area in 1969 to 1973) and low density rhododendron (LR; less than 2% rhododendron basal area in 1969 to 1973). Rhododendron was not tallied in the 1934 to 1935 survey. Density–diameter distributions for the five dominant tree species were determined from the 1934 to 1935 and 1969 to 1973 inventories of HR and LR plots.

Oak and red maple regeneration, which was abundant in 1934 to 1935 due to past disturbance, decreased by 1969 to 1973 as the canopy closed. Total tree reproduction was lower in HR plots than in LR plots and the magnitude of the difference increased with time (Table 10.2). There were no significant differences between HR and LR plots in species composition, canopy tree basal area, understory basal area, or basal area of chestnut killed by the blight. This suggests that the differential decrease in tree reproduction over time was due to an increase in the density and basal area of rhododendron. This in turn may have been fostered by a combination of logging, chestnut blight, and cessation of burning.

At the time of the later survey, chestnut oak and white oak reproduction was depressed in HR plots relative to LR plots, whereas red maple was only slightly affected. Scarlet oak and black oak regeneration was poor at all sites, regardless of rhododendron density.

Rhododendron and mountain laurel represent the two most important evergreen components in these "deciduous forests," though lesser amounts of hemlock, pitch pine,

Table 10.2. Total Density (stems/ha) of Tree Saplings in the 1.3–8.9 cm DBH Class

	LR	HR	Percent Difference	p
Mixed Oak type				
1934–1935	2324	2257	3	NS
1969–1972	1566	793	49	0.0024
% decrease	33	65		
p	0.0108	0.0009		
Chestnut Oak type				
1934–1935	2657	2343	12	NS
1969–1972	1198	660	45	0.0001
% decrease	55	72		
p	0.0005	0.0001		

Shrubs and small tree species with no individuals >11.4 cm DBH were omitted. LR, low rhododendron; HR, high rhododendron; NS, not significant ($p > 0.05$).

American holly (*Ilex opaca*) and dog-hobble (*Leucothoe axillaris*) may be present. These evergreen species (mostly rhododendron and mountain laurel) contribute between 20 to 35% of the total standing crop of leaf biomass (Monk and Day 1984). With one-fourth to one-third of the leaf biomass present as evergreen leaves, it becomes evident that some aspects of mineral cycling will be modified by their presence. Some of the rhododendron leaves are held for as long as 7 years. Thus, these two clonal evergreen shrub species may influence forest regeneration and the rate of mineral flow within the forest (Day and McGinty 1975).

Table 10.3. Composition of Woody Vegetation on WS 18

Species	Basal Area m²/ha	Relative Basal Area (%)	Density No. Stems/ha	Relative Density (%)
Quercus prinus	5.5	21.3	190.8	6.3
Acer rubrum	2.4	9.3	181.8	6.0
Quercus coccinea	2.0	7.9	44.5	1.5
Rhododendron maximum	1.9	7.4	887.0	29.2
Quercus rubra	1.7	6.8	21.4	0.7
Liriodendron tulipifera	1.6	6.4	53.7	1.8
Carya glabra	1.3	5.1	70.4	2.3
Kalmia latifolia	1.3	5.1	890.9	29.3
Quercus velutina	1.2	4.8	30.1	1.0
Oxydendrum arboreum	1.1	4.4	75.5	2.5
Nyssa sylvatica	1.0	3.7	70.0	2.3
Cornus florida	0.8	3.2	182.7	6.0
Betula lenta	0.7	2.7	62.1	2.0
Tsuga canadensis	0.4	1.4	41.0	1.3
Hamamelis virginiana	0.2	0.7	71.4	2.3
Others (27 spp.)	2.5	10.0	171.0	5.2
Totals	25.6	100.0	3044.3	100.0

Species arranged in order of contribution to percent basal area. Only species with ≥0.1 m²/ha basal area and ≥20 stems/ha are listed.

Species Distributions

An intensive study of the vegetation on an undisturbed watershed (WS 18) was conducted in 1970 by sampling 25 plots, each 25 × 50 m. The overstory on this watershed was dominated by oaks (42.7% of total basal area) of which chestnut oak was the most prominent, followed in importance measured by relative basal area by scarlet oak, red oak, and black oak (Table 10.3). The hickories occurred as codominants in the overstory with pignut hickory (*Carya glabra*), mockernut hickory (*C. tomentosa*), and red hickory (*C. ovalis*) comprising 5.1%, 2.2%, and 1.3% respectively of the total basal area on the watershed. Red maple was also an important codominant in the overstory (9.3% of total basal area). The oaks, red maple, and hickories constituted only 9.6%, 6%, and 3.2% respectively of the total number of stems >2.5 cm dbh. The most important understory species were mountain laurel and rhododendron (58.5% of the stems >2.5 cm dbh), followed in relative basal area by dogwood (*Cornus florida*) and witch hazel (*Hamamelis virginiana*). The herb layer was relatively sparse, with ferns composing much of the ground vegetation.

Distribution maps based on absolute basal areas of the major overstory species reveal some of the general patterns on the watershed (Figure 10.2). The oaks and pignut hickory were distributed primarily high on the slope away from the stream. Red maple was distributed over most of the watershed. In two areas, at the base and near the stream halfway up the NW-facing slope, the composition of the overstory was atypical. Instead

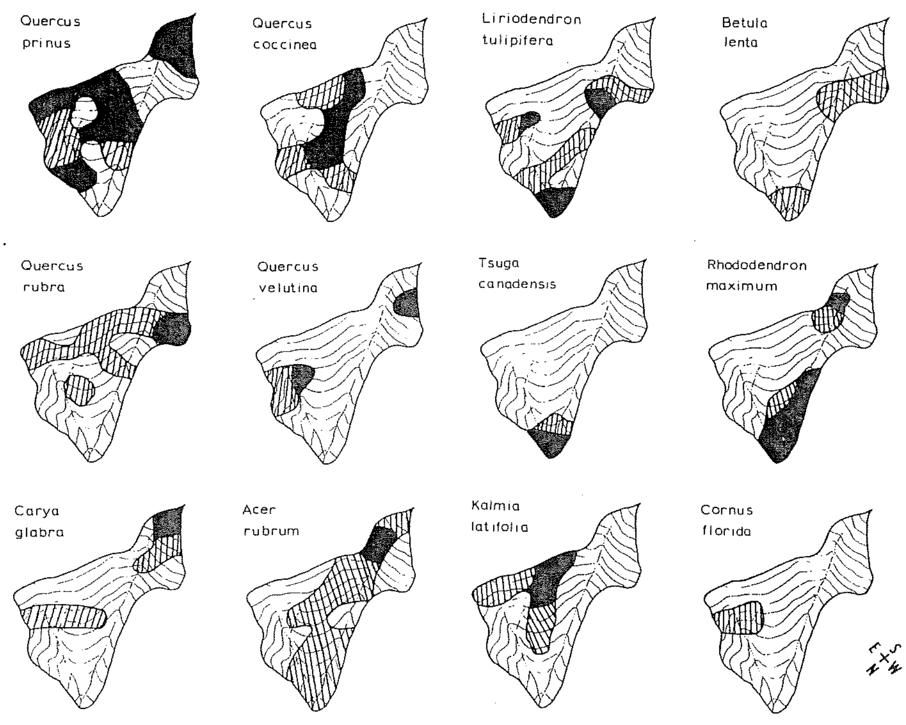

Figure 10.2. Species distribution patterns on WS 18 based on absolute basal area. Solid shading = >5 m²/ha, slashed = 2–5 m²/ha, remaining area = <2 m²/ha.

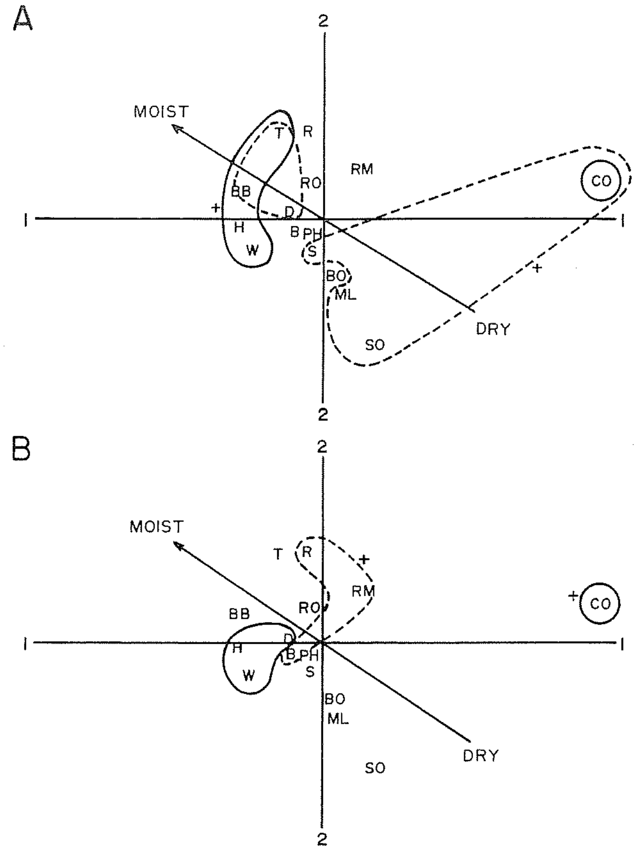

Figure 10.3. Plot of species on the plane of the first two principal components. *A*. The solid lines group species significantly correlated with distance from the water divide; the dashed lines group species correlated with distance from the stream. *B*. The solid lines group species significantly correlated with elevation; the dashed line groups species correlated with aspect. A + indicates that the group is positively correlated. The moisture gradient is arbitrarily sketched in. Species codes: CO, Chestnut Oak; RM, Red Maple; SO, Scarlet Oak; R, Rhododendron; RO, Red Oak; T, Tulip Poplar; PH, Pignut Hickory; ML, Mountain Laurel; BO, Black Oak; S, Sourwood; B, Blackgum; D, Dogwood; BB, Black Birch; H, Hemlock; W, Witch Hazel.

of being composed of oaks or hickories, much of the overstory consisted of tulip poplar, hemlock, and black birch. The patterns of understory species are striking (Figure 10.2) and were readily apparent in the field. Rhododendron was distributed primarily on the lower NE-facing slopes and areas near the stream, mountain laurel occurred near the ridges, and dogwood was concentrated mostly in an area near the stream. The understory species had very distinct distributions, and were virtually exclusive of each other in a given area.

In a principal components ordination of species based on basal area (Day and Monk 1974; Goldstein and Grigal 1972), the species significantly correlated with distance from the stream and distance from the water divide were grouped (Figure 10.3A).

Those species positively correlated with distance from the divide included tulip poplar, black birch, hemlock, and witch hazel. These species increased in basal area as the distance from the ridge increased, thus occupying moist sites. Overlapping this group was the group of species negatively correlated with distance from the stream; these included tulip poplar, black birch, and dogwood. Thus, those species occupying moist sites based on these two topographic gradients were grouped together in the ordination and were at one extreme of the ordination plot. At the other extreme were the species occupying the drier sites based on these two topographic gradients. The one species negatively correlated with distance from the divide was chestnut oak. Those species positively correlated with distance from the stream were chestnut oak, scarlet oak, mountain laurel, and sourwood. The two groups of species occupying the more moist sites were both located at one extreme of the arbitrary moisture gradient, while the two groups occupying drier sites were at the other extreme. Thus, the spatial arrangement of most species on the watershed as depicted by the ordination seems to align regularly with these two topographic gradients, which probably produce a moisture gradient.

The species grouped in Figure 10.3B were significantly correlated with aspect moisture value and elevation. There were no species negatively correlated with aspect moisture value. Those positively correlated with aspect moisture value, thus occupying more moist sites, were rhododendron, red maple, and blackgum. However, red maple had been observed widely distributed over the watershed, and blackgum was found on upper slopes and ridges. Also, densities of red maple and blackgum were positively correlated with elevation and distance from the stream channel, and blackgum density was negatively correlated with distance from the water divide. Therefore, we are less than satisfied with the manner in which aspect was quantified in the analysis. A relative moisture scale for aspect may be inappropriate for Coweeta; a measurement of solar radiation with respect to slope aspect would probably be a better quantification of this parameter. The only species positively correlated with elevation was chestnut oak, which was at one extreme of the gradient. Dogwood, hemlock, and witch hazel were negatively correlated with elevation, thus occupying the moist base of the watershed. Again, the groups associated with moist sites based on these two topographic gradients were located together at one extreme of the ordination plot and chestnut oak was at the other extreme.

Summary

The four major vegetation types at Coweeta (northern hardwoods, cove hardwoods, oak (–chestnut), and oak–pine) are apparently still undergoing change following major disturbances (logging, fire, chestnut blight). Over a 35 year period following loss of chestnut by blight, replacement was predominantly by species already codominant with chestnut. Chestnut oak should continue to be important, except perhaps in areas of high *Rhododendron* density, but there may be declines in white oak, scarlet oak, and black oak. Red maple will probably remain prominent as it does in many eastern forests following disturbance. The evergreen understory seems to be quite important in inhibition of regeneration of some canopy species. Individual species appear to be distributed along complex moisture gradients.

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