SURFACE LITTER, SOIL ORGANIC MATTER, AND THE CHEMISTRY OF MINERAL SOIL AND FOLIAR TISSUE: LANDSCAPE PATTERNS IN FORESTS LOCATED ON MOUNTAINOUS TERRAIN IN WEST VIRGINIA

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Abstract.--The topography of the landscape forms a foundation upon which variations in ecosystem structure and function arise. These variations are evident in the detritus component of forests located in highly dissected mountainous terrain, e.g., amidst the steep slopes and narrow valleys of the Appalachian Mountains. In this paper we describe the pattern of surface leaf litter distribution across a ridge-slope-valley landform and the concomitant effects on soil development and foliar elemental concentrations. The results of this study have direct ecological implications toward understanding the chemical status within a stand, the calculation of elemental turnover rates, and the determination of elemental budgets for watersheds.

A greater amount of surface leaf litter was measured on toeslopes and footslopes than on midslopes. This pattern is a direct consequence of downslope leaf transport by wind and not differences in litter deposition or litter decomposition. Litter accumulation on ridge crests was higher than that found at midslopes but not consistently higher, equal to, or lower than that at footslopes. Leaf transport out of stands centered on broad ridge crests is probably low.

The pattern for soil development along the fall line of the slope reflected the pattern in surface litter distribution. Higher concentrations and larger pools of organic matter, total nitrogen, calcium, magnesium, and potassium were found in the mineral soil at the footslopes than at midslopes. Foliar tissue analyses, in turn, reflected the chemical status of the soil. Higher concentrations of total nitrogen and calcium were found in leaves of *Quercus rubra* and *Q. prinus* growing at footslopes compared to similar data obtained at midslopes.

Keywords: Appalachian Mountains, elemental cycling, foliar tissue chemistry, forest floor, landscape, leaf litter, mineral soil chemistry.

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INTRODUCTION

Theoretical and empirical studies of forest floor detritus traditionally have considered the accumulation of litter to be the result of the difference between litter deposition and litter decomposition (e.g., Olson 1963, Lang 1974, Gosz et al. 1976). In stands located on level terrain, wind dispersal of litter inputs along the forest floor occurs (Zinke 1962, Phillipson 1975, Stone 1977) but presumably results in no net litter loss or accretion within the stand. Natural microsites, such as fallen logs, small topographic depressions (see Dwyer and Merriam 1981), large boulders, and bases of shrubs and trees, tend to trap and hold litter and help explain the inherent spatial variation in the distribution and the mass of forest floor detritus. Recently, Orndorff and Lang (1981) and Welbourn et al. (1981) independently documented the importance of wind-caused redistribution of surface litter along mountain slopes. Both studies showed the net loss of leaf litter from the forest floor at steep midslope positions with a concomitant accretion in footslope positions. Ostman and Weaver (1982) also noted this same phenomenon. The role of natural microsites for retaining litter in situ becomes increasingly important on steep slopes (Orndorff and Lang 1981), while the deposition-decomposition mass balance approach to calculating forest floor mass becomes inappropriate in mountainous landscapes.

This paper is an extension of the results of our earlier paper (Orndorff and Lang 1981). Our purpose here is 1) to further analyze and describe the spatial variation that exists in the distribution of surface litter both within and among forested stands located across a ridge-slope-valley landform in the mountainous landscape of West Virginia, and 2) to assess the effect of the distribution pattern on the chemical status of the mineral soil and, in turn, that of the foliar tissue.

STUDY AREA

Our data were collected in the Allegheny Mountain section of the unglaciated Appalachian Plateau physiographic province (Fenneman 1938), near Morgantown, West Virginia. The landscape in this area is strongly dissected, with steep slopes (slope angles range from 10-40°) and narrow valleys formed through fluvial processes. The land ranges in altitude from 262-792m and is covered with second growth forest of varying species composition. Mean annual precipitation is approximately 140cm; mean January and July temperatures are -1°C and 20°C, respectively.

Two sites were chosen for detailed study. The Sunset Beach (SB) site (39°40'N, 79°52'W) is a very steep southwest (225°)-facing slope, 120m in length (Figure 1). The actual lower portion of the slope is presently covered by Cheat Lake, a reservoir formed in 1926 by the damming of the Cheat River. This site is underlain entirely by upper Pennsylvanian aged shales and sandstones of the Conemaugh series (Hennen and Reger 1913). The mineral soil along the ridge crest and midslope is a fine-loamy, mixed, mesic Typic Hapludult, Gilpin series (Wright et al. 1982). Gilpin soils are well drained, moderately deep (50 to 100cm), acidic (pH 4.5-5.5), low to moderate in natural fertility, and usually without an organic horizon, especially on steep slopes. At the footslope, the soil is a fine-loamy, mixed, mesic Aquic Fragiudults, Shelocta series. This soil developed from material of colluvial origin, and is deep and moderately well drained.

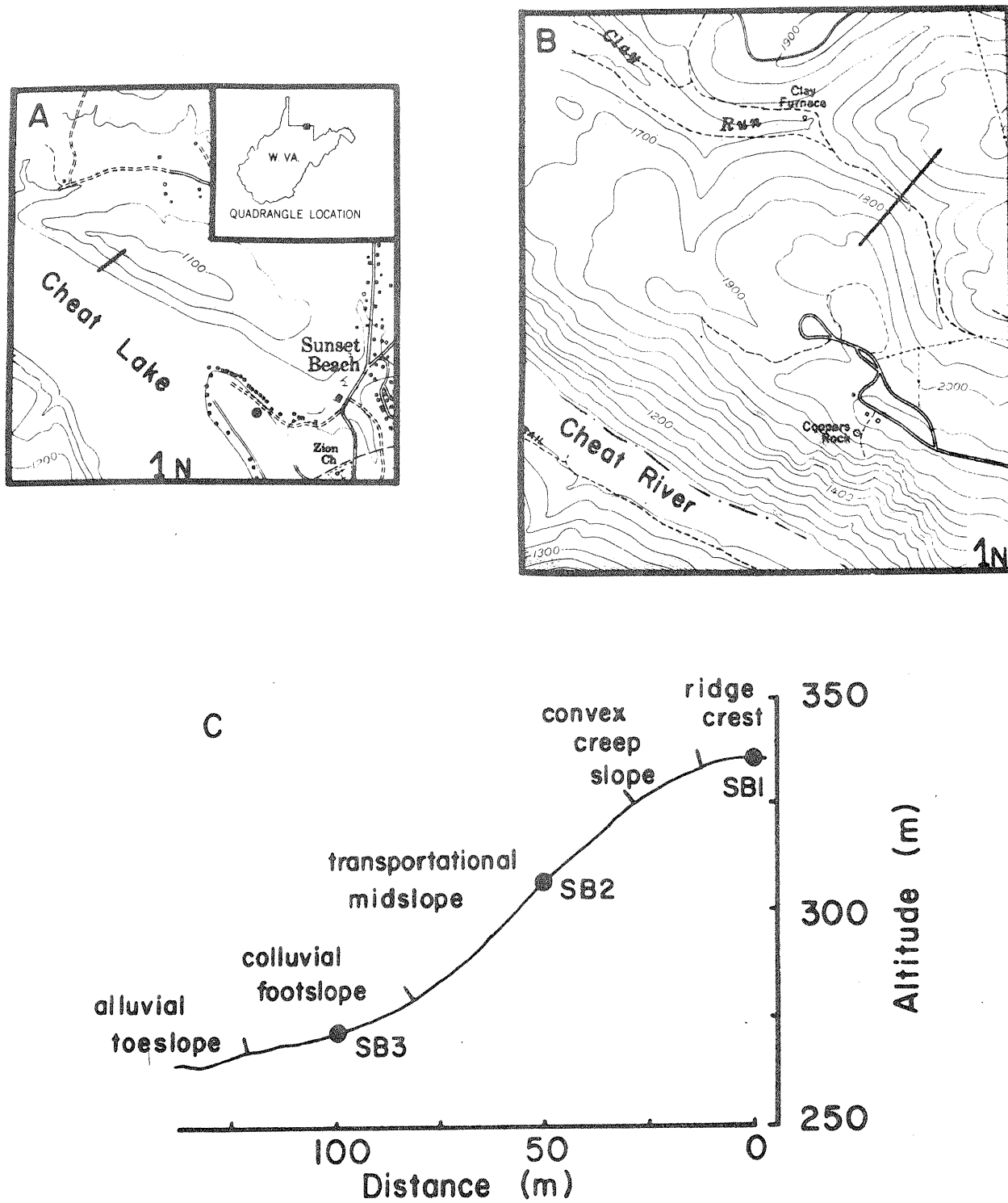

Figure 1.--A and B. Topographic data are from the Lake Lynn Quadrangle, West Virginia-Pennsylvania. The actual locations of the original study stands described in Orndorff and Lang (1981) and transect lines are shown in bold ink. C. Profile of the Sunset Beach site showing the position of the three original stands; the geomorphological slope charaterization is from Dalrymple et al. (1968).

The Clay Run (CR) site (39°38'N, 79°49'W) is composed of adjacent southwest (215°)- and northeast(35°)-facing slopes that laterally dissect the main trending ridge of the Appalachian Plateau (Figures 1 and 2). The main ridges and upper slopes are underlain by Upper Connoquenessing sandstones of the Pottsville series (Hennen and Reger 1913). These highly resistant early Pennsylvanian sandstones are responsible for the bold cliffs along the slopes and the talus that covers the lower slopes and streams. The lower portion of the Clay Run site is underlain by upper Mississipian shales interspered with sandstone layers of the Mauch Chunk series. The overlying mineral soil across the ridge crest and midslope is a loamy-skeletal, mixed, mesic Typic Dystrochrept, Dekalb series (Wright et. al. 1982). These soils are physically very similar to the Gilpin soils, but are slightly more acidic (pH 3.6-5.5), shallower, and contain more sand and coarse rock fragments. At the footslope, the soil is a fine-loamy, mixed, mesic Aquic Fragiudults, Buchanan series. This soil is similar to the Shelocta soils, having formed colluvial material, but from upland Dekalb soils. No chemical data were given for any of the soils by Wright et al. (1982).

METHODS

Surface Litter and Humus

Eighteen stands plus eight individual windthrow pits at Clay Run and three stands at Sunset Beach were targeted for detailed sampling of surface litter and in some instances humus. The 21 stands were located so as to represent major landscape features and to characterize differences in slope position and slope aspect. Forest cover was visually determined for each stand. From 8 to twenty-four 20x20cm quadrats were then sampled in each stand. Within each quadrat litter cover was estimated by cover classes: 0-25%, 26-50%, 51-75%, 76-99%, and 100%. After next measuring litter depth, a combined sample of the leaf portion of the L and F layers of the forest floor (sensu Lutz and Chandler 1946) was collected. Humus samples were taken to depth using a 5.7cm diameter soil core. Both the litter and humus samples were dried at 80°C before weighing. Oven dried material was ground and a subsample was combusted at 250°C for 2 hours and then 450°C for 4 hours. All mass data are given on an ash-free basis. Field collections were made in early September 1979, prior to autumn leaf deposition.

Two parallel line transects, 25m apart, were run along the fall line of the southwest-facing slopes at both sites (Figure 1). Litter cover to the nearest 5% was estimated for each 1m of transect line. The frequency and type of microsite which tended to trap litter were recorded. Microsites included logs, twigs, depressions (old tree fall pits or topographic concavities), and the bases of multistemmed shrubs.

Litter Deposition

Autumn leaf litter deposition was collected biweekly from ten $0.2m^2$ litter traps, distributed in a stratified random design, from September to mid-November 1979 in each of four 20x50m stands in the Clay Run site (Figure 2). Each trap was 50cm deep and the opening was oriented parallel to the horizontal and approximately 0.5m above the forest floor. Litter collections were dried at 80°C and weighed. The location of these four stands expressed the greatest available contrast in both topographic position and forest vegetation within the site.

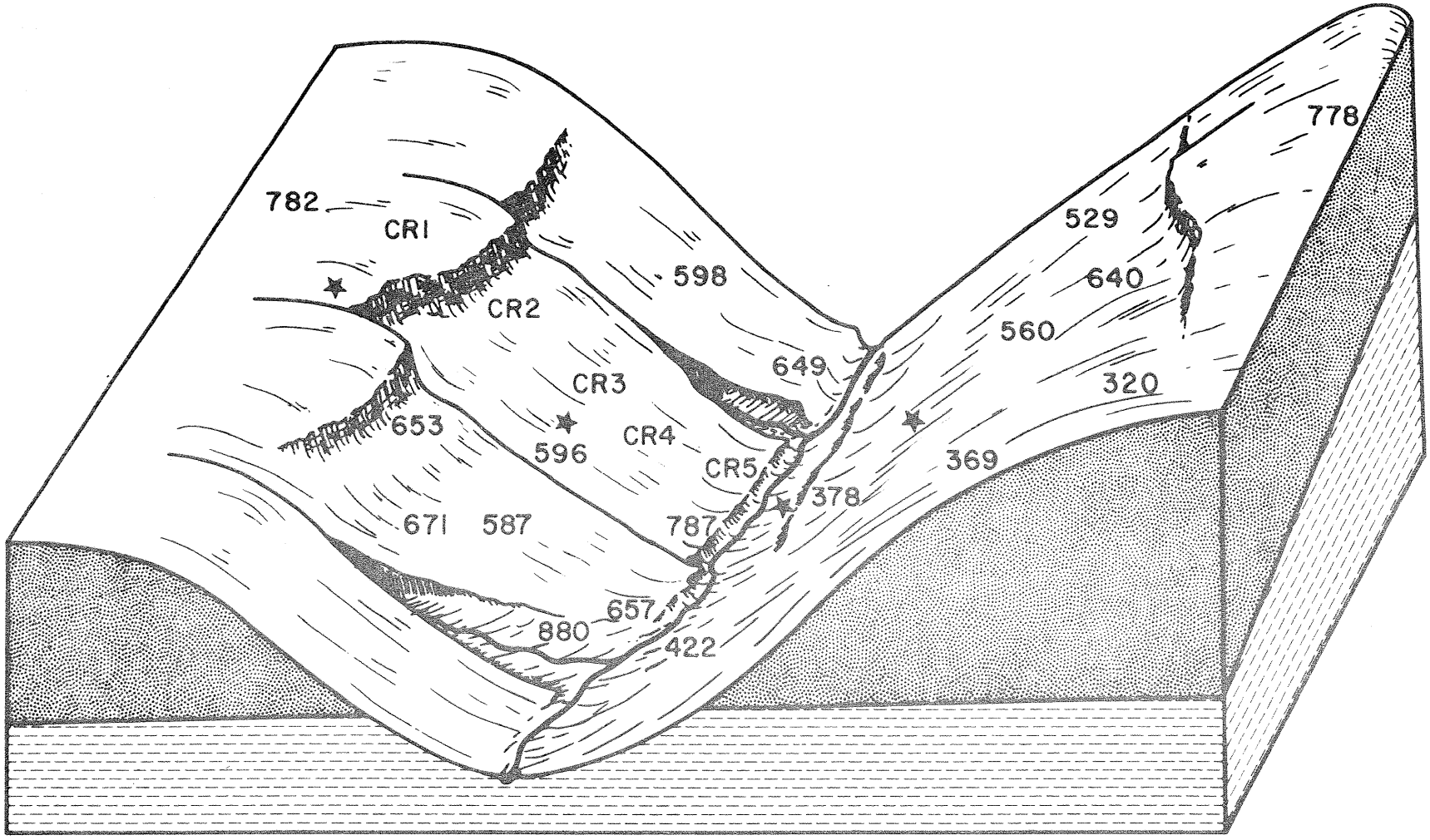

Figure 2.--Idealized block diagram of the Clay Run site with approximate position of the five original stands (CR1-CR5). Stars indicate the general topographic position at which litter deposition was measured. Values for litter mass from targeted stands (Table 1) are superimposed to reflect the topographic position from which they were obtained. depicts Upper Connoquenessing sandstone of Pottsville deposition; depicts Mauch Chunk shale and sandstone.

Soil Pits

To examine the chemical development of the soil along these mountain slopes, three 20x50cm soil pits were dug in the center of stands SB1-SB3 at Sunset Beach and CR1-CR5 at Clay Run (Figures 1 and 2) in September 1977. These stands are the same as described in Orndorff and Lang (1981), and our use of the stand codes remains consistent with this earlier paper. The fine earth portion of one pit was removed from the A, B and B_2 soil horizons and was weighed in the field. For the other two soil pits, the fine earth material was separated by horizon but not weighed. A subsample of fine earth material was taken from each horizon from each soil pit and returned to the laboratory. The pH of this material was measured on a 2:1 slurry of distilled water:wet soil by mass. Extractable cations were displaced from 50g of soil at field moisture using 200ml of 10% NaCl (Black 1965). Ion concentrations in the resulting solutions were analyzed using atomic absorption spectrophotometry. Soil moisture percentage was determined in order to convert field wet mass to dry mass values and to convert extractable ion concentrations to a dry mass basis. Soil organic matter content was determined from the loss on ignition of oven dried material as earlier described for the litter and humus. Total nitrogen was determined using Technicon Industrial Method No. 334-74 W/B.

Foliar Samples

Foliar samples of red oak (*Quercus rubra*) were collected at stands CR3, CR5, SB2, and SB3; samples of chestnut oak (*Q. prinus*) were collected only at CR3 and CR5. Three individual trees of each species were marked in each stand in order to repetitively sample the same individuals over time. Collections occurred on three dates during the growing season and once following the formation of the leaf abscission layer. On each date 20 within-crown leaves per tree, five from each cardinal position, were collected and pooled. Tissue samples were dried, ground in a Wiley mill to pass a 20 mesh screen, and then dry ashed and digested with HCl using the method described by Likens and Bormann (1970). Cation concentrations in the resulting solutions were determined by atomic absorption spectrophotometry. Total nitrogen and total phosphorus were determined using the method referenced for soil nitrogen. Plant tissue samples from the National Bureau of Standards were used to verify our methodology and analytical techniques.

Statistical Analyses

An analysis of variance was used to compare values for surface litter mass, litter deposition, and foliar concentration. Duncan's multiple range test ($P \leq 0.05$) was used to make the subsequent multiple comparisons (Sokal and Rohlf 1969). Correlation analysis was used to determine if there was a significant relationship between two sets of data.

RESULTS AND DISCUSSION

Surface Litter Distribution

Information on the forest cover of the study sites is shown in Table 1. The change in the dominant tree species composition among the different topographic positions is related to the differences in microclimate associated with north- and south-facing slopes (Wolfe *et al.* 1949), especially water

Table 1.--Characteristics of surface litter and humus at different topographic positions (see Figure 1).

Topographic Position[1]	Dominant Tree Species[2]	Surface Litter Cover (%)	Surface Litter Depth (cm)	Surface Litter Mass[3] (g/m^2)	Humus Mass[5] (g/m^2)
		CLAY RUN			
windthrow pits (SW)	----	100	10.3	2609(25,8)a	NM[4]
SW, toeslope	Ar-Lt-Ps-Fg	91	6.1	880(45,16)b	4781(60)
SW, footslope	Ar-Qr-Qv-Lt	100	4.0	787(23,8)bc	NM
ridge crest (SW)	Qp-Qr-Ar	100	3.7	782(39,24)bc	5207(32)
ridge crest (NE)	Qp-Qr-Ar	100	3.3	778(26,24)bc	4511(42)
SW, upper midslope	Qp-Ar-Qr	75	3.3	671(35,8)cd	NM
SW, footslope	Lt-Bl-Fg	97	3.7	657(46,24)cd	4938(89)
SW, midslope terrace	Ar-Qp-Qr-Ns	93	3.5	653(41,24)cd	4232(60)
SW, footslope	Fg-Lt-Qa-Fa	95	3.3	649(62,24)cd	8261(125)
NE, midslope terrace	Ar-Ta-Lt-As	84	2.7	640(40,24)cd	2616(25)
SW, midslope	Qp-Ar-Qr	82	2.6	598(49,8)cd	NM
SW, midslope	Qp-Ar-Qr	69	2.8	596(57,24)cd	4213(40)
SW, midslope	Ar-Qp-Qr	76	2.8	587(37,8)cd	NM
NE, midslope	Ar-As-Ta	93	2.3	560(50,8)d	NM
NE, upper midslope	As-Ar-Lt	98	2.3	529(17,8)de	NM
NE, toeslope	Lt-Ar-Ps	93	2.1	422(32,16)ef	3445(43)
NE, footslope	Lt-Ta-Ps-Ar	91	2.0	378(43,24)ef	4154(86)
NE, midslope	Ar-Lt-Ta-Ps	95	2.4	369(41,24)ef	4644(55)
NE, upper midslope	As-Ta-Lt-Ps	98	1.9	320(29,8)f	NM
		SUNSET BEACH			
SW, footslope	Ar-Fa-Qr-As	100	8.2	1067(30,10)x	NM
SW, ridge crest	Fa-Qr-Ar	87	2.2	449(68,23)y	NM
SW, midslope	Qp-Qr-Ar	<5	0.9	124(234,24)z	NM

[1] SW and NE designate southwest-facing and northeast-facing slopes, respectively.

[2] Species codes are: Ar, *Acer rubrum*; As, *A. saccharum*; Bl, *Betula lenta*; Fa, *Fagus grandifolia*; Lt, *Liriodendron tulipifera*; Ns, *Nyssa sylvatica*; Ps, *Prunus serotina*; Qa, *Quercus alba*, Qp, *Q. prinus*; Qr, *Q. rubra*; Qv, *Q. velutina*; Ta, *Tilia americana*. Nomenclature follows that of Strausbaugh and Core (1977).

[3] Data in parentheses are the coefficient of variation and the number of quadrats; for each site, statistically similar mass values have the same letter.

[4] Not measured

[5] Value in parentheses is the coefficient of variation.

availability (Bush et al. 1980). In general, oak species dominate the more xeric ridge crest and southwest-facing midslopes while more mesic species are associated with the footslopes and northeast-facing midslopes. Red maple (Acer rubrum) is ubiquitous in its distribution throughout the forest.

The average cover, depth, and mass values for surface litter within the individual stands are given in Table 1. Cover values were determined by averaging the mid-point values from the cover class data. Several points are noteworthy. First, for the litter mass there was no relationship between increasing the number of quadrats sampled and decreasing the coefficient of variation. Thus eight quadrats chosen at random was as adequate as 24 quadrats for representing the litter mass. The mean coefficient of variation for the 18 stands at the Clay Run site was 37%.

Second, windthrow pits are unique microsites located within stands at all slope positions on the landscape. The litter mass value from these pits was from 3- to 4.5-times greater than the average mass value for a stand on the southwest-facing slope at Clay Run. These results compliment those of Dwyer and Merriam (1981) who measured significantly more litter in topographic low areas, 0.5m in depth, compared to high areas in an Ontario woodlot. This topographic heterogeneity was produced by natural undulations in the underlying glacial till.

Third, at each site the stands were ranked in decreasing order of the values for litter mass. A 3- and 10-fold difference between the extremes is evident at the Clay Run and Sunset Beach sites, respectively. The statistical separation of the stands is clearly seen. At Clay Run, the mass values are significantly correlated with depth (r=0.95) but not with cover (r=0.03). A relationship with cover was expected but the small variation in cover values among the stands prevented any trend from appearing. In fact, all of the average cover values were greater than 90% except for those on the southwest-facing midslope and the northeast-facing midslope terrace.

Fourth, the effect of aspect is also evident at the Clay Run site. All but one stand on the northeast-facing slope segregated out with the lowest mass values while stands on the southwest-facing slope had the higher values. This trend is related to the differences in the vegetation found along each slope and within the individual stands and will be discussed later. The ridge crests do not face southwest or northeast but are so designated in parentheses to show their location with respect to the slopes.

Fifth, overlying the effect of aspect is a pattern associated with topographic position. At Clay Run, both midslope terrace stands had similar mass values. These two stands were located at similar positions on the opposing slopes (Figure 2) and received inputs of predominantly oak litter from the convex creep slope and ridge crests above the sandstone cliffs. Both ridge crest stands had nearly identical mass values; these values were also comparable to those measured in stands located at the southwest-facing footslope and toeslope positions, while stands at the midslope had the least amount of litter. The reduction in litter mass, and concomitant decrease in depth, is explained by the wind-caused downslope movement of leaf litter (cf. Orndorff and Lang 1981, Welbourn et al. 1981, Ostman and Weaver 1982). This midslope-footslope pattern is less striking on the northeast-facing slope, while the Sunset Beach site represents the extreme example. Here the short steep slope magnifies the

pattern of litter export from the midslope and accumulation in the footslope position. The transect data for litter cover, irrespective of the presence of microsites, also show this pattern well (Table 2). The midslope position is the most interesting with its low litter cover and very high coefficient of variation. These results mimic those for the Sunset Beach stands in Table 1, especially the midslope stand where only five of the 24 samples had any litter. The larger values for litter cover reported for the Sunset Beach site in Table 1 compared to those in Table 2 are a result of comparing stand data with transect data. The stand data are derived from quadrats located in a homogeneous area which characterizes a topographic position. On the other hand, the transect data are taken from contiguous 1m intercepts of the transect line distributed across the entire slope and a posteriori compiled by topographic position. This manner of sampling inherently has greater variability and leads to the lower cover values. In addition, some of the discrepancy may be the result of sampling two different but adjacent areas at Sunset Beach. On the whole, the data for Clay Run are more typical of the general landscape in the area.

Table 2.--Surface litter cover along the Sunset Beach slope.

Topographic Position[1/]	Litter Cover[2/]
Ridge crest	55 (51)
Creep slope	24 (78)
Midslope	14 (79)
Footslope	66 (55)
Toeslope	99 (2)

[1/] See Figure 1

[2/] Mean % cover with coefficient of variation in parentheses.

Litter cover in the midslope stands at Clay Run is lower than that in the footslope stands (Table 1) but higher than might be expected considering the export of litter downslope. This observation is explained by the presence of microsites within the midslope stands which act to trap and accumulate litter, thereby, keeping the average stand values for litter mass and especially litter cover high. For example, along the southwest-facing slope at Clay Run, 80 microsites (28 logs, 23 branches and twigs, 20 multistemmed shrubs and 9 topographic depressions) were intersected by the two transect lines. This amounts to one microsite every 4.4m or 23% of the line. For the 1m length of transect line upslope of a microsite, a litter cover value $\geq$ 90% was associated with 46 (58%) of the 80. Along the 77% of the transect line that did not have microsites, 58% also had litter cover values $\geq$ 90%. However, if the transect data from the ridge crest and toeslope are excluded, the percentage of the transect data having litter cover values $\geq$ 90% changes to 53% for the microsites and only 35% for the remaining portion of the transect line. This difference illustrates the importance of the microsites for maintaining litter cover and mass, higher than expected, at midslope stands.

But, not all microsites have high litter cover. Six (7%) of the microsites had < 30% cover and all were located at the midslope where downslope litter movement is maximum. Five were logs at large angles from the contour, which trapped less litter (Orndorff and Lang 1981).

In general, microsites have greater mass values than that for the stand as a whole. For logs this increase may be up to 11-times that for the stand (Orndorff and Lang 1981) while windthrow pits were up to 4.5-times greater (Table 1). Through random selection, it is highly likely that a microsite will be sampled. Since the values for litter cover and mass associated with the microsites are high, inclusion of these data helps to keep the stand average high. Furthermore, the presence of microsites maybe especially important in midslope stands. The redistribution of litter, and thus the internal heterogeneity, within a stand is at a maximum in late summer prior to autumn leaf deposition (Orndorff and Lang 1981). High cover and mass values at the microsites plus concomitant low values (e.g., from topographically raised areas, (Dwyer and Merriam 1981, Orndorff and Lang 1981)) contribute to the variation in the values among the quadrats within a stand and account for the large values for the coefficient of variation (Table 1).

Litter Deposition

Autumn leaf deposition data are given in Table 3. It is during autumn that 90% of the annual leaf deposition occurs within this eastern deciduous forest (Orndorff and Lang 1981). The values from the four stands for 1979 are comparable to those reported for eastern temperate forests (Bray and Gorham 1964, Cole and Rapp 1980). The value for the southwest-facing midslope stand is 1.4-times greater than that measured in the same stand in 1978. This difference is not unusual since up to a 2-fold difference in leaf deposition can occur from year to year (Bray and Gorham 1964). More importantly, the pattern of deposition across the landscape was similar to the pattern shown for the mass of recently fallen leaf litter collected from the forest floor in November 1978 (i.e., by rank, litter deposition on southwest-facing midslope>ridge crest>footslope). The deposition value for northeast-facing midslope fell intermediate in rank.

There are two principle points to be drawn from these data. First, the mass of autumn leaf deposition is not the same at different topographic positions located only short distances apart in mountainous landscapes. Differences in litter deposition values is attributed to differences in the total mass of leaves within a stand which is controlled by stand density, canopy development, and species composition (see Table 1), variables we did not measure. Of special importance is the variation in leaf mass per leaf area among species. For example, the mass per unit area of black oak (*Q. velutina*) leaves is 3.2-times greater than that for red maple (*A. rubrum*) leaves (Lang unpublished data). Such differences alone illustrate how differences in the mass of litter deposition can occur among stands with canopies of equal leaf areas and all other variables being similar. Second, the observed differences in leaf deposition are not correlated with the general pattern of surface litter distribution across the landscape (Table 1). In fact, the mass of litter is greatest at positions of lowest deposition.

Landscape Pattern In Surface Litter

Although leaf litter decomposition was not measured in this study, results

Table 3.--Autumn leaf deposition by topographic position (see Figure 1).

Topographic Position	Dominant Tree Species[1/]	Mass[2/] (g/m^2)
Southwest-facing, midslope	Qp-Ar-Qr	478a
Northeast-facing, midslope	As-Lt-Ta	418b
Ridge crest	Qp-Ar-Qr	398b
Valley bottom, toeslope	Lt-Tc-Ps	338c

[1/] Species codes are given in Table 1.

[2/] Statistically similar mass values have the same letter.

of our earlier work showed that on southwest-facing slopes, decay was slower in the midslope position than at the footslope or ridge crest. This pattern plus that for increased litter deposition at the southwest-facing midslope than at the footslope or ridge crest is contrary to the observed patterns for the mass data. This paradox is explained by the redistribution of the litter deposition along the slope. Wind-driven downslope movement of litter causes a net loss of litter off the midslope and an accumulation in the footslope.

Decomposition rates for leaves on the northeast-facing slope are not available but are expected to be fast, however, based on the tissue chemistry of the vegetation. Leaves of the dominant mesophytic species (Acer saccharum, Liriodendron tulipifera, Tilia americana, and Prunus serotina) generally have lower C/N ratios, less lignin, and a higher nutrient status than leaves of the xerophytic oaks. These mesophytic leaves will decompose faster regardless of the microclimatic differences that exist between the two slopes (see data of Witkamp and Olson 1963, Meentemeyer 1978, Aber and Melillo 1980, Melillo et al. 1982). Faster decomposition rates plus reduced litter inputs (Table 3) would lead to less litter mass (Table 1) on a northeast-facing slope compared to a southwest-facing slope. Furthermore, leaves of the mesophytic species on the northeast-facing slope remain moister longer, lose their integrity more rapidly, and adhere to the forest floor surface more readily. Thus these leaves do not blow around as much and there is less litter redistribution. On the southwest-facing slope, wet oak leaves dry quickly, keep their integrity longer and thus are subject to greater wind dispersal. The net effect is a less striking pattern on the northeast-facing slope. Welbourn et al. (1981) observed less transport on a northwest-facing leeslope (comparable to our northeast-facing slope) but suggested that the results were attributed to differences in wind flow patterns.

The patterns described herein support 1) our earlier work (Orndorff and Lang 1981), but with a much broader data base, 2) the complementary studies of Welbourn et al. (1981) and Dwyer and Merriam (1981) and 3) the observations of Wolfe et al. (1949), Finney et al. (1962), Franzmeier et al. (1969), and more recently Ostman and Weaver (1982). These results question the validity of using the standard deposition-decomposition mass balance approach to modeling forest floor detritus in mountainous terrain since any given stand

can have potentially significant inputs or outputs through wind-caused litter redistribution. In addition, these results illustrate the importance of understanding the geomorphological features of the land form in mountainous terrain as a framework for describing patterns in litter mass. Deviations to the broad landscape pattern can arise if the stands that are sampled are located on topographic discontinuities along the slope or have unique microsite properties.

Humus And Soil Organic Matter Accumulation

The accumulation of humus and the incorporation of organic matter into the soil, especially the A horizon, is strongly influenced by the presence of surface detritus and its decomposition. One consequence of leaf litter redistribution should be the development of a pattern for humus and soil organic matter accumulation that parallels that for surface litter mass. A trend, albeit weak, occurred on the southwest-facing slope, with higher humus values in the ridge crest and southwest-facing footslope stands than in the southwest-facing midslope stand (Table 1). The midslope-footslope trend is reversed on the northeast-facing slope but data from other stands are necessary to determine if this trend is real or an artifact of the low number of stands that were sampled. Replicate collections were more variable for the humus than for the surface litter. The rockiness of the terrain prevented a uniform humus layer from developing within a stand and accounted for the higher coefficients of variation.

Data from the soil pits must be considered with caution since the sample size is small. The data do show, however, that the incorporation of the organic matter into the soil is related to slope position (Tables 4 and 5). The Sunset Beach data illustrate this consequence most pronouncedly. Both the concentration and total content of organic matter in the A horizon is greatest in the footslope stand (SB3) compared to the midslope stand (SB2) (cf. Welbourn *et al.* 1981). The content value for the entire pit at stand SB3 is much greater than reported values in the literature (Schlesinger 1977, Cole and Rapp 1980), but this stand is subjected to localized influences to the extreme.

At Clay Run, mean litter mass values for stands CR1 through CR5 were 480, 540, 500, 670, and 400 g/m^2, respectively (Orndorff and Lang 1981). The organic matter concentration values in Table 4 are significantly correlated ($r=0.98$) to the surface litter mass values. Stand CR2 was an upper midslope terrace and had high litter and also a high concentration of organic matter in the soil. The CR4 stand was on a terrace in the footslope; litter accumulated in this stand and did pass further downslope to stand CR5. The deep A horizon at stands CR4 and CR5 reflect the colluvial nature of these stands compared to that at CR3 (Table 5). Total mass values for the A horizon show a strong midslope-footslope pattern, but the ridge crest data do not conform (Table 5). The large mass of organic matter in stand CR5 is a result of the horizon depth compensating for the low concentration values, suggesting that the latter may be the result of a dilution from the inorganic colluvium. If the data for the A-horizon are relativized to account for the differences in depth, the stand ranking becomes: midslope<footslope<ridge crest.

Mineral Soil Chemistry

The fact that the distribution patterns for surface litter affect soil organic matter development in a predictable way would further suggest that the

chemical status of the soil might also be affected in a similar manner. The mean concentration data for total N and the extractable cations at the three soil pits at Sunset Beach reflected the expected trends (Table 4). At Clay Run, the midslope-footslope pattern occurred for all elements except potassium, which showed no trend across all five stands. The concentration data for the ridge crest stand resembled that in the midslope stand (CR3). Cation data from the Clay Run site fell within the range of the values reported by Frank (1981) for Dekalb soils.

Table 4.--Chemical characteristics of mineral soil at the Clay Run and Sunset Beach sites.

Stand	Horizon	Soil pH	% Organic Matter	Mean Concentration[1/]			
				N	Ca	Mg	K
CR1	A	3.5	7.1	1.8	28	10	32
	B	-	4.6	1.0	40	2	29
	B_2	4.2	2.8	0.6	44	3	28
CR2	A	3.5	7.9	1.7	36	11	30
	B	4.1	2.6	0.4	5	2	27
	B_2	4.2	2.3	0.4	3	2	26
CR3	A	3.5	6.7	1.8	40	11	31
	B	4.3	3.3	0.7	12	3	28
	B_2	4.3	2.9	0.5	9	3	27
CR4	A	4.4	9.7	3.3	185	24	34
	B	4.5	3.8	1.0	24	5	30
	B_2	4.5	2.9	0.8	20	6	28
CR5	A	4.3	5.7	2.1	182	15	31
	B	4.4	3.4	1.0	77	8	29
	B_2	4.4	2.7	0.6	74	11	28
SB1	A	6.2	12.9	3.2	5110	691	180
	B	5.0	7.8	1.0	2810	513	152
	B_2	4.5	5.0	0.2	1830	446	138
SB2	A	4.7	9.0	1.2	2130	271	135
	B_2	4.7	5.6	0.1	300	92	101
SB3	A	7.0	19.7	6.6	12600	1010	323
	B	7.1	10.8	2.0	6090	482	201
	B_2	-	8.8	1.6	5460	455	160

[1/] N data are mg/g, dry soil; cation data are for extractable ions in ppm, dry soil.

Table 5.--Organic matter and elemental contents in mineral soil horizons at the Clay Run and Sunset Beach sites.

Stand	Horizon	Horizon Depth(cm)	Contents (kg/ha) Organic Matter	N	Ca	Mg	K
CR1	A	2	13400	340	5	2	6
	B	10	28300	640	25	1	18
	B_2	32	58600	1180	92	6	57
		44	100300	2160	122	9	81
CR2	A	2	10300	220	5	1	4
	B	10	21800	370	4	1	23
	B_2	28	55700	1040	8	4	64
		40	87800	1630	17	6	91
CR3	A	5	18200	490	11	3	8
	B	25	58700	1190	22	5	50
	B_2	30	90600	1670	28	10	85
		60	167500	3350	61	18	143
CR4	A	8	29000	980	56	7	10
	B	10	27400	540	17	4	20
	B_2	37	125000	3190	84	26	118
		55	181400	4710	157	37	148
CR5	A	20	82100	3070	263	22	45
	B	8	22800	670	51	5	19
	B_2	40	112000	2850	353	51	132
		68	216900	6590	667	78	196
SB1	A	7	78700	1930	3120	420	110
	B	10	59000	780	2140	390	120
	B_2	50	384000	1300	14000	3400	1050
		67	521700	4010	19260	4210	1280
SB2	A	3	20800	270	490	60	30
	B_2	23	61200	110	330	100	110
		26	82000	380	820	160	140
SB3	A	16	166000	5570	10600	850	270
	B	21	262000	4770	14700	1170	490
	B_2	60	637000	11400	39500	3290	1160
		97	1065000	21740	64800	5310	1920

Total elemental contents of the soils are given in Table 5. The patterns are again evident for the three Sunset Beach stands. At Clay Run, there was, in general, an increase in the total elemental contents from the ridge crest (CR1) to the footslope (CR5). The nitrogen data mimic the organic matter contents, while each cation behaved independently. If the elemental contents for the A horizon are relativized to account for differences in depth, the midslope stand (CR3) has the smallest pool size compared to the ridge crest and footslope stands. Welbourn et al. 1981 reported similar trends in the mineral soil.

Foliar Tissue Chemistry

The chemistry of foliar tissue often reflects the chemical status of the soil substrate (van den Driessche 1974). As a consequence of the observed pattern in soil chemistry, we would expect differences to appear in the chemistry of foliar tissue collected from different topographic positions (Orndorff and Lang 1981).

Since no changes in the elemental concentrations in leaves of either Q. prinus or Q. rubra were noted among the three summer collections, the data were pooled (Table 6). The leaves were fully expanded and mature during the time when the three collections were made, which may account for the absence of any seasonal pattern. The data of Ostman and Weaver (1982) also showed no seasonal changes during August and September. Average late summer concentration values for Q. prinus leaves from a midslope stand were 1.7% for N, 0.16% for P, 1.1% for K, and 0.9% for Ca (Ostman and Weaver 1982). These values correspond quite well with the data in Table 6 for the midslope stand CR3.

The effect of topographic position is evident in the foliar concentration values (Table 6). For Q. prinus, all elements except magnesium were significantly greater in the footslope stand (CR5) than in the midslope stand (CR3). For Q. rubra, only nitrogen and calcium were significantly greater in the footslope stands (CR5 and SB3). The differences in the foliar tissue concentrations between the two positions reflects the soil substrate differences (Table 4 and 5). Welbourn et al. (1981) also showed increased nitrogen and calcium concentrations in the foliage at lower slope positions.

A comparison of the concentration values in senescent leaves to those in green, late summer leaves will give an estimate of retranslocation. This approach is open to two criticisms that act to over estimate retranslocation--1) leaching of elements from senescent leaves, and 2) not accounting for mass changes per unit of leaf area. Ostman and Weaver (1982) reported that the effect of leaching in Q. prinus was<5% for nitrogen, phosphorus, and calcium; for potassium the value was 10%. Nevertheless, we calculated an estimate for retranslocation as the difference in concentration values between pre- and post-senescent leaves. No differences were noted among the stands and thus by landscape position for either species. Our estimates for retranslocation, averaged across the different stands, were 59, 67, and 43% for N, P, and K, respectively, for Q. rubra, and 65, 68, and 67% for N, P, and K, respectively, for Q. prinus. Calcium, an immobile element, showed an enrichment of 1.43 and 1.48% for Q. rubra and Q. prinus, respectively. Our values for retranslocation correspond in magnitude to those reported by Ostman and Weaver (1982)--79% for N, 55% for P, and 63% for K--who suggested that retranslocation is an important mechanism for conserving elements in nutrient poor sites, i.e., midslope stands.

The absence of a trend for greater retranslocation in midslope position may be an artifact of the limited number of samples, or, if real, a consequence of the long standing genetic characteristics of the species overriding the recent increase in the chemical status of the footslope stand.

CONCLUSIONS

The observed patterns in the mineral soil and foliar tissue chemistry were related to the redistribution and accumulation of surface litter. The data for Sunset Beach represent the extreme case, and, as such, are useful to illustrate clearly these patterns. For Clay Run, the chemical data also showed clearly the midslope-footslope trends on the southwest-facing slope but the relationship to the ridge crest was confounded. Data for the northeast-facing slope are lacking and further investigation is needed. On the whole, the chemical data from the Clay Run site probably will be more characteristic of the landscape.

Table 6.--Chemical characteristics of foliar tissue before senescence.

Species	Stand	Mean Concentration (% on dry mass basis)[1/]				
		N	P	Ca	Mg	K
Q. rubra	CR3	2.03a	0.112a	0.63a	0.128a	1.62a
	CR5	2.55b	0.120a	0.77b	0.118a	1.39b
Q. rubra	SB2	1.82a	0.147a	0.79a	0.182a	1.36a
	SB3	2.05b	0.131a	1.23b	0.179a	1.27a
Q. prinus	CR3	1.98a	0.132a	0.82a	0.128a	1.39a
	CR5	2.31b	0.190b	0.89b	0.143a	1.58b

[1/] For each pair of values, statistically similar means (n=9) have the same letter.

Several ecological implications arise, however, from the observed patterns. First, as inappropriate as it is to calculate a model for detritus dynamics on the basis of litter deposition and litter decomposition alone, so is it also inappropriate to calculate similar estimates for elemental turnover rates. The cycling of elements is complicated by the downslope movement of leaves which acts to transport elements as well, especially those bound in the structural component of the leaf. For example, a large portion of the elements mineralized in a footslope stand originated from the midslope. In the midslope stand, a continual net loss of elements would occur and potentially lead to a condition of generally diminished nutrient status.

Second, input-output budgets for a watershed may also be affected. In footslope and toeslope stands, nitrogen mineralization may exceed total immobilization because the import of nitrogen is greater than the relatively high, but limited, uptake. As such, even aggrading stands adjacent to streams

might be net exporters of nitrogen, whereas in all other landscape positions the reverse would occur and nitrogen would be conserved in incrementing biomass. Thus the elemental budget for an entire watershed could be significantly influenced by the functional processes occurring in stands adjacent to streams.

Third, as a result of the differences in the chemical status among stands, key variables, including species composition and productivity, would shift. Different combinations of species occur across the ridge-slope-valley landform. Midslope stands on southwest-facing slopes generally have the lowest site index whereas in the footslope the index is much higher. The relative importance of the chemical status to account for these patterns will be hard, if at all possible, to separate from the importance of microclimate and hydrology.

Fourth, from a historical perspective the Clay Run site has been disturbed by open-pit iron mines, logging (last clearcut occurred in 1938), and fires. The observed patterns have developed within 40 years, regardless of the previous perturbations. If we assume that a steady-state exists, then within watersheds in mountainous terrain, spatial heterogeneity rather than homogeneity across short distances on the landscape will be a more appropriate model of ecological structure and function both within and among stands. Thus understanding that heterogeneity becomes paramount to making any management decisions.

LITERATURE CITED

Aber, J.D. and J.M. Melillo. 1980. Litter decomposition: measuring relative contributions of organic matter and nitrogen to forest soils. Canadian Journal of Botany 58:416-421.

Black, C.H. 1965. Methods of soil analysis. American Society of Agronomy. Madison, Wisconsin.

Bray, J.R. and E. Gorham. 1964. Litter production in forests of the world. Advances in Ecological Research 2:101-157.

Bush, G.S., C. Lenk, and J. Smith. 1980. The natural forests of Maryland: an explanation of the vegetation map of Maryland. Ecological Monographs 50:77-92.

Cole, D.W. and M. Rapp. 1980. Elemental cycling in forest ecosystems. In: D.E. Reichle, editor. Dynamic properties of forest ecosystems. Cambridge University Press, Cambridge, England.

Dalrymple, J.B., R.J. Blong, and A.J. Conacher. 1968. An hypothetical nine-unit landsurface model. Zeitschr. fur Geomorph. 12:60-76.

Dwyer, L.M. and G. Merriam. 1981. Influence of topographic heterogeneity on deciduous litter decomposition. Oikos 37:228-237.

Fenneman, N.M. 1938. Physiography of eastern United States. McGraw-Hill, New York.

Finney, H.R., N. Holowaychuk, and M.R. Heddleson. 1962. The influence of microclimate on the morphology of certain soils of the Allegheny Plateau of Ohio. Soil Science Society of America Proceedings 26:287-292.

Frank, P.S. 1981. Forest biomass predicted by soil-site factors. Dissertation. West Virginia University, Morgantown, West Virginia.

Franzmeier, D.P., E.J. Pedersen, T.J. Longwell, J.G. Byrne, and C.K. Losche. 1969. Properties of some soils in the Cumberland Plateau as related to slope aspect and position. Soil Science Society of America Proceedings 33:755-761.

Gosz, J.R., G.E. Likens, and F.H. Bormann. 1976. Organic matter and nutrient dynamics of the forest and forest floor in the Hubbard Brook Forest. Oecologia 22:305-320.

Hennen, R.V. and D.B. Reger. 1913. West Virginia Geological Survey. County Reports. Marion, Monongalia and Taylor Counties. Wheeling News Lithological Company, Wheeling, West Virginia.

Lang, G.E. 1974. Litter dynamics in a mixed oak forest on the New Jersey Piedmont. Bulletin of the Torrey Botanical Club 101:277-286.

Likens, G.E. and F.H. Bormann. 1970. Chemical analyses of plant tissues from the Hubbard Brook ecosystem in New Hampshire. Yale University School of Forestry Bulletin No.79.

Lutz, H.J. and R.F. Chandler, Jr. 1946. Forest soils. MacMillan Publishing Company, Incorporated, New York.

Meentemeyer, V. 1978. Macroclimate and lignin control of decomposition rates. Ecology 59:465-472.

Melillo, J.M., J.D. Aber, and J.F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621-626.

Olson, J.S. 1963. Energy storage and the balance of production and decomposers in ecological systems. Ecology 44:322-331.

Orndorff, K.A. and G.E. Lang. 1981. Leaf litter redistribution in a West Virginia hardwood forest. Journal of Ecology 69:225-235.

Ostman, N.L. and G.T. Weaver. 1982. Autumnal nutrient transfers by retranslocation, leaching, and litter fall in a chestnut oak forest in southern Illinois. Canadian Journal of Forest Research 12:40-51.

Phillipson, J., R.J. Putnam, J. Steel, and S.R.J. Woodell. 1975. Litter input, litter decomposition and the evolution of carbon dioxide in a beech woodland--Wytham Woods, Oxford. Oecologia 20:203-217.

Schlesinger, W.H. 1977. Carbon balance in terrestrial detritus. Annual Review of Ecology and Systematics 8:51-82.

Sokal, R.R. and F.J. Rohlf. 1969. Biometry. Freeman and Company, San Francisco, California.

Stone, D.M. 1977. Leaf dispersal in a pole-size maple stand. Canadian Journal of Forest Research 7:189-192.

Strausbaugh, P.D. and E.L. Core. 1977. Flora of West Virginia. Second Edition. West Virginia University Bulletin, Morgantown, West Virginia.

van den Driessche, R. 1974. Prediction of mineral nutrient status of trees by foliar analysis. Botanical Review 40:347-394.

Welbourn, M.L., E.L. Stone, and J.P. Lassoie. 1981. Distribution of net litter inputs with respect to slope position and wind direction. Forest Science 27:651-659.

Witkamp, M. and J.S. Olson. 1963. Breakdown of confined and non-confined oak litter. Oikos 14:138-147.

Wolfe, J.N., R.J. Wareham, and H.T. Scofield. 1949. Microclimates and macroclimate of Neotoma, a small valley in Ohio. Ohio Biological Survey Bulletin No. 41.

Wright, E.L., C.H. Delp, K. Sponaugle, C. Cole, J.T. Ammons, J. Gorman, and F.D. Childs. 1982. Soil survey of Marion and Monongalia Counties, West Virginia. United States Department of Agriculture. Soil Conservation Service.

Zinke, P.J. 1962. The pattern of influence of individual forest trees on soil properties. Ecology 43:130-133.