About 95% of the annual net primary production of mature Coweeta forests is directly transferred to the detrital food web as foliar litter and woody debris. The decomposition of these plant substrates and the release of elements contained within the litter are necessary for the continued productivity of the forests. Most of the chemical energy released during decomposition is processed by bacteria and fungi; however, interactions with a host of invertebrates (primarily protozoans, nematodes, annelids, and arthropods) are responsible for the patterns of nutrient immobilization and mineralization observed in litter and soil.

Three sites in North America have extensive data sets on soil invertebrates and their effects on decomposition and mineralization processes. These sites include the Jornada desert studied by Whitford and his colleagues (Santos and Whitford 1981; Steinberger et al. 1984), the shortgrass prairie ecosystem studied by Coleman and his associates at Colorado State University (Anderson et al. 1981; Coleman et al. 1983; Ingham et al. 1985), and the Southeastern deciduous forests of Coweeta studied by Crossley and his students (Crossley 1977a,b). The Coweeta site has focused almost entirely on arthropods, in part because of investigator interests, but also because the arthropod fauna at Coweeta is particularly diverse and abundant (Gist and Crossley 1975a,b; Cornaby et al. 1975; Reynolds 1976; Abbott et al. 1980; Seastedt and Crossley 1981) (see Table 17.1). The relatively low pH of the weathered soils has favored arthropods over fauna such as earthworms that require a higher soil pH. The moderate levels of acid precipitation presently occurring at Coweeta dictate an even larger role for certain arthropod species in the future (Hagvar and Kjondal 1981).
Table 17.1. Soil Macrornvertebrate Numbers and Biomass in the Forest Floor of a Defoliated Hardwood Forest (WS 27) and an Undisturbed Forest (WS 7)\textsuperscript{a}

<table>
<thead>
<tr>
<th>Arthropod Taxa</th>
<th>WS 27 (n = 171)</th>
<th>WS 7 (n = 211)</th>
<th>F Value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean Number</td>
<td>Biomass</td>
<td>Mean Number</td>
</tr>
<tr>
<td></td>
<td>per m(^2)</td>
<td>(mg×m(^{-2}))</td>
<td>per m(^2)</td>
</tr>
<tr>
<td>Isopoda</td>
<td>0.1</td>
<td>0.1</td>
<td>0.5</td>
</tr>
<tr>
<td>Chilopoda</td>
<td>25.6</td>
<td>105.5</td>
<td>12.9</td>
</tr>
<tr>
<td>Diplopoda</td>
<td>31.6</td>
<td>92.8</td>
<td>10.0</td>
</tr>
<tr>
<td>Araneida</td>
<td>11.2</td>
<td>15.3</td>
<td>13.6</td>
</tr>
<tr>
<td>Orthoptera</td>
<td>0.4</td>
<td>3.6</td>
<td>0.5</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>0.6</td>
<td>12.5</td>
<td>0.5</td>
</tr>
<tr>
<td>Total macroarthropods\textsuperscript{b}</td>
<td>70.4</td>
<td>230.8</td>
<td>45.0</td>
</tr>
<tr>
<td>Mollusca</td>
<td>7.2</td>
<td>278.9</td>
<td>13.4</td>
</tr>
<tr>
<td>Annelids</td>
<td>3.6</td>
<td>10.6</td>
<td>0.6</td>
</tr>
<tr>
<td>Total invertebrates\textsuperscript{b}</td>
<td>81.2</td>
<td>520.5</td>
<td>60.0</td>
</tr>
</tbody>
</table>

\(F\) values based on tests of log-transformed values.

\(\text{**}p < 0.05, \text{***}p < 0.01, \text{****}p < 0.001, \text{*****}p < 0.0001\)

\(\text{WS 7 was subsequently clearcut. Results presented here were obtained prior to logging.}\)

\(\text{bIncludes taxa not listed separately.}\)

The studies of Gist (1972), Cornaby (1973), and Cromack (1973) at Coweeta provided some of the first empirical evidence supporting the hypothesis that arthropods have large effects on nutrient cycling processes; far larger impacts than are apparent by measurements of the arthropods' contribution to community respiration. Their work preceded the large number of consumer papers that began to appear in the mid 1970s and that have remained abundant in the literature. Their work also provided the conceptual framework for many of the studies that followed at the site. In this chapter we attempt to summarize the important findings of the Coweeta research by reporting on soil arthropod abundance and response to substrate quantity, substrate quality, and perturbations. We then discuss how arthropods influence litter chemistry and decay rates. These different subjects demonstrate the interdependence between the biotic and abiotic components of the forest floor, and show that arthropods are both regulated by and regulators of forest floor nutrients and organic matter.

The Effects of Substrate Quantity, Quality, and Perturbations on the Arthropod Community

Global patterns of arthropod densities and composition in relation to substrate quantity have been addressed by Harding and Studdard (1974) and Swift et al. (1979). The general pattern is one of macroarthropods such as millipedes diminishing in importance and abundance as one goes from the tropics to the poles. Conversely, microarthropods such as mites and collembolans tend to be much more numerous in northerly environments. Macroarthropods are believed to be more important in the direct breakdown of
litter than are microarthropods (Anderson 1973; Herlihtzius 1983). The response of the macroarthropod group to disturbances affecting amounts of litter is therefore likely to be larger than the response of the microarthropods. Conversely, microarthropods are believed to be much more sensitive than are macroarthropods to changes in litter quality via their interactions with microorganisms. Thus, microarthropod densities should fluctuate greatly with substrate quality changes, but macroarthropod biomass should be inversely correlated with litter standing crops. Here, we examine the relationship between arthropod standing crops and detritus variables measured within several Coveeta watersheds.

In the early 1970s an outbreak of a defoliator, the fall cankerworm (Alsophila pometaria), was discovered on one of the Coveeta watersheds. Several ecosystem processes were subsequently measured for this and a reference watershed. Among the variables were litterfall, litter standing crops, and macroarthropod densities and biomass along several transects within several distinct plant community types. Comparisons between the defoliated watershed (WS 27) and the reference hardwood watershed (WS 7) yielded a number of differences (Table 17.1). Annelid and centipede numbers and biomass were greater on WS 27, while isopteran, spider, and orthopteran numbers and biomass were greater on WS 7. Millipede biomass was greater on WS 7, as was total arthropod biomass. Narceus annularis, a large spiribolid millipede, was abundant on portions of WS 7 but was not found on WS 27. When Narceus was excluded from the analysis, no differences were observed between watersheds for either millipede or total arthropod biomass. Of course, only site differences are indicated by these statistics; treatment differences cannot be statistically evaluated (Hurlburt 1984).

We examined the relationship between invertebrate biomass to litter standing crops using the three transects on WS 27 and the four plant community types on WS 7 (Table 17.2). The mesic oak–hickory area on WS 7 had significantly more macroinvertebrate biomass than did all other areas. The pine-hardwood and xeric oak–hickory associations had less macroinvertebrate biomass than the two mesic strata on WS 7, but did not differ from the biomass estimated for the transects on WS 27. The ratio of standing crops of invertebrate biomass to litter standing crop varied almost five fold, with WS 27 values intermediate among those observed for WS 7. Macroinvertebrate biomass appeared inversely proportional to litter standing crops on WS 7, but not on WS 27. Overall, there was a nonsignificant negative relationship between macroinvertebrate biomass and litter standing crops ($r = -0.44$).

Partial defoliation by the cankerworms on WS 27 resulted in many measurable changes in nutrient export and internal elemental dynamics (Swank et al. 1981). The arthropod response, based on comparisons with WS 7, remains difficult to interpret. Differences in macroarthropod densities between WS 27 and WS 7 were observed, but these could not necessarily be attributed to the defoliation. An examination of within-watershed differences on WS 7 does, however, allow for some generalizations. Based on litterfall and litter standing crop data (Table 17.2), WS 7 can be divided into two areas: A productive zone with relatively high litterfall and low litter standing crops (the cove hardwood and mesic oak–hickory associations), and a low productive zone with low litterfall and high litter standing crops (the pine-hardwood and xeric oak–hickory associations). The productive zone had high standing crops of invertebrates, while the
### Table 17.2. Estimates of Litter, Litterfall in 1974, and Soil Invertebrates in Summer 1975 on Defoliated and Control Watersheds.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Defoliated (WS 27)</th>
<th>Control (WS 7)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Lower</td>
<td>Middle</td>
</tr>
<tr>
<td>Litterfall (g m⁻²)</td>
<td>424.2</td>
<td>360.9</td>
</tr>
<tr>
<td>(sample size)</td>
<td>(4)</td>
<td>(4)</td>
</tr>
<tr>
<td>Litter standing crop (g m⁻²)</td>
<td>686.4 AB</td>
<td>680.4 AB</td>
</tr>
<tr>
<td>Total arthropods (mg m⁻²)</td>
<td>273.4 BC</td>
<td>230.1 C</td>
</tr>
<tr>
<td>Total macroinvertebrates</td>
<td>533.8 BC</td>
<td>607.9 BC</td>
</tr>
<tr>
<td>Ratio of macroinvertebrates biomass to litter standing crop (× 10⁻⁴)</td>
<td>0.69</td>
<td>0.89</td>
</tr>
<tr>
<td>Litterfall/litter standing crop</td>
<td>0.62</td>
<td>0.53</td>
</tr>
</tbody>
</table>

Means followed by different letters are significantly different at \( p < 0.05 \) (Duncan's Multiple Range Test).
unproductive area had lower standing crops (Table 17.2). This correlation between forest productivity, low standing crops of litter, and large standing crops of forest macroarthropods is similar to relationships observed in European forests (e.g. Wallwork 1976; Swift et al. 1979). The absence of such a relationship on WS 27 probably resulted from the disturbance of defoliation. A time lag likely occurred between increased litter inputs and the subsequent increase in the detritivore standing crop (Seastedt, unpubl. data); thus, equilibrium conditions implicit to the relationship observed on WS 7 were not present on WS 27.

Microarthropod densities range from about $1.25 - 2.25 \times 10^5$ individuals per m$^2$ in the top 5 cm of litter and soil at Coweeta (Gist and Crossley 1975a; Crossley 1977b; Seastedt and Crossley 1981). A high percentage of microarthropods are fungivores, and these organisms are thought to have only a small direct effect on litter comminution (e.g. Anderson 1973; Swift et al. 1979). Microarthropod densities are not always positively correlated with litter decomposition rates (Seastedt 1979). Nonetheless, their contributions to decomposition and mineralization are usually measurable and often substantial (Crossley 1977a; Seastedt 1984). At Coweeta as in other ecosystems, densities appear roughly correlated with substrate quality, and, we believe, microbial activity (Seastedt and Crossley 1981; Abbott and Crossley 1982). Densities of microarthropods at Coweeta have been increased either by adding additional substrate (Webb 1976) or by enriching litter by adding artificial canopy leachates (Seastedt and Crossley 1983). The highest naturally occurring densities of microarthropods that we have observed on 1-year-old foliar litter (in litterbag studies) were about 100 individuals per gram (Seastedt et al. 1983). However, by fertilizing this litter with an N, P, K, Ca, Mg mixture we significantly increased densities to over 160 individuals per gram of litter (Seastedt and Crossley 1983). In spite of this increase in microarthropod densities, we did not observe a significant increase in the decomposition rate of the fertilized litter over that of the unfertilized controls.

The Effects of Microarthropods on Substrate Chemistry

The first microarthropod exclusion study to be conducted at Coweeta was reported by Cromack (1973). His results, along with subsequent findings, indicated that the presence of microarthropods always increases the nitrogen content of the litter (Figure 17.1). There is little doubt that this result occurs from microarthropod stimulation of microbial respiration (Hanlon and Anderson 1979. Either the microorganisms themselves or their waste products (which are assumed to be intimately mixed with the decaying litter) contain the nitrogen. These findings need to be evaluated in respect to the reports of Aber and Mellilo (1980) and Mellilo et al (1982) that initial substrate quality (either nitrogen, lignin or nitrogen:lignin ratios) predict subsequent changes in the nitrogen and mass of the litter. Aber and Mellilo (1980) reported an inverse linear relationship between litter decay and the initial nitrogen content of the litter, with an average correlation coefficient of $-0.93$ based on the analysis of 30 data sets. A graphical analysis of Cromack's data (see Mellilo et al. 1982) indicates a modest lack of fit to their linear models. High nitrogen-low lignin substrates such as dogwood foliage decayed too rapidly relative to other litter types. Indeed, it is difficult to understand
why initial lignin or nitrogen concentrations should be such a strong predictor of amounts of litter remaining after one year in the field. If decay is evaluated as a function of biotic activity, perhaps most simply expressed by the use of a correlate such as evapotranspiration (Meentemeyer 1978), then an explanation for the increased variability and lack of fit of the Coweeta data is apparent (Figure 17.2). Decay in a single year is much more rapid, and substrate quality much more altered, in the warmer and wetter environment of the Southeast. Microhabitat and microenvironmental influences on decomposition tend to be cumulative (Seastedt et al. 1983). Thus, initial substrate quality is of lesser importance to decay rates during the second half of the year in the Southeast than it is in the Northeast. Faunal effects are not shown in Figure 17.2, but they are implicit. Furthermore, the seasonality of temperature and moisture regimes may influence decay rates (e.g., Seastedt et al. 1983). Differences in nitrogen content of substrates with or without fauna may be large or small, but this faunal effect also contributes a source of variation that diminishes the usefulness of using initial substrate characteristics as predictors of decomposition and mineralization rates. Of course, if initial substrate quality was correlated with subsequent microbial and microarthropod activity, a strong relationship would be expected. Meentemeyer (1978) combined initial lignin content of litter with actual evapotranspiration values to predict decomposition rates. However, this relationship remains useful only if the actual evapotranspiration values are correlated with biotic activity (Whitford et al. 1981). If the biota circumvent temperature or moisture constraints, then actual evapotranspiration measurements lose much of their usefulness as predictors of litter decay rates.

We have continued to analyze the influence of microarthropods on the concentrations of nitrogen and other elements in foliar litter. Feeding activities of microarthropods appear to consistently increase the concentrations of most elements (Table 17.3).
Concentrations of elements increase if the absolute amounts of the measured elements remain constant in litter while the absolute amounts of carbon, hydrogen, and oxygen of the substrate diminish. Concentrations may also increase by inputs of elements in canopy leachates or by the recruitment of nutrients from the soil by fungal hyphae. Previously (e.g., Seastedt and Crossley 1980, 1983), we argued that the increased nutrient concentrations observed in litter with fauna are a consequence of stimulation of microbial respiration by fauna. In the absence of leaching of the litter substrate, an increase in the concentration of all mineral elements is predicted. With leaching, however, only those elements concentrated or immobilized by the microorganisms should remain within the litter-microbial system. This interaction between fauna, microorganisms, and microclimatic conditions was established by Witkamp and his colleagues (e.g., Patten and Witkamp 1967; Witkamp 1969; Witkamp and Frank 1970), but the consequences of these interactions for biogeochemical cycles remains somewhat controversial (Seastedt 1984). All else being equal, enhanced nutrient concentrations in litter indicates that elements are being immobilized, and this result has been observed in field studies (e.g., Seastedt and Crossley 1980). Effects of fauna on
Table 17.3. Concentrations of Nutrients in Decaying Dogwood (*Cornus florida*) Litter

<table>
<thead>
<tr>
<th>Element</th>
<th>Day 0</th>
<th>Day 180</th>
<th>Day 364</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>With Fauna</td>
<td>Without Fauna</td>
<td>With Fauna</td>
</tr>
<tr>
<td>N</td>
<td>1.25</td>
<td>1.61</td>
<td>1.27</td>
</tr>
<tr>
<td>P</td>
<td>0.09</td>
<td>0.11</td>
<td>0.08</td>
</tr>
<tr>
<td>K</td>
<td>0.92</td>
<td>0.71</td>
<td>0.68</td>
</tr>
<tr>
<td>Ca</td>
<td>2.40</td>
<td>2.72</td>
<td>2.74</td>
</tr>
<tr>
<td>Mg</td>
<td>0.29</td>
<td>0.26</td>
<td>0.25</td>
</tr>
</tbody>
</table>

Unpublished data from a study reported by Seastedt and Crossley (1983). Fauna were excluded by application of Naphthalene (100 g m⁻²).

Elemental budgets cannot be assessed on the basis of nutrient concentrations alone. Nonetheless, comparisons of litter nutrient concentrations with and without fauna and with and without throughfall still provide useful insights into biotic processes occurring on the forest floor.

Results shown in Table 17.3 illustrate the effects of throughfall (in this example artificial canopy leachate additions) on litter nutrient concentrations. Occasionally, throughfall additions appear to mask a faunal effect (i.e., K, Mg in Table 17.3), and also show that a portion of the elements in litter originate from throughfall rather than from the litter itself. Also, the effect of fauna on the seasonality of nutrient immobilization and mineralization patterns appears to differ for the different elements. For example, increased N and P concentrations are very evident after 180 days of litter decomposition, while similar effects of fauna on Ca and Mg concentrations are not apparent until later. Such results may indicate a faunal-mediated change in either the successional sequence or composition of the microflora of litter (Parkinson 1980). The effect of microarthropods on enhanced P concentrations in litter appears to diminish later in the year. Such changes generally indicate a pulse of mineralization (e.g., Seastedt and Crossley 1984).

The Effects of Arthropods on Nutrient Cycling

We have conducted a number of studies of microarthropod effects on nutrient dynamics of litter, but have regretfully devoted little time doing similar studies on the effects of macroarthropods. The modeling efforts conducted using Coweeta data all suggest a substantial macroarthropod effect (e.g., Gist and Crossley 1975a; Cornaby et al. 1975; Webb 1976, 1977). More recently, Anderson and Ineson (1983) and J. M. Anderson
(personal communication) have suggested that macroarthropod effects on the nutrient flux of such elements as nitrogen are equal to the entire contribution of the microflora and mesofauna. The subsequent discussion, then, may be regarded as a conservative evaluation of arthropod effects on nutrient budgets.

A generalized nutrient cycling model used by Seastedt and Crossley (1984) (Figure 17.3) illustrates that the arthropods may directly influence elemental cycling by ingestion rates, storage within living tissue, and storage within dead tissues and feces. The works of Gist (1972) and Cornaby (1973) suggested that arthropods function as a modest sink for elements such as calcium. Subsequent work by Seastedt and Tate (1981) and Seastedt et al. (1981) indicated that soil fauna exoskeletons composed a slightly larger elemental sink than that found in living fauna, but that this amount, when elevated on the basis of total system standing crops, remained relatively small. Only a few species of detritivores appeared to specialize on invertebrate carrion and exoskeleton fragments; most of the species appeared to be generalist litter feeders. Exoskeletons of millipedes and oribatid mites represent concentrated calcium sources (e.g., Cromack et al. 1977; Crossley 1977b), and may be fed upon by a number of organisms.

Webb (1976, 1977) studied the effects of feces from a large millipede species on decomposition and cation mineralization processes of litter. His results were similar to those reported by Nicholson et al. (1967b): feces did not decompose faster than the

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**Figure 17.3.** Conceptual model of an ecosystem emphasizing the presence and activities of the forest floor fauna. Direct effects of fauna are represented by the flows of material through the faunal component. A potential nutrient and energy sink is created by feces production. For microarthropods, at least, the dominant effect of the fauna is expressed by stimulation of microbial respiration and mineralization activity.
initial litter substrates, and the addition of feces to the forest floor did not stimulate
decomposition or mineralization processes of other litter. The relatively small surface
area of the fecal pellets, which supported a relatively small microbial population, was
suggested as a reason for these negative results. Webb’s findings appear very different
from those reported by Anderson and Ineson (1983), who demonstrated large increases
in ammonium–nitrogen leaching from litter containing feces of a millipede. The source
of the nitrogen was believed to have originated from heterotrophic bacteria on the feces
themselves. These bacteria produced a pulse of N mineralization in spite of a relatively
high carbon to nitrogen ratio of the substrate. No similar studies have been conducted
using microarthropod feces; however, both Anderson and Ineson (1983) and Petersen
and Luxton (1982) cite studies suggesting lower rates of decomposition of the feces
than that measured for the original litter or microbial substrates.

As previously stated, microarthropods are primarily microbivores and therefore the
dominant effect of microarthropods on nutrient budgets results from direct and indirect
effects of their feeding activities on microflora. Net mineralization is largely decided
by whether microbial immobilization accompanies the increase in microbial respira-
tion that usually results from faunal activities (e.g., Hanlon and Anderson 1979;
Anderson and Ineson 1983). Seastedt (1984) developed a procedure to quantify this
faunal effect, i.e.:

\[
\text{Net faunal effect} = \frac{\text{CONC}_f}{\text{CONC}_w} \times \frac{\text{MASS}_f}{\text{MASS}_w}
\]

where \( \text{CONC}_f \) = concentration of a nutrient in litter containing fauna; \( \text{CONC}_w \) =
concentration of a nutrient in litter without fauna; \( \text{MASS}_f \) = mass remaining of litter
containing fauna; and \( \text{MASS}_w \) = mass remaining of litter without fauna. This proce-
dure combines both the effect of the arthropods on the concentrations of elements
within the detritus and its effect on mass loss. Ironically, fauna may occasionally
increase nutrient concentrations of the litter and decrease the mass of the substrate such
that their effect on net mineralization is negligible. Of course, such substrates that have
been grazed by microarthropods have different chemical constituents (generally higher
nutrient content per unit of mass) than litter without fauna (e.g., Figure 17.1), and can
be expected to subsequently mineralize at a more rapid rate. A summary of the Coweeta
data (Seastedt 1984; Seastedt and Crossley 1984) indicates that the microarthropod
effect on microbial respiration and therefore mass loss usually exceeds the increase in
nutrient concentration in litter by stimulation of microorganisms. Thus, net minerali-
zation is the usual result. However, the patterns observed for all elements are by no means
the same, and, to date, no consistent pattern has been observed for some of the cations.

Conclusions

The Coweeta studies, along with many others conducted elsewhere, suggest that litter
and soil arthropods are directly and indirectly responsible for a 20% to 40% increase
in the cycling rates of most elements. The mechanisms responsible for these increased
mineralization rates remain poorly known. We do not know if the net faunal effect is
due to more efficient processing of nutrients by a continually cropped (hence, younger
and more physiologically active) microflora, or if the response is primarily caused by
a shift in the species composition of the microflora (e.g., Parkinson 1980; Newell 1984a,b). Our current conclusions are drawn from studies of relatively short duration. An untested assumption is made that the faunal effects measured in the short-term studies can be extrapolated using standard exponential decay models. Recently, Mellilo (pers. comm.) suggested that decomposition apparently ceases when the ratio of lignin to lignin plus cellulose approaches a given value. He suggested that physical mixing or some other process that reduces overall lignin content of a substrate must occur. His findings concur with data previously presented by Howard and Howard (1974). Soil fauna may not only speed decomposition, but perform a function that is ultimately responsible for the continued decay and mineralization of plant substrates.

Current research at the ecosystem level has indicated that the ratios of important elements such as C:N:P ratios may result in certain predictable patterns of energy allocation by plants. These patterns have subsequent consequences to consumers. Herbivores appear to both respond to plant C/N ratios (Mattson 1980), and also cause changes that influence other consumers (e.g., Hutchinson and King 1980; Smolik and Dodd 1983). A similar process also occurs within the detrital food web. Feeding activities of soil fauna produce measurable changes in the chemical content of the detritus (e.g., Table 17.3), and this chemically modified material influences the subsequent activities of detritivores and microbivores. At any given time, a system or subsystem such as the forest floor may therefore be represented by a nutrient and energy matrix that, free from extrinsic perturbation, will interact with the microclimate and generate a subsequent matrix. The soil arthropod fauna at Coweeta clearly represents a major factor in the regulation of this nutrient and energy reservoir. Continued studies of soil invertebrates at Coweeta will undoubtedly contribute to our knowledge of these emerging patterns.