

Microflora Activities and Decomposition

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INTRODUCTION

Decomposition results in the disintegration and mineralization of organic residues. Most physical and chemical changes that occur in and around the decomposing substrate cannot be separated from the effects of microbial activity. However, degradation of plant and animal remains may be well advanced before significant ingress of microbes occurs (Dowding 1974, Flanagan and Veum 1974). Losses of weight and specific chemical constituents, which are often considered as measures of decomposition, may be initiated by plant-soil environment interactions that induce senescence and autolysis in moribund tissue. Important ecological phenomena that cause loss of weight from organic residues but occur somewhat independently of microbial activity include leaching, microfaunal activities, and chemical reactions that influence mineralization.

Soil invertebrates and protozoans are considered to influence decomposition rates indirectly by modifying the activities of the decomposer organisms or microbes. They modify the environment through comminution of organic matter, and the microbial populations by grazing upon them (Chapter 11). Plant components like soil algae and the roots of vascular plants alter the environment through the provision of particular substrates and physical structure, and by modification of pH and supply rates for oxygen and other chemical compounds.

Decomposition of organic matter is accompanied by synthesis of microbial tissues which themselves decompose, contributing to further microbial production. If the amount of substrate is limited, the potential for production of microbial biomass is dependent upon the efficiency of the microbial population in solubilizing, assimilating and incorporating organic remains, i.e. the efficiency of conversion of grams substrate to grams microbe, or the yield coefficient. The yield coefficient is influenced by climatic and substrate variables and is decreased significantly by the maintenance demands of preformed and forming tissues (Gray

and Williams 1971). These aspects of microbial activities are best related to inputs from primary production.

Under aerobic conditions, microbes decomposing a substrate break down complex organic molecules to end-products that are primarily inorganic (carbon dioxide, water and minerals); under anaerobic conditions the end-products assume a variety of organic and inorganic forms. The breaking down is accompanied by a loss in weight and energy content of the substrate as well as disintegration of its physical structure. An observer of the decomposition phenomenon thus witnesses physical and chemical as well as biological changes. Measures of decomposition incorporate varying features of these changes, and no one measure quantifies decomposition perfectly. Belowground events are especially difficult to decipher because of the simultaneous respiration of heterotrophic and autotrophic organisms and the complex geometry of hundreds of substrates and microorganisms showing vastly different responses. Soils of the coastal tundra at Barrow are frozen for a large part of the year and this further complicates examination of biological processes within them.

Given the complex of physical, chemical and biological processes comprised in decomposition, diverse methods have been employed to relate the findings of individual, specialized techniques to general concepts. The concepts of decomposition used recognize that different microbes have different enzymatic potentials or capacities to utilize various chemical constituents of naturally occurring substrates. Not only do microbes have different capacities to exploit substrates, but their enzymatic potential, growth and respiration rates also respond differently to the temperature, moisture, oxygen and pH in their environment. Thus the capacity to decompose inherent in a particular microbial population is at any time modified by the environment.

Acknowledging this conceptual framework, our studies of decomposition have examined the physiological potentials of different microfloral constituents to utilize particular chemical compounds as substrates; the response of these potentials to environmental conditions; the biomass, biomass yield per gram of substrate, and maintenance demands of major microbial species; the response of rates of respiration and growth to changes in important environmental variables such as temperature, moisture, oxygen and dissolved nutrients; and the resultant loss rates of particular chemical constituents, carbon, calories and net weight. Measures of ability to utilize particular chemical compounds are *in vitro* assessments of an organism's ability to exploit selected natural substrates. Responses of respiration and growth to selected environmental variables and measures of biomass yields and maintenance demands are also evaluated, primarily by laboratory techniques, particularly Gilson respirometry. Laboratory measures are related to field observations by simulation models (Flanagan and Bunnell 1976, Bunnell

et al. 1977a, b). Field measures of decomposition and decomposition-related phenomena are primarily measures of rates of loss of specific substrate components. Four field measures have been employed.

Weight losses from litter bags measure the rate at which litter becomes sufficiently disintegrated that it disappears from the litter bag. A portion of this loss is due to microbial activity but some weight is lost by leaching and physical comminution by invertebrates and by the freeze-thaw cycle. Ingress of microbial, plant, animal and mineral matter can confound estimates of weight loss.

Chemical analyses of substrate composition coupled with measured weight loss estimate the rate of disappearance of major chemical compounds such as cellulose or phosphorus. These measures are also an inaccurate estimate of microbial activity. Not only are other processes also acting (e.g. leaching) but the microbial populations and their chemical composition are inseparable from the substrates.

Measurements of rates of evolution of carbon dioxide represent the rate of mineralization of complex organic compounds to carbon dioxide, water and residual constituents such as minerals, and are perhaps the best measure of aerobic microbial activity. Depending on the substrate measured and the method used, various inaccuracies are introduced, either by the effects of methodology, as with the physical disturbance in Gilson respirometry, or by inclusion of carbon dioxide evolved from plant roots and soil invertebrates. Anaerobic decomposition processes are incompletely measured by carbon dioxide evolution and may present an important omission in some habitats.

Measurements of microbial biomass during decomposition of above- and belowground substrates permit one to relate the abundance of major decomposer agents to substrate availability and quality. These measures, coupled with laboratory data on microbial growth and yield from varying substrates and information indicating microbial maintenance demands, allow approximation of the microbial production in the field. Microbial biomass and production may then be compared with similar measures from leaves, roots, microfauna etc. Additionally, studies of microbial biomass permit compensation for underestimates of weight loss caused by growth of microbial tissue in litter bags. By knowing microbial mineral content per gram we can approximate values for mineral immobilization and cycling in microbial biomass and production, respectively.

In the subsequent discussion, both field and laboratory measures are employed to help define patterns of decomposition. Since decomposition is equated with the microbial mineralization of carbon, these measures are to varying degrees inaccurate. No one measure discretely encompasses decomposition as defined, but integrated with a knowledge of microbial biomass, dynamics, and physiology the measures contribute to a

synthetic view of decomposition. Tools of integration include correlative analyses and computer simulation models. Although these tools are in some instances novel and sophisticated, the conceptual framework employed owes much to the seminal work of Douglas and Tedrow (1959) (see Bunnell and Tait 1974).

The approach in the following discussion moves through the conceptual framework as it is presented above, first examining the potential to exploit particular substrates that different microfloral constituents possess. Then we examine the manner in which this potential and other critical activities such as respiration are influenced by environmental variables such as temperature, moisture and oxygen. The discussion in the section on *Decomposer activities and decomposition* utilizes simulation models to combine the responses of microbial respiration to individual environmental variables and compares the predictions with integrative measures such as weight loss. Measures of microbial biomass, yield and efficiency are related to substrate availability and potentials for mineral cycling and immobilization.

POTENTIAL OF THE MICROFLORA TO UTILIZE SUBSTRATES

The decomposition of organic remains proceeds mainly through the action of microorganisms that can use them as a source of energy and nutrients. Most soil microbial populations are heterotrophic and the organisms compete for available substrates. In the coastal tundra at Barrow, microbial saprophytes are more competitive and abundant than are parasites and the present discussion ignores the latter. Not all saprophytic microorganisms utilize and compete for the same substrates. Although an individual microorganism may be encouraged by the presence of a specific substrate that it can use, its potential to exploit that substrate is further modified by environmental conditions and "competitive saprophytic ability" (Garrett 1963). The composition of the microbial population inhabiting a particular substrate and thus the decomposition rate of the substrate are therefore dependent upon the environmental conditions and competitive ability of the microorganisms as well as the measured potential to utilize specific substrates. The data presented here are based almost entirely on *in vitro* measurements. The discussion is biased towards treatment of the mycoflora rather than of the total microbial population.

Major substrates for decomposer organisms at Barrow can be divided into two main categories on the basis of their chemical composition, pattern of dissolution and utilization by microorganisms. These categories are 1) low molecular weight, water- and/or 80%-ethanol-soluble frac-

tions that are readily leachable, and 2) the more recalcitrant compounds, such as lignin, cellulose, hemicellulose, pectin and starch. The first, more soluble group contains approximately 25% of aboveground plant products, exits as leachate from moribund tissues and contains the bulk (> 80%) of plant leaf nitrogen, phosphorus and potassium. The second group represents the bulk of the available organic substrate and is relatively poor in nitrogen, phosphorus and potassium (Flanagan and Veum 1974, Van Cleve 1974). Substrates of the more soluble group are frequently utilized by organisms decomposing the more resistant group.

Microflora in all Biomes display a broad diversity of enzymatic potential to decompose the various organic substrates. Tundra microflora share this capacity, with the restriction that the cold-dominated environment has selected for taxa or strains that utilize these substrates under cooler conditions. The restricted number of taxa may or may not reduce the potential to complete a given phase of decomposition such as conversion of cellulose to carbon dioxide, but it does reduce the number of modes that such a reaction can follow in the ecosystem.

As in many temperate zone habitats, bacteria in tundra are often weak competitors with the fungi for those substrates that both groups have the enzymatic potential to metabolize. The competitive difference is especially obvious in such habitats as standing dead and litter, and in drier surface soils. Conversely, in wet habitats bacteria play a proportionately greater role in decomposition. In extremely wet or anaerobic habitats, such as sediments of tundra ponds or soils at depth, bacteria are the dominant group of decomposers. The potentials to utilize specific forms of nitrogen and phosphorus are addressed in Chapters 7 and 12; here we consider only carbon.

Bacteria

The sources of carbon most commonly exploited by soil bacteria are of intermediate molecular size (Table 9-1). Large molecules such as pectin and cellulose, which form major structural entities of plant cells, can be decomposed by relatively few of the plateable bacteria. *Cytophaga* appears important among the cellulose-decomposing bacteria since it frequently occurs on plate isolations. Enrichment studies of "most probable number" show *Cytophaga* populations varying from 10^5 (gdw soil)⁻¹ after thaw to 10^6 (gdw soil)⁻¹ at mid-season. No cultures of indigenous aerobic bacteria that could decompose humic substances were obtained.

The relative ability to utilize humic substances is one of the major enzymatic differences that separate bacteria from fungi (cf. Table 9-1 and Figure 9-1). Widden (1977) has documented similar differences between bacteria and fungi at Devon Island. Enzymes that cleave the aro-

TABLE 9-1 *Percentage of Bacterial Types at Barrow Capable of Utilizing Specific Carbon Sources*

Carbon source	Bacteria (%)
Succinic acid	92
Citric acid	84
Glucose	78
Maltose	66
Starch	42
Pectin	28
Lactic acid	25
Cellulose	5
Lactose	0
Lignin	0
Tannic acid	0

Note: Based on 200 randomly selected aerobic types isolated from the 0- to 2-cm soil depth in wet meadows and tested at 15 °C.
Source: Benoit (unpubl.).

matic ring of humic materials require the presence of oxygen. Thus, as humic materials move from the surface into the less aerobic subsurface layers of the soils, the probability of their decomposition is markedly reduced. The differential capacities of bacteria and fungi to survive low amounts of oxygen and to exploit humic material are instrumental in the accumulation of organic matter in the soil horizon.

The strictly anaerobic portion of the microflora remains the least known in terms of physiology and in situ activity. Rapid development and intense activity of anaerobes on the soil plots heated to 15 to 20 °C illustrates the potential of this group. Enrichment cultures of strictly anaerobic cellulose-decomposers and methane-producers were obtained from anaerobic soils on these plots. There is no evidence that anaerobic bacteria can degrade humic materials; therefore the activity of the anaerobes becomes limited when the pool of rapidly decomposable material originating from the death of belowground parts is exhausted. Continued decomposition requires the action of other microorganisms and a change of abiotic conditions.

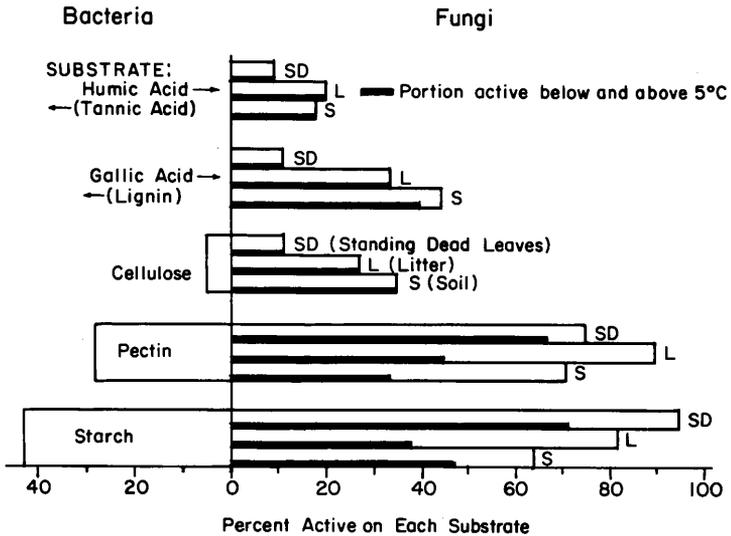


FIGURE 9-1. Percentages of fungi and bacteria capable of exploiting specific organic substrates. Bacterial percentages are based on 200 randomly selected, aerobic types isolated from the 0- to 2-cm soil depth in wet meadows and tested at 15°C. Fungal percentages are based on percent frequency of major species and their ability to utilize specific substrates as sole carbon sources in vitro. (Benoit and Flanagan, unpubl.)

Fungi

The major taxonomic groups of phyllosphere, litter and soil fungi have been discussed (Chapter 8). The ability of these groups to utilize pectin, starch, cellulose and lignin has been tested (Flanagan and Scarborough 1974). Comparison among the mycoflorae of the phyllosphere, litter and soil reveals different enzyme potentials for substrate degradation as integrated over the season (Figure 9-1). Generally, the mycoflorae of litter and soil are better able to degrade the more recalcitrant substrates than is the mycoflora of the phyllosphere. Fungi in standing dead leaves are infrequently cellulolytic (10%), while in litter and soil 27% and 35% respectively are cellulolytic. The pattern is repeated for polyphenol oxidizers, some of which (gallic acid oxidizers) are better represented in litter and soil than are cellulolytic forms. The potential to utilize humic acids also is represented better among litter and soil fungi than among fungi of the phyllosphere. Fungi decomposing pectin and starch make up the greatest portion of the mycoflora, whether from phyllosphere, litter

or soil. The potential for decomposition of pectin is lower in the phyllosphere than in litter while the opposite is true in the case of potential amylase activities. Both the phyllosphere and litter contain more utilizers of pectin and starch than do soils. This pattern is the reverse of the trend in distribution of utilizers of lignocellulose. In summary, a trend of increasing ability to degrade larger molecules is apparent proceeding from the phyllosphere into the soil.

ABIOTIC VARIABLES AND MICROFLORA ACTIVITIES

Despite the low annual input of energy to tundra, the active layer of the soils is rich in carbon (9 to 20 kg m⁻² to 20 cm depth) and contains much energy. The energy contents of wet meadow soils range from 13.8 kJ (gdw soil)⁻¹ in the 0- to 2-cm horizon to 9.6 kJ (gdw soil)⁻¹ at depths of 12 to 18 cm. These resources of carbon and energy could sustain substantial microbial production, provided other environmental conditions were satisfactory. Potentially limiting factors include low temperatures and reduced availability of moisture, oxygen and inorganic nutrients.

Here we treat two themes: 1) potentially adaptive responses to low temperatures, and 2) relationships between measured soil oxygen, associated moisture levels, and activities of microbial groups.

Responses to Temperature

Temperature influences microbial activity in at least three ways. Both growth rates and respiration rates of microorganisms are affected as well as the activities of specific enzymes used to degrade substrates. Cardinal influences of temperature on organisms and their enzymes determine the upper and lower temperature thresholds. The form of the response may differ between cardinal points. We have examined the influence of temperature on tundra microorganisms within the framework of two broad hypotheses:

- 1) Tundra microorganisms gain cold tolerance by extending their range of metabolism towards lower temperatures.
- 2) Tundra microorganisms enhance their effective metabolic range by showing linear rather than exponential responses to low temperature (Bunnell et al. 1977a).

The first hypothesis addresses the depression of the lower cardinal temperature; the second addresses the form of response to changing temperature. Both hypotheses relate to psychrophily. Definitions of psychrophily and mesophily vary (Ingraham 1958, Griffin 1972, Christophersen

1973). Psychrophilic organisms are here defined as having a growth optimum at or below 20°C (Griffin 1972).

Temperature Influences on Microbial Growth and Respiration

Metabolic processes of decomposers are generally adapted to the cold-dominated environment. Respiration within soil and litter is measurable down to -6.5°C and substantial increases in fungal biomass have been measured in soils when temperatures were between 0° and 2°C. Data on growth and respiration of individual bacteria from the Biome research area and other cold-dominated systems (Boyd 1967, Christensen 1974, Mosser et al. 1976) have shown that strict psychrophiles are present, but their incidence is less than 5 to 10% of the total plateable flora.

Most fungi are cold-tolerant mesophiles able to respire heterotrophically to -6.5°C but with optima for growth and respiration between 20° and 30°C (Figure 9-2). Minimum and maximum temperatures at which

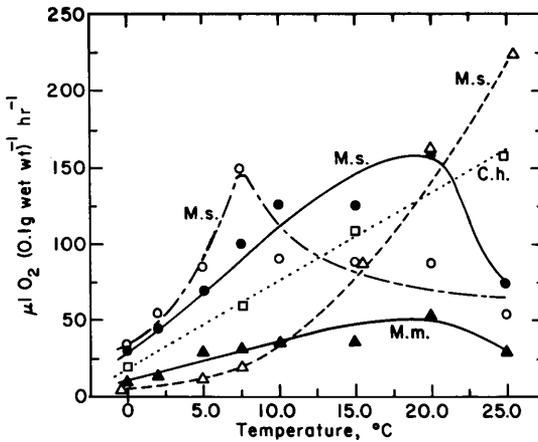


FIGURE 9-2. Influence of temperature on respiration of tundra fungi growing on potato extract in Gilson respirometers (1 m extract: 0.1 g mycelium). M.s. = three different Mycelia sterilia from Barrow tundra soil; C.h. = Cladosporium herbarum; M.m. = Mucor microsporus. Each point is a mean of three samples; six readings per sample. Standard deviations ranged from 5 to 7.5% of mean. (After Flanagan and Scarborough 1974.)

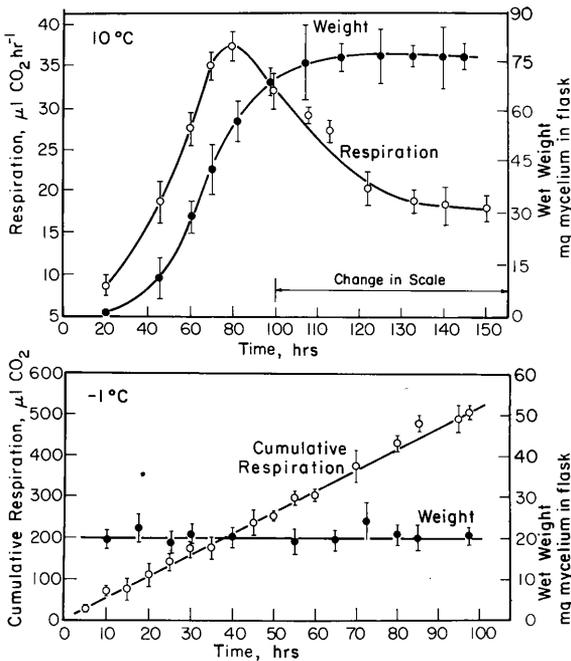


FIGURE 9-3. Respiration and growth (wet weight) of a common tundra soil fungus, *Myceliun steriliun B18*, at 10° and -1°C , growing on a mineral salt medium containing a known amount of glucose. Vertical bars represent the standard errors ($n = 6$). (After Flanagan and Bunnell 1976.)

respiration was measurable using individual fungi were -6.5°C and $+48^\circ\text{C}$. Some psychrophilic fungi were present. Corresponding with the temperature gradient, there is a general increase in psychrophilic fungi from the phyllosphere (5.5%) to the litter (7.5%) and into the soil (15.6% of the mycoflora). Even among psychrophilic forms, however, growth of most organisms was not measurable below -3°C . At 0°C the psychrophiles cultured on potato extract broth did produce measurable growth; average growth rate of four psychrophiles at 0°C was $3.6 \text{ mg g}^{-1} \text{ day}^{-1}$. Fungi from other Alaskan sites, Eagle Summit and Prudhoe Bay, showed similar responses (Flanagan and Scarborough 1974), leading to the conclusion that both bacteria and fungi in tundra are capable of growth and respiration at subzero temperatures. These observations support hypothesis one.

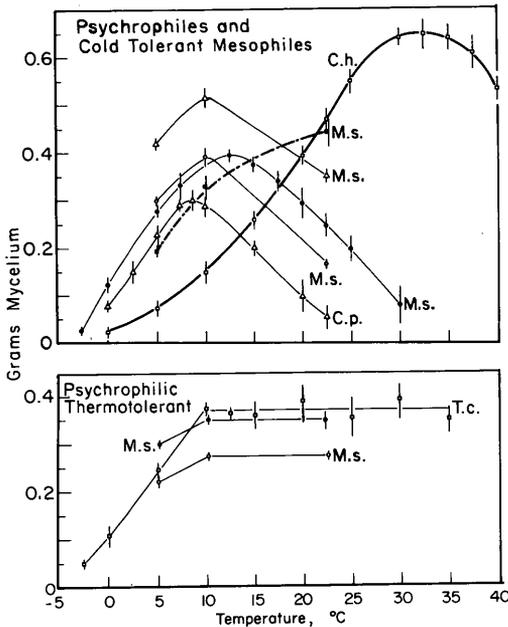


FIGURE 9-4. Fungal growth responses to temperature among several different sterile forms (*M.s.*), *Chyso sporium pannorum* (*C.p.*), *Cladosporium herbarum* (*C.h.*), and *Trichosporiella cerebriformis* (*T.c.*) growing in liquid potato dextrose extract. Vertical bars represent the standard errors ($n = 8$). (Flanagan, unpubl.)

Growth rates of fungi are not always closely coupled with rates of respiration (Figure 9-3), especially in the senescing phase of growth or at low temperatures (-3°C) when growth has ceased but respiration is still measurable. The relationship between respiration and temperature can be either linear or exponential, depending on the isolate. Furthermore, certain fungi, e.g. CC8, may show an exponential relationship between respiration and temperature while the relationship of growth to temperature is linear, or the reverse may be the case as with *Cladosporium herbarum* (cf. Figures 9-2 and 9-4). Therefore no one specific organism or randomly collected group of organisms will emulate completely the response of respiration or growth to temperature found among field populations.

Summing individual rates of respiration (cf. growth) for the major fungal species shows an average Q_{10} (ratio of the rates at 10° and 0°C) of 3.6. The measured Q_{10} for respiration of total litter over the same temperature range is between 3.8 and 4. Temperature fluctuations decrease and temperatures are generally lower with depth. According to the second hypothesis it is expected that with increasing depth microorganisms would show flatter and more linear responses to temperature for their various biological activities. A linear rather than exponential response to

temperature can result in a higher rate of activity near the minimum temperatures (Bunnell et al. 1977a). In support of the second hypothesis it is noted that observed relations between respiration and temperature in soils do not depart statistically from linear, and computed Q_{10} values in the soil are frequently less than 2.0. Q_{10} values for respiration decrease from the surface litter downwards into the soil. Numbers of psychrophiles increase from the phyllosphere to the 10-cm depth in soil, and the majority of psychrophiles and several important cold-tolerant mesophiles have linear responses to increasing temperature (Figures 9-2 and 9-4). Because such organisms have not been recorded for temperate regions it would seem that the second hypothesis is further supported.

Temperature Influences on Substrate Utilization

About 80 to 90% of the tundra bacteria that are cellulolytic at 15 °C are unable to use cellulose as a sole source of carbon at 0 °C. But 82% of these same bacteria use glucose as a sole source of carbon at 0 °C. These observations are similar to those made in Canadian arctic lakes by Christensen (1974), who found 6% of the cellulolytic *Cytophaga* to be psychrophilic. The bacteria capable of decomposing hydrocarbons that were isolated from plots treated with oil at the Biome research area illustrate similar relations with temperature. Bacteria that could use mineral oil as a sole source of carbon at 15 °C could not metabolize the same substrate at 0 °C (Campbell et al. 1973). They could, however, use succinic acid or glutamic acid as sole sources of carbon at 0° and 15 °C.

The limited data suggest that a temperature near 0 °C eliminates specific metabolic pathways of bacteria while other metabolic activities, e.g. respiration, in the same organisms are only depressed. At low temperature bacteria can sustain themselves on substrates which at higher temperature they might ignore in favor of larger molecular compounds. Comparable data are not available for temperate forms of the organisms found at Barrow, but one interpretation of such a switch between substrates is that the tundra organisms are responding to the demands of a colder environment. Such a response broadly conforms to hypothesis one, and suggests that tundra bacteria extend their capabilities at lower temperature by exploiting compounds of lower molecular weight.

The influences of temperature on the potentials for substrate utilization by fungi are greatest for simple substrates (Figure 9-1). Utilization of cellulose and phenolic compounds does not cease below 5 °C and in most cases continues to sub-zero levels, although usually at lower rates. Potentials for fungal utilization of pectin and starch are substantially decreased when the temperature falls below 5 °C but do not cease. Decomposers of hemicelluloses have not been fully examined, but prelimin-

ary data suggest that the fungal potential for hydrolysis of hemicellulose resembles the pattern for utilization of pectin and starch.

The response of the fungi thus contrasts directly with that of bacteria which apparently use less recalcitrant substrates preferentially as temperature decreases. Widden (1977) made similar observations on Devon Island. The byproducts of fungal cellulolysis may serve as substrates for bacteria at temperatures below 5 °C and coevolution of interdependent cold acclimations may result in closer relationships between bacteria and fungi at lower temperatures.

Our second hypothesis relates to the form of response with changing temperature. Different enzymes produced by pure cultures of specific tundra fungi have very different responses to temperature (Figure 9-5). The low temperatures (< 10 °C) commonly encountered may encompass simultaneously the optimal range for utilization of one substrate and the unfavorable range for utilization of another. Flanagan and Scarborough (1974) have shown that some cellulolytic fungi decompose cellulose optimally below 10 °C, while in the same organism optimal amylase and pectinase activity occurs above 30 °C. The pectinase activities of four fungal isolates (Figure 9-5) have temperature optima between 18° and 30 °C, while those for cellulase activities are between 6° and 14 °C.

If such differences in enzyme activity through varying temperature ranges occur *in vivo*, then the optimum temperature range for cellulose decomposition in the field may be wider than for some other enzyme systems, e.g. pectinase and amylase. These observations help explain why pectinolytic and amylolytic fungi are less frequently isolated or active at low temperature than are cellulolytic forms (Figure 9-1).

Literature on fungi from temperate regions often examines temperature as a regulator of fungal respiration, but relationships between temperature and utilization of substrate have received less attention. Thus both hypotheses presented here are not fully testable with regard to utilization of substrate. However, tundra fungi at Barrow do appear to extend their effective metabolic activity over a wide temperature range, by incorporating different temperature optima for utilization of different substrates.

Temperature influences on microbial utilization of substrate, growth and respiration seem to fall into three broad groups (Figures 9-2, 9-3 and 9-4). All three groups have a range of activity that extends below 0 °C, while at the same time the population as a whole has the flexibility to take advantage of mesic and higher temperatures. One group, including several sterile soil fungi together with *Mucor microsporus*, shows very gradual responses of growth and respiration to temperature values in the range from -3° to +20 °C. The second group shows a positive response to increasing temperature up to an optimal point, but thereafter shows no further response to increasing temperature in the range exam-

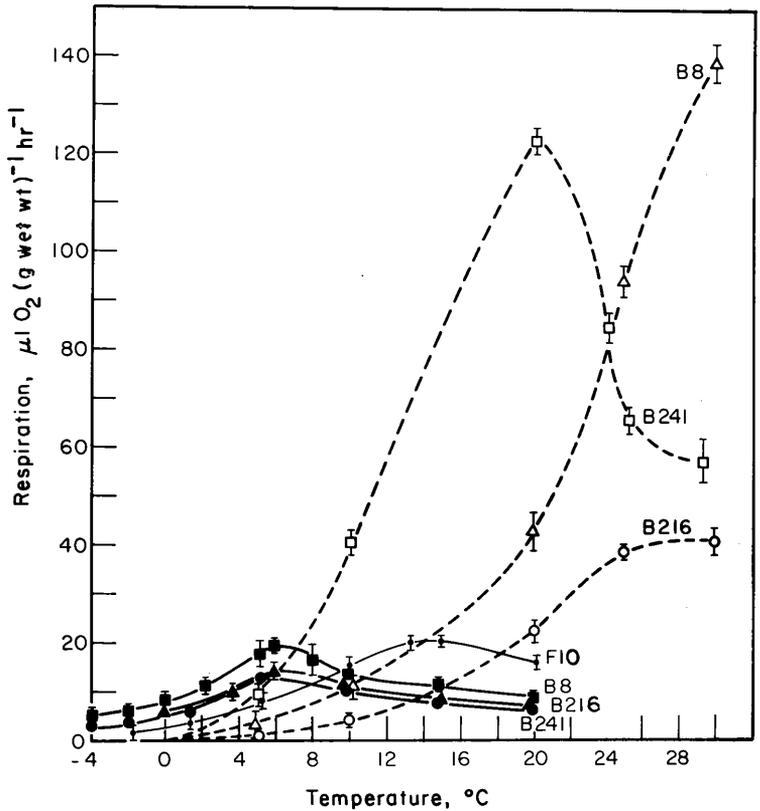


FIGURE 9-5. Influence of temperature and substrates on fungal respiration for *Cylindrocarpon magnusianum* (B8), *Cladosporium cf. cladosporoides* (B216), *Phialophora hoffmannii* (B241) and *Chrysosporium pruinatum* (F10) in Gilson respirometers growing on media with cellulose (—) and pectin (---) as the sole sources of carbon. Substrate moisture content was 250% (dry weight) in all cases. Flasks contained 0.1 g fungus (wet weight). Measures began 48 hours after substrate inoculation. (After Flanagan and Scarborough 1974.)

ined, e.g. *Trichosporiella cerebriformis* and several sterile forms like B1, CC17 and CSS4 (Figure 9-4). Fungi with responses to temperature like that of *T. cerebriformis* are new to the literature in microbial ecology and could be termed “psychrophilic thermotolerant.” Roots of plants such as *Eriophorum angustifolium* show a similar response to temperature for uptake of phosphorus (Chapin 1974a). A third group of soil fungi displays psychrophilism, but demonstrates high exponential increases of

respiration in its minimum–optimum temperature range, e.g. CC8 (Figure 9-2).

Together, the two hypotheses address extension of the lower temperature limits and the form of response with changing temperature. The microflora appears to have extended its capacity to degrade substrates, respire and grow at low temperatures. Respiration continues to -7.5°C , growth is positive at 0°C , and oxidation of cellulose and phenols probably continues well below $+5^{\circ}\text{C}$, possibly to -7.5°C , because psychrophilic and psychrophilic thermotolerant organisms show a propensity for utilizing these substrates at low temperature. Both interspecific differences and individual responses serve to increase the effective metabolic range of the microflora, by broadening the near-optimal metabolic range or form of response with changing temperature. Bacteria appear to increase their effective metabolic range by shifting to compounds of lower molecular weight (6-C compounds) at lower temperature, while fungi continue oxidation of cellulose and phenols. In terms of growth and respiration, evidence from tests of individual soil fungi and the calculation of the percentage of psychrophiles in soil as compared to above ground (7.5% in litter, 15.6% in soil) strongly suggests that soil organisms at Barrow are cold-adapted, while aboveground populations with wider ranges of near-optimal temperature occur. Adaptation to cold rather than acclimation is indicated. Progressing from aboveground to belowground environments, relations between temperature and respiration tend from exponential to linear, suggesting another form of adaptation to cold. Computed values of Q_{10} from soils of the Biome research area are typically lower (closer to linearity) than are values from temperate soils (Macfadyen 1970, de Boois 1974). Neither the first nor the second hypothesis can be rejected.

Responses to Moisture and Oxygen

As with temperature, moisture levels for microbial activity assume minimum and maximum thresholds and optima. These cardinal moisture levels differ between organisms and within a single organism for different processes. While there are some notable exceptions (Pitt and Christian 1968), most microbial activities in soil are limited by moisture potentials below -100 bars. The lower limit for bacteria generally is believed to be higher than that for fungi (Dommergues 1962, Griffin 1972). It is unlikely that soils of the Barrow research area were dry enough to restrict the activities of microorganisms, but in the standing dead canopy decomposition may be limited by lack of moisture. Within the soils, moisture effects are more likely to be indirect and associated with reduced flux of oxygen (Chapter 8).

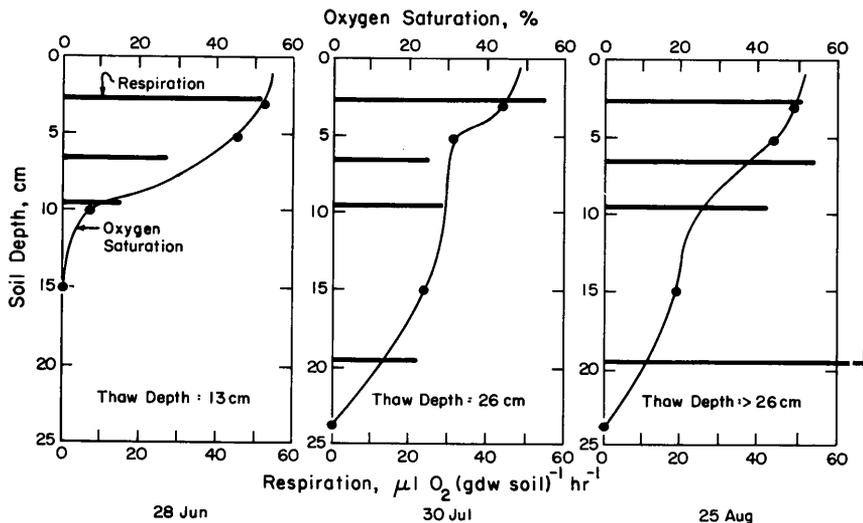


FIGURE 9-6. Depth profiles of soil respiration and oxygen saturation on three days in wet meadows. Oxygen saturation measured by Polarographic analyses; respiration measured by Gilson respirometry. (Based on data from Benoit and Gersper, unpubl.)

Oxygen concentrations are influenced by root metabolism and the associated rhizosphere effect as well as by soil moisture and respiration by decomposers. Because of the intense respiratory activity of the roots and the associated bacteria, the rhizosphere has a high demand for oxygen. Since tundra plants typically have high root-to-shoot ratios there is high demand for oxygen throughout the active layer.

Microaerobic or anaerobic conditions depress the overall activity and eliminate some functions of the soil microflora. Over short periods anaerobic conditions reduce the rate of decomposition because of the buildup of end-products which inhibit microbial activity. In the long term, anaerobic conditions may be the major reason organic matter can accumulate. All natural products except aromatic compounds can be decomposed under anaerobic and aerobic conditions. The aromatic compounds generally cannot be utilized as microbial substrates under anaerobic conditions. Furthermore, the decomposition of large molecular weight compounds is largely the province of the fungi. Therefore, lignicolous and phenolic polymer compounds will be decomposed primarily in the surface soil where oxygen values are higher and the fungal biomass is greatest (Chapter 8). When phenolic compounds reach the lower levels of the soil profile, either by leaching or transfer by microfauna, they enter a zone of changed abiotic conditions where oxygen levels and tem-

peratures are lower. Here they can accumulate and thereby affect the long-term carbon balance of the system. Under anaerobic conditions these aromatic products may change their chemical structure, repolymerize and become highly recalcitrant organic matter.

However, decomposition occurs throughout the active layer (Figure 9-6) and the numbers of facultative and anaerobic bacteria appear sufficient to prevent rapid accumulation of carbon in the wetter microtopographic units. Roots that follow the thaw front down presumably can exploit nutrients mobilized by microbial activity.

Moisture and Microfloral Metabolism

Because of the interaction between moisture and temperature, a general optimal moisture level for microbial respiration in organic residues is indeterminable, but an optimal moisture range is determinable at optimal temperatures (Douglas and Tedrow 1959, Flanagan and Veum 1974). When moisture is less than 20% of the dry weight residues it is not possible to measure respiration at any temperature; thus moisture levels above 20% dry weight seem necessary to initiate microbial metabolism. The metabolic rates continue to increase throughout the moisture range 20 to 500% of dry weight. High moisture levels (> 500% dw) may depress microbial respiration. In a Gilson respirometer the depressant effect can be eliminated by increasing available oxygen (Flanagan and Veum 1974) and is likely associated with reduced rates of supply of oxygen. As temperatures increase, respiration in some substrates shows saturation of metabolic moisture demand at amounts of moisture less than 400% dw. Temperature-moisture interactions, as demonstrated by studies of microbial respiration from plant remains, may reflect differences in oxygen diffusivity in water or changes in microbial oxygen demand as temperature varies.

Oxygen and Microfloral Metabolism

Oxygen is critical in microbial metabolism because it serves as an electron acceptor in the breakdown of organic matter. In the soils at Barrow the potential alternate electron acceptors such as nitrate and sulfate are present in such low concentrations (< 1 ppm) that they can support little activity. Diffusion of oxygen into the soil is often below levels required for optimal microbial activity, and in very wet soils pore spaces become filled with moisture. The effect is decreased microbial activity among the aerobic component; the cause is not too much moisture, but apparently too little oxygen. It is equally plausible that carbon dioxide

operating separately from or in concert with a deficiency of oxygen reduces microfloral metabolism (Burgess 1958, Griffin 1972).

The highest oxygen levels measured within the upper 20 cm of soil were observed in the soils of the basins and rims of low-centered polygons and the tops of high-centered polygons (Figure 7-6). It is surprising to find that on the dates they were sampled the basins of low-centered polygons had high oxygen values throughout the soil profile. Soil thin sections from basins, unlike rims, indicate a structure that should impede drainage and aeration (Everett, pers. comm.). The data for both *in vitro* respirometry and measured evolution of carbon dioxide indicate that basins of low-centered polygons have low rates of decomposer activity (Figure 9-9). For example, in 1972 the mean seasonal rate of respiration, as measured by Gilson respirometry, for 0- to 2-cm basin soils was $10.06 \mu\text{l O}_2 (\text{gdw soil})^{-1} \text{hr}^{-1}$ whereas the values from similar depths in the trough and very wet meadow were 31.37 and $43.15 \mu\text{l O}_2 (\text{gdw soil})^{-1} \text{hr}^{-1}$ respectively. The consistently low decomposer activity and low primary productivity probably act to maintain relatively high levels of oxygen in the basin soils.

The shift of bacteria-to-fungi ratios along the oxygen gradient (Chapter 8) suggests that anaerobiosis does not eliminate decomposition of the soil organic matter but changes the quality of that decomposition. In the wet meadow, depressed oxygen concentrations in the deeper soils were associated with high levels of decomposer activity measured by Gilson respirometry (Figure 9-6). Thus the high values for respiration from subsurface samples represent activity of facultative bacteria after full induction of potential for oxidative phosphorylation in the Gilson respirometer. The rapid response to oxygen indicates the active enzymatic state of the cells. The zone of anaerobiosis at the front of the thaw zone appears to be a result of the rapid decomposition of readily available substrates.

Experiments with heated soil further demonstrate that anaerobic conditions *per se* do not prevent decomposer activity in tundra soils. Oxygen saturation in the soil solution in heated soils declined to 0% by the 3-cm depth. On these plots methane routinely composed 60% (with a range of 42 to 65% of the gas released), with the balance primarily of carbon dioxide. Methane production provides good evidence for anaerobic activity because methane producers represent one of the most strictly anaerobic groups, and can be killed easily by transitory exposure to oxygen. Despite anaerobic conditions, rates of decomposition were high in heated soils. Evolution of carbon dioxide over a 33-day period in late summer was 39% higher in heated soils, and after 12 months the energy content in the heated soil was less than in control soils by 21% in the upper 2 cm and by 16% at depths of 7 to 12 cm. The higher rates of microbial respiration in the heated soils are a result of the increased tempera-

tures and approximate the rates expected, given the respiratory Q_{10} of 1.78 measured from unheated soils and a 4° to 6°C increase in mean daily soil temperature. The heat treatment documents the in situ potential for anaerobic decomposition present in tundra soils suggested by the high number of facultative bacteria relative to strictly aerobic species (Chapter 8).

DECOMPOSER ACTIVITIES AND DECOMPOSITION

Two general approaches are used in analyzing the response of decomposer organisms to temperature, moisture and other environmental phenomena. The first approach employs integrative measures of all microbial groups. The evolution of carbon dioxide, the rates of weight loss from selected substrates, and the patterns of nutrient concentration are each considered direct or indirect functions of the activities of all microbial groups. The second, more direct, approach examines the individual activities of specific microbial groups. The specific activities suggest the contribution particular groups make to the general integrative measures such as carbon dioxide evolution. We discussed some specific responses earlier in this chapter without relating them to patterns of weight loss or carbon dioxide evolution measured in the field. The present discussion illustrates how these activities are enacted in the changing environment to produce the observed patterns of weight loss or decomposition.

Decomposition of aboveground parts of graminoids begins at the time when necrotic patches appear on the leaves and stem bases. The necroses are most apparent from mid-August onwards. Before or concurrent with visual signs of senescence the leaves lose up to 12% of their weight as green healthy tissue (Figure 9-7). The initial loss, which occurs prior to substantial microbial ingress, and whether or not rain has fallen, is apparently caused by translocation to belowground parts. The freeze-thaw cycle and the physical throughput of water remove up to 18% of the dry weight of overwintering leaves by the spring. During and prior to the period of leaching substantial microbial activity may take place, contributing to overall weight loss, but microbial contributions to weight loss in this and the previous phase of aboveground plant weight losses are undetermined. During the period from mid-August to the end of spring runoff, up to 30% dry weight may be lost from leaves of graminoids (Figure 9-7, Table 9-5).

Three simulation models relate microbial activities quantitatively and unambiguously to the environmental phenomena that govern them. One model, GRESP (Bunnell et al. 1977a), relates the respiratory response of microbial populations to changing temperature and moisture. The second, DECOMP (Bunnell et al. 1977b), expresses the respiration rate as a

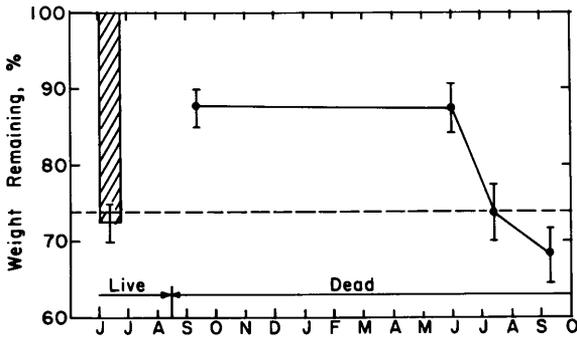


FIGURE 9-7. Progression of leaf weight of *Carex aquatilis* and *Eriophorum angustifolium*, combined. Hatched bar shows the amount of material removed in vitro by warm water and 80% ethanol. Vertical bars indicate the standard errors. The dashed line indicates the weight loss before ingress of microorganisms is well under way. (Flanagan, unpubl.)

function of substrate chemistry. The third, ABISKO II (Bunnell and Scoullar 1975), integrates the effects of changing meteorological conditions and substrate chemistry within an ecosystem framework. The models document relationships between weight loss and microbial activities, as they are influenced by abiotic variables and substrate chemistry and the relationship of the biomass of microbial populations to primary production and turnover of organic matter. Although the development of these models was based on tundra research, their predictive abilities have also been tested for conditions found in the taiga and moors (Bunnell et al. 1977a, Bunnell and Scoullar 1981).

Temperature, Moisture, and Microbial Respiration

The function GRESP represents a formal statement and complex hypothesis of the manner in which temperature, moisture and substrate features influence aerobic respiration of microbes. It treats aerobic respiration as a function of the supply rates of water, oxygen and organic nutrients. The critical features of the hypothesis are presented:

$$R(T, M) = [M/(a_1 + M)][a_2/(a_2 + M)] a_3 a_4^{(T-10)/10}$$

where $R(T, M) = \mu\text{l CO}_2$ respired $(\text{g substrate})^{-1} \text{hr}^{-1}$ at temperature T and moisture M

T = temperature, °C

M = moisture, percent dry weight

a_1, \dots, a_4 = substrate specific parameters.

The rationale of the GRESP function has been presented elsewhere (Bunnell and Tait 1974, Bunnell et al. 1977a) and only a summary is repeated here. Microbial respiration is assumed to be related to the moisture potential of the substrate via two saturation processes. The first process is related to the metabolic water requirements of decomposer organisms and embodies a convention of soil mycologists, that is, the expression of water content on a relative basis, or as a percentage of the value when the soil is saturated (Griffin 1966). This process is expressed as $M/(a_1 + M)$, where M represents the percent water content on a dry weight basis and a_1 represents the percent water content at which the substrate is "half-saturated" with water or respiratory activity is at half its optimal level.

The second saturation process occurs at high moisture levels. It is assumed to represent the effect of water on gas exchange with the atmosphere either of oxygen, carbon dioxide or both. The simplest formulation is employed (Bunnell and Tait 1974). Since the degree to which gas exchange is inhibited can be expressed as $M/(a_2 + M)$, the degree to which it is not inhibited can be expressed as:

$$1 - [M/(a_2 + M)] \quad \text{or} \quad a_2/(a_2 + M).$$

Again M represents the moisture content, and a_2 represents the percent water content at which gas exchange is limited to half its optimal value.

The third and fourth factors, temperature and substrate characteristics, are treated as a substrate-specific Q_{10} relationship:

$$a_3 \times a_4^{(T-10)/10}$$

where a_3 is the substrate specific respiration rate that occurs at 10°C when neither moisture nor oxygen are limiting and a_4 is the Q_{10} coefficient. Alternative formulations for both moisture and temperature influences on rates of nutrient supply are discussed by Bunnell et al. (1977a); the treatment of substrate characteristics is pursued later in this chapter. According to the GRESP function any one of the major determinants of rates of respiration (moisture, oxygen, temperature and substrate) can effectively reduce the rate of microbial respiration independently of the other factors. Thus, the rate determinants are combined multiplicatively.

Evaluation of the complex hypothesis represented by the GRESP function indicates that it predicts carbon dioxide evolution more accurately from aboveground substrates than from tundra soils. In the somewhat more aerobic soils of the taiga the model accounts for 78 to 84% of the variability in respiration rates (Bunnell et al. 1977a). The generality

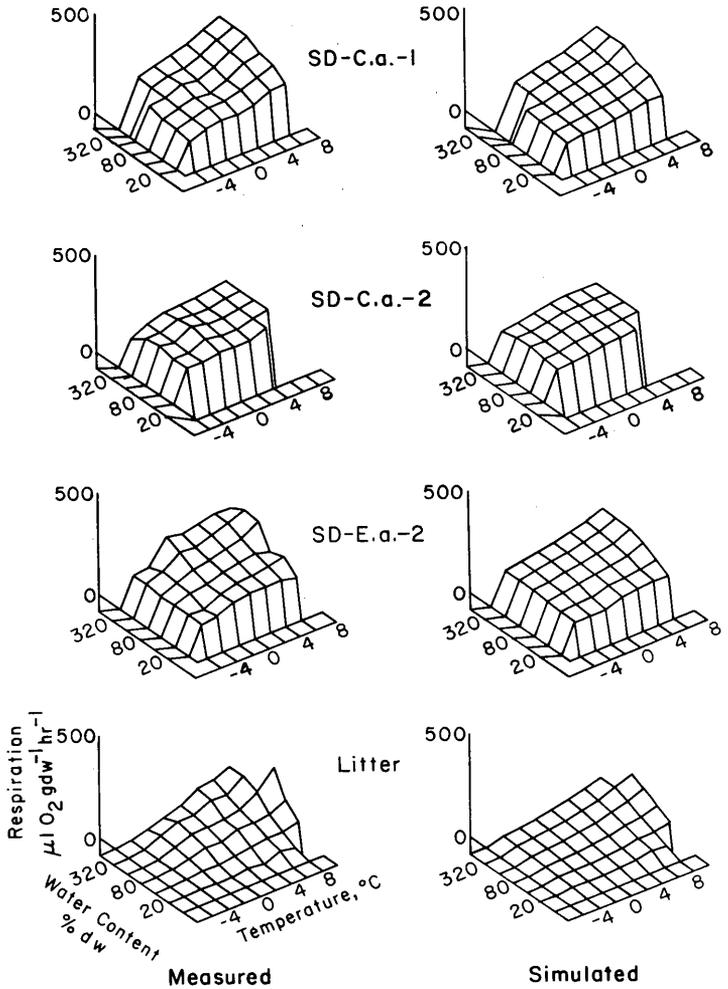


FIGURE 9-8. Measured and simulated rates of microbial respiration in relation to moisture and temperature for: 1-yr-old standing dead of *Carex aquatilis* (SD-C.a.-1); 2-yr-old standing dead of *C. aquatilis* (SD-C.a.-2); 2-yr-old standing dead of *Eriophorum angustifolium* (SD-E.a.-2); and mixed graminoid litter. (After Bunnell et al. 1977a.)

TABLE 9-2 *Parameter Values Giving the Best Fit of the GRESP Function to Data from Seven Substrates and Coefficients of Determination*

Substrate	No. of obs.	a_1 water (%)	a_2 dry wt)	a_3 ($\mu\text{l O}_2$ $\text{g}^{-1} \text{hr}^{-1}$)	a_4 (Q_{10})	r^2	r_a^{2*}
<i>Carex</i> (1 yr old)	96	59	NE	204	3.33	0.79	0.86
<i>Carex</i> (2 yr old)	45	213	822	296	2.18	0.63	0.71
<i>Eriophorum</i> (newly dead)	54	416	416	777	8.79	0.65	0.96
<i>Eriophorum</i> (1 yr old)	79	74	NE	184	2.56	0.64	0.72
<i>Eriophorum</i> (2 yr old)	65	19	NE	107	2.79	0.72	0.77†
<i>Dryas</i> (2 yr old)	38	160	160	158	1.75	0.36	0.43
Total Barrow litter	346	116	2820	232	3.74	0.66	0.71

* r_a^2 is an estimate of the accountable variation explained by a nonlinear model.

† An optimum solution was not found.

NE—No estimate; number of measurements at moisture contents >500% moisture (% dry wt) are <10. Therefore $a_2/(a_2 + M)$ was set equal to 1.

Source: After Bunnell et al. 1977a.

and accuracy of the model in predicting measured microbial respiration from aboveground substrates, assessed visually (Figure 9-8) and statistically (Table 9-2), suggest that the hypothesis is applicable to a diversity of aboveground substrates.

Coefficients a_1 and a_2 assess the moisture range over which microbial respiration is little affected by changes in moisture levels. The range encompassed by these coefficients extends beyond the optimal moisture regime determined for individual species, particularly at the upper end. Excluding the poorly constrained values (NE in Table 9-2) the weighted mean of the mid-point between a_1 and a_2 for aboveground substrates is 461% moisture on a dry weight basis. For the microbial community *in toto*, respiration from dead vegetation is depressed far more as amounts of moisture approach the lower thresholds than near the upper thresholds. Within plant litter where aquatic fungi are more abundant, the upper limits to the moisture range may be greatly extended (Table 9-2; Flanagan and Veum 1974).

Some substrates, particularly in taiga soils, have computed half-saturation values that are equal for both a_1 and a_2 (e.g. newly dead *Eriophorum angustifolium*, Table 9-2). The resulting model with a_1 set equal to a_2 has only three parameters but accounts for 96% of the variation in respiration from that substrate (Bunnell et al. 1977a). However, Bunnell et al. (1977a) noted that equal values of a_1 and a_2 are likely an artifact of the model. Given the multiplicative form of the GRESP function, a

narrow-peaked response of respiration versus moisture can be obtained only by having a_1 equal a_2 .

Despite an uneven data base, trends in coefficients a_1 and a_2 are revealing. With increasing age and pitting within the substrate, the moisture range for effective respiration appears to broaden (see *E. angustifolium*, Table 9-2). Bunnell and Tait (1974) stated that the volume of water relative to the amount of organic matter was critical. Thus, they predicted that the moisture range over which respiration was unconstrained would broaden with age in aboveground substrates and narrow with increasing depth and bulk density below ground. The trend below ground has been documented most rigorously for aspen forest floor in the taiga, and does show a gradual decrease in the effective moisture range with depth (Bunnell et al. 1977a).

Coefficient a_3 represents the respiration rate at 10°C when moisture and oxygen are not limiting. It is assumed to be a measure of substrate quality and as such should decline with the age of the substrate. Bunnell et al. (1977a) documented the expected pattern within the taiga forest floor; among substrates of the Biome research area it is evident among the *E. angustifolium* age classes (Table 9-2). The exponential response of respiration with temperature, defined by coefficient a_4 , assumes Q_{10} values ranging from 2.2 to 8.8, with younger substrates showing a higher Q_{10} than older substrates (Table 9-2). There are two possible reasons. 1) Newly senescent substrates have not experienced a winter and may not be well colonized by psychrophilic organisms; thus they would show lower rates of respiration at lower temperatures and higher Q_{10} values. 2) Younger substrates contain greater proportions of constituents of low molecular weight which appear to have higher Q_{10} values associated with their utilization as discussed earlier in this chapter. Over the range 0° to 10°C the weighted average of Q_{10} values for all aboveground substrates tested at the Biome research area is 3.65.

Observations suggest that while younger aboveground substrates have the chemical potential for higher respiration rates than do older substrates, respiration is more likely to be constrained by temperature and moisture. The high Q_{10} values from younger substrates imply a population poorly adapted to low temperatures. The narrower moisture range suggests that drying by wind frequently may reduce realized respiration. These environmental constraints act to ensure that nutrients present in newly dead standing vegetation are not released into the system until the spring thaw.

The same clear pattern of carbon dioxide evolution with temperature and moisture is not observed for decomposition processes below ground. The best fit of the GRESP function to Gilson respirometry measures of wet meadow soil accounts for only 10 to 20% of the variation. The computed Q_{10} is near 2.0 for a variety of soils and the optimal mois-

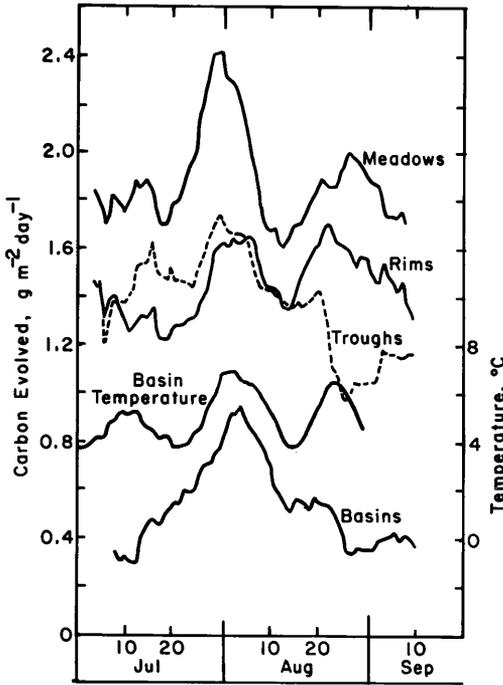


FIGURE 9-9. Seasonal courses of the evolution of carbon dioxide from soils of four microtopographic units and soil temperature near the surface in the basin of a low-centered polygon. Carbon flux measured by KOH titrations in darkened lysimeters. Data are ten-day running means for 1973. (Benoit, unpubl.)

ture level is about 75 to 80%. Few measures incorporating higher moisture levels were available and the estimate is likely low. Rates of soil respiration as measured by Gilson respirometry can be extrapolated only tenuously to estimate decomposition rates in the field. At best they represent a potential rate of decomposition that may not be realized.

Another estimate of field decomposition rate and the factors which control it can be made from in situ measurements of carbon dioxide evolution although these measures include respiration of roots as well as microflora. Field data were obtained by daily potassium hydroxide titration of gas collected from plastic cores sunk into the soil in 1973. Measures of carbon dioxide evolution from different microtopographic units all peak in early August (Figure 9-9). Although the peak appears correlated with temperature, early August is also the time of maximum above-ground biomass of vascular plants and intense activity by soil fauna. Logarithmic regression of the daily evolution of CO_2 m^{-2} , as measured by lysimeters in wet meadow soils, against mean daily soil temperature estimates a Q_{10} of 1.89:

$$R = 1465.6 \times 1.89^{T_{\text{mean}}/10} \quad r^2 = 0.37, \alpha \leq 0.01$$

where R is $\text{ml CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ and T_{mean} is the mean daily temperature.

Linear regression with the same data produces:

$$R = 1476 + 117.4 \times T_{\text{mean}} \quad r^2 = 0.39, \alpha = 0.01.$$

For all microtopographic units, linear regressions of carbon dioxide evolution versus mean daily temperature and maximum daily temperature consistently provided higher coefficients of determination, r^2 , than regressions involving $2^{T/10}$ and $e^{T/10}$ (where T = temperature). The observed linear response to temperature may be a result of the summation of a number of exponential responses.

The contribution of plant roots to observed carbon dioxide production was analyzed by comparing undisturbed soil cores with cores effectively stripped of primary producers. Linear regressions of carbon dioxide evolution from stripped cores also provide better fits than do exponential models for the effect of temperature. The relative response (the predicted response at 10°C divided by the predicted response at 0°C) is higher for stripped cores than for cores on which the graminoid and moss canopy was left intact. Removing the plant cover increased the relative response from 2.08 to 3.1 in basins of low-centered polygons and from 1.59 to 1.89 on rims of low-centered polygons. The intercepts of equations for stripped cores of basin and rim soils were 155 and 634 ml CO₂ day⁻¹, about half the level of the intercepts of untreated cores (353 and 1121 ml CO₂ day⁻¹).

Direct comparisons between treated and untreated cores should be viewed with caution because microbial populations in treated cores are not experiencing the same environment as the controls. Further, there may have been increased root respiration associated with clipping. However, the results do suggest that the near-linear response of carbon dioxide evolution to temperature changes in soils is in part due to the influence of primary production. The lower relative response of soils on rims, which support higher primary production than do soils in basins, corroborates the suggestion, as do the high Q_{10} values observed for microbial respiration in standing dead and litter substrates (Table 9-2). In short, microbial activity below ground appears to respond more strongly to changes in temperature than do processes of primary production below ground.

Undoubtedly some of the differences in carbon dioxide evolution observed among microtopographic units (Figure 9-9) are associated with differing primary productivity. Rims of low-centered polygons and polygon troughs evolve approximately twice as much carbon dioxide as basins of low-centered polygons and support considerably greater primary production. Evolution of carbon dioxide from meadow soils is still greater, possibly reflecting the higher biomass of bacteria in these soils. We cannot distinguish between the influences of soil moisture and primary

production on measured respiration, but acknowledge that the difference in soil respiration among microtopographic units is greater than that expected from differences in primary productivity alone.

In taiga soils coefficient a_3 and total respiration decrease with depth in the profile, while the measured Q_{10} increases (Bunnell et al. 1977a). Such findings suggest that the relative contribution from primary production in the taiga declines with depth and that the effect of temperature on microbial populations increases with depth. In both tundra and taiga, microorganisms in the litter layer continue respiration at lower temperatures than do organisms at depth in the soil. Surface layers are subject to wider ranges in both temperature and moisture than are deeper layers. Thus it is not surprising to find deeper communities apparently adapted to narrower ranges of temperature and moisture than surface communities. The tendency within tundra soils for more linear relationships with temperature may reflect an adaptation to low temperatures.

The sensitivity analyses of the model based on the function GRESP that were conducted by Bunnell et al. (1977a) have been extended using other substrates from tundra. In all cases the model is most sensitive to coefficient a_4 , which determines the predicted Q_{10} . Relative sensitivities to other coefficients vary with the substrate. For those substrates where the overall fit of the model is close ($r^2 \geq 0.80$) we observe that the broad

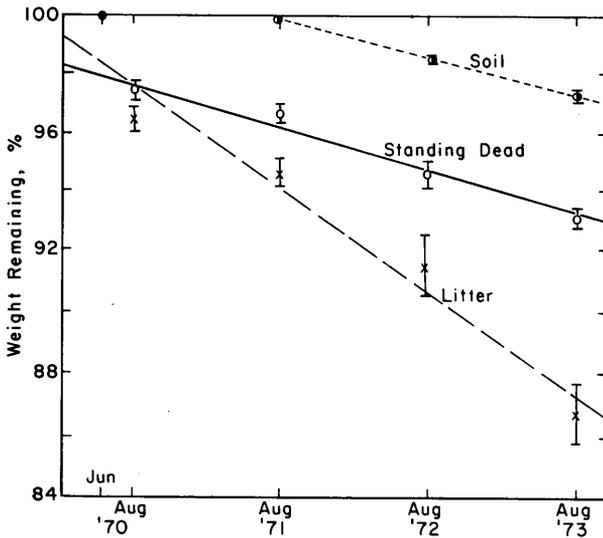


FIGURE 9-10. Progression of weights of cellulose placed in surface soil, litter and standing dead material. Vertical bars give standard error. (After Bunnell et al. 1977b.)

response of microbial respiration in substrates from tundra and taiga is most sensitive to temperature, then to substrate chemistry, and least sensitive to amounts of moisture, particularly high levels of moisture. Despite the variable response to moisture, elimination of moisture effects from the model reduces its predictive ability by a minimum of 23 to 31% (Bunnell et al. 1977a). Also, it is important to note that while respiration rates are relatively insensitive to moisture over the range of respirometry data collected, moisture levels in the field may become high enough to reduce respiration significantly. Temperature, moisture and oxygen are all important modifiers of the rate of respiration of tundra microorganisms.

The overall effect of the microbial population and micrometeorological factors can be seen in the relative decomposition rates of a uniform substrate, cellulose, placed in three different microhabitats (Figure 9-10). Over several years, the weight loss from the cellulose was greatest in the litter, intermediate in the standing dead, and lowest in the soil. As both soil and litter have more cellulolytic decomposers than standing dead (Figure 9-1), the results support the hypothesis that moisture may be limiting in the standing dead (Chapter 8). The considerable decrease in decomposition rate noted for the soil suggests that conditions in the soil are less favorable overall to decomposition than those above ground.

Substrate Chemistry and Microbial Respiration

Microbial respiration is assumed to be influenced by substrate chemistry as well as by temperature and moisture. This assumption is broadly accommodated by coefficient a_3 in the function GRESP. Coefficient a_3 represents the respiration rate at 10°C when neither moisture nor oxygen are limiting, and is employed to establish the upper level or amplitude of the response surface for respiration. The "quality" of the substrate is thus directly proportional to the magnitude of a_3 , which in turn is directly correlated with the percentage of ethanol-soluble compounds or percent glucose (Bunnell et al. 1977a). The significance of a_3 to broad patterns of respiration is estimated by the preceding sensitivity analyses.

Earlier works (Henin et al. 1959, Minderman 1968) proposed that observed rates of weight loss result from the summation of rates from specific chemical components, but did not relate these rates to microbial activities. Bunnell et al. (1977b) extended these earlier models of decomposition to encompass not only the observed patterns of weight loss, but the microbial activities producing these patterns. Ethanol-soluble compounds disappear five to six times as fast as other constituents of natural substrates (Figure 9-11). Combination of these two chemically defined groups produces the common departure from a simple exponential

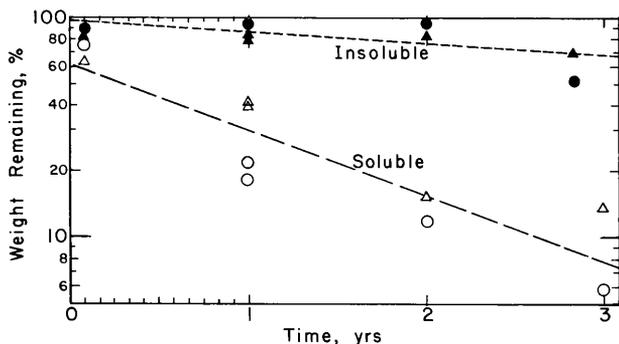


FIGURE 9-11. Percentage of ethanol-soluble and ethanol-insoluble compounds remaining in decomposing *Carex aquatilis* (▲, △) and *Eriophorum angustifolium* (●, ○). Percentages are based on weight per unit area. (After Bunnell et al. 1977b.)

illustrated by many decomposing substrates (Burgess 1958, Minderman 1968, Satchell 1974).

Here we address the manner in which the phenomenon of substrate "quality" represented in the function GRESP by the single coefficient a_s can be related to substrate chemistry more directly. In accordance with earlier workers different constituents are assumed to have their own chemical-specific rates of decomposition. In addition the decomposition rate of each chemical constituent is assumed to be a function of the temperature and moisture-dependent respiration rate of the microflora, and thus changes seasonally or even daily. The observed decomposition rate of a substrate is assumed to be the sum of the temperature-moisture-chemical-specific rates of utilization times the amount of each chemical constituent present. Observed rates of decomposition thus change with the meteorologically induced changes in rates of microbial respiration and the changing capacity of the substrate to provide energy to the microbial population.

As developed by Minderman (1968), the decay rate of a substrate can be expressed as:

$$(dY/dt) = \sum_{i=1}^n (dy_i/dt)$$

$$(dY/dt) = \sum_{i=1}^n -k_i y_i$$

where Y = total weight of the decomposing substrate

$$y_i = \text{weight of substrate component } i; \sum_{i=1}^n y_i = Y$$

$$k_i = \text{decay rate of substrate component } i.$$

The above equation states that each substrate component decomposes at a constant rate of decay specific for that substrate constituent and independent of the amount of other substrate components present. The relation of decomposition to temperature and moisture discussed earlier suggests that the above equation can be written

$$R(T, M) = \sum_{i=1}^n r_i(T, M)y_i$$

where $R(T, M)$ = respiration rate of the total substrate at temperature T and moisture M

$r_i(T, M)$ = respiration rate of substrate component i , a function of temperature and moisture

y_i = amount of substrate component i present, as before.

As expressed in the above equation, the model of decomposition not only accounts for the observed differences in response surfaces of respiration versus temperature and moisture for substrates of different chemical composition, but also accounts for the observed differences in rates of loss of different chemical components from a substrate in the field. To document the relative contributions of different chemical constituents to total respiration, the influences of temperature and moisture must be reduced or removed. Bunnell and Tait (1974) proposed several methods for separating the temperature and moisture effects from chemical-specific effects. Three methods have been evaluated by Bunnell et al. (1977b). Their evaluation suggests that dominating influences on the pattern of respiration for any specific constituent are levels of temperature and moisture. Only 1 to 4% of the variation in instantaneous respiration rates is due to chemical composition. These observations are not incompatible with the preceding sensitivity analyses, which suggest that the overall response surface of microbial respiration versus temperature and moisture is sensitive to substrate quality. The general amplitude of the response surface, and thus its overall shape, are sensitive to substrate quality (Bunnell et al. 1977a). Variations in temperature and moisture, however, account for more of the variation of the total surface (Figure 9-8) as it rises to the amplitude set by substrate quality. When summed over a year, even small differences associated with substrate chemistry will produce distinctly different annual rates of loss.

In their evaluation of the relationships expressed in the last equation, Bunnell et al. (1977b) initially treated five different substrate components: ethanol-soluble cellulose, lignin, pectin, starch and volatiles.

Several important points emerge from their analyses. The coefficients associated with the volatile and lignin components were occasionally negative, implying negative respiration. Analyses yielding negative coefficients for respiration usually had a disproportionately large number of *Dryas* substrates. The observations imply 1) that respiration rates of total substrates from any botanical taxon cannot be predicted consistently from independent consideration of the five substrate components mentioned above, and 2) that some substrate components may have an inhibitory effect on the respiration rate of other components.

In addition to generating inhibitory effects, specific substrate components also may provide energy for the degradation of more recalcitrant components. For example, the observed rates of weight loss from pure cellulose filter papers placed in the field are lower than rates of loss of cellulose from natural substrates.

As well as indicating the failure of the five selected chemical constituents to contribute independently to microbial respiration, the analyses of Bunnell et al. (1977b) indicate that the predictability of regression equations within temperature-moisture classes is little altered by ignoring amounts of pectin, starch and volatiles in the substrate being respired. When broader chemical groups (e.g. percent ethanol-soluble and percent ethanol-insoluble) are employed, and *Dryas* substrates are omitted, regression coefficients for the two substrate components are consistently different and significantly greater than 0 ($\alpha \leq 0.001$). Rates of respiration of ethanol-soluble components are about 5 to 10 times greater, depending on temperature, than the rates associated with other chemical constituents. It is noteworthy that ethanol-soluble compounds make a greater contribution to total respiration at higher temperatures.

The discussion of microfloral potential to utilize substrates noted that several fungal isolates show higher temperature optima for utilization of substances of lower molecular weight than they do for utilization of the more recalcitrant substances such as cellulose. The analyses associated with the last equation suggest that the phenomenon is general within the mycoflora of the coastal tundra at Barrow and applies to associated rates of respiration as well as to the physiological potential to degrade these substrates (Bunnell et al. 1977b). At lower temperatures tundra fungi not only maintain their competence to degrade more recalcitrant chemical constituents (Figure 9-1), but also have a greater proportion of their respiration associated with these constituents.

Microbial Respiration as a Measure of Weight Loss

Implicit in the preceding discussion is the assumption that the general form of the response surface for microbial respiration against temper-

ature and moisture is characterized by the physical and chemical nature of the substrate. The model GRESP closely mimics this response surface for a variety of substrates (Figure 9-8, Table 9-2). Ignoring hysteresis effects and microbial succession, the assumption can further be made that given the initial characterization for a specific substrate one can predict the instantaneous respiration rate under any temperature and moisture condition during a year. Unfortunately, in situ measures of respiration from the soil are confused by plant and invertebrate activity, and there are no measurements of the pattern of weight loss during a specific annual cycle. However, annual measures of weight loss from a variety of substrates under markedly different meteorological conditions are available. These data were collected from different International Tundra Biome research sites.

Bunnell et al. (1977a) and Bunnell and Scoullar (1981) have compared measures of total weight loss from different litters with losses due to microbial respiration as simulated by the model. To project simulated weight losses due to microbial respiration they first estimated coefficients a_1 through a_4 (p. 310-311) from respirometry data collected at the specific site using the non-linear optimization techniques described by Bunnell et al. (1977a). The GRESP model was then used to project rates of microbial respiration during the year. Temperature and moisture data used in the projection were those collected from the appropriate site. Computations of weight loss assume that the substrate is 45% carbon and has a respiratory quotient of 1.0.

The annual weight losses computed from the simulated daily respiration rates are compared with the rates of weight loss as measured by litter bags (Table 9-3). Bunnell and Scoullar (1981) discuss the implications of computed coefficients a_1 through a_4 for each substrate and site. The hypothesis relating microbial respiration to measures of temperature and moisture accounts for 71 to 98% of the variation in rates of respiration measured from a variety of natural substrates and predicts annual loss rates under a wide range of environmental conditions that are 70 to 90% of the measured loss from litter bags. The values for loss of weight seem reasonable, given the additional losses due to leaching and physical reduction.

The equation on page 320 explicitly encompasses the additional influence of substrate chemistry. In nature, rates of weight loss from ethanol-soluble compounds and ethanol-insoluble compounds show a ratio of 5.75:1. When the effects of temperature and moisture are incorporated according to the central equation of GRESP, rates of respiration from the two chemical groups show ratios ranging from 5.1:1 to 8.7:1 (Bunnell et al. 1977b). Thus the rates of microbial respiration associated with the two chemical constituents show approximately the same ratio as rates of weight loss from these constituents in the field. If the simplifying

TABLE 9-3 *Annual Weight Losses of Various Litters Measured and Predicted from the Simulated Microbial Respiration*

Research area	Substrate	Weight loss (% of initial weight)		Simulated as a percentage of measured
		Measured	Simulated	
Abisko, Sweden	<i>Rubus chamaemorus</i> leaves	32 ¹	23.3	73
Barrow, Alaska	<i>Dupontia fisheri</i> leaves	15 ²	13.4	89
	<i>Carex aquatilis</i> leaves	14.6 ³	13.4	
Moor House, United Kingdom	<i>Calluna vulgaris</i> shoots	15-20 ⁴		
	<i>Calluna vulgaris</i> stems	8 ⁴	7.1 ⁵	92
	<i>Rubus chamaemorus</i> leaves	36-38 ⁴	20.1	81

Note: Abiotic and respirometry data for the research areas were collected during development of the ABISKO model (Bunnell and Dowding 1974).

¹Rosswall (1974).

²Benoit et al. (unpubl.).

³Benoit (unpubl.).

⁴Heal and French (1974).

⁵Shoots and stems combined in model.

Source: Bunnell et al. (1977b).

assumption is made that both chemical groupings contain the same percent carbon as the parent material, 45%, the respiration rates can be converted directly to weight loss. The rate of weight loss of ethanol-soluble compounds is:

$$\text{weight loss hr}^{-1} = 3.8 \text{ GRESP}(T,M)1.19WE$$

where GRESP = central equation of the model (p. 310) with coefficients appropriate to the specific substrate

1.19 = conversion factor from $\mu\text{l CO}_2$ to g substrate

WE = weight of ethanol-soluble compound in grams.

Following the same approach the rate of weight loss of ethanol-insoluble compounds is:

$$\text{weight loss hr}^{-1} = 0.76 \text{ GRESP}(T,M)1.19WNE$$

where WNE represents the weight of ethanol-insoluble compounds in grams. The annual rate of weight loss is given by:

$$1 - \prod_{i=1}^{365} (1 - k_i)$$

TABLE 9-4 *Measured and Simulated Chemical Composition After One Year and Rates of Weight Loss of Eriophorum angustifolium Standing Dead Material*

	Percentage	
	Measured*	Simulated†
Chemical composition of the substrate after one year:		
ethanol-soluble	7	10
ethanol-insoluble	93	90
Loss per year:		
ethanol-soluble	49	48
ethanol-insoluble	11	12
Total weight loss	27	31

*Measured values use changes in identified age classes.

†Simulated values used abiotic data from 1973.

Source: Bunnell et al. (1977b).

where k_i is the computed daily rate of weight loss due to respiration. The three equations above make up the model DECOMP. Using meteorological data from the Barrow site, Bunnell et al. (1977b) computed daily values of the function GRESP as determined by temperature and moisture and applied these to the chemical-specific coefficients. They obtained annual rates of weight loss of -0.66 and -0.13 for ethanol-soluble and ethanol-insoluble constituents respectively. Measured weight losses from the total litter in the field are -0.69 and $-0.12 \text{ g g}^{-1} \text{ yr}^{-1}$. The rates of weight loss computed from temperature-moisture-chemical-specific rates of respiration are thus in very close agreement with measured rates of weight loss. Because the loss rates are chemical-specific (Bunnell et al. 1977b), the model DECOMP can project not only total substrate weight loss but also chemical composition, which is also very similar to the observed value (Table 9-4).

The model DECOMP provides a framework that permits extrapolation of laboratory measures of microbial activity to predict total loss of substrate weight and changing composition of substrate. The concepts of decomposition embodied in the model appear supported by combined laboratory and field evidence. The reasonably close agreement between simulated and measured values for standing dead material (Table 9-4) suggests that at least during the initial period of decomposition many of the changes in substrate weight and chemical composition result from changing rates of microbial respiration which are chemical-specific and independently influenced by temperature and moisture (Bunnell et al. 1977b).

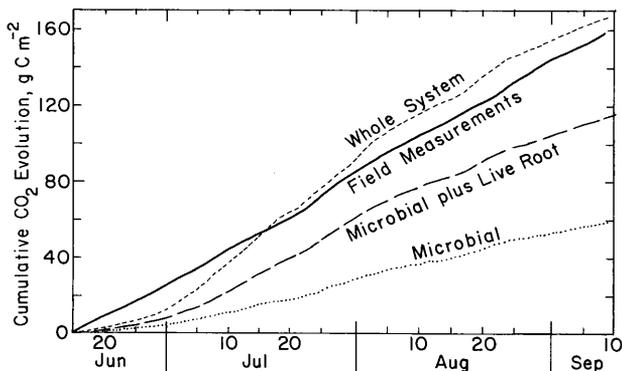


FIGURE 9-12. Cumulative CO₂ release over a single growing season, simulated for soil microbes, microbes plus roots and the whole system, and measured by KOH titrations in darkened lysimeters. Root respiration includes that of microbes associated with the rhizosphere. Whole-system CO₂ evolution includes the flux from soil microbes, roots, above-ground decomposers and respiration of aboveground plant biomass. (After Bunnell and Scoullar 1975.)

For the more advanced stages of decomposition, such as belowground substrates, the relationships of microbial activities to decomposition are not as well quantified. No data are available on the chemical composition of belowground substrates. Furthermore, measures of microbial activity are confused by the activities of invertebrates and vascular plants. To evaluate the hypothesis concerning decomposition below ground, a broader approach incorporating more ecosystem components but less chemical detail has been employed. The model ABISKO II (Bunnell and Scoullar 1975) incorporates the temperature and moisture influences expressed but also simulates contributions from dying roots and respiration of vascular plants.

Bunnell and Scoullar (1975) have evaluated the model ABISKO II for the Biome research area comparing in situ measures of carbon dioxide evolution with the cumulated totals of simulated respiration from relevant components of the system (Figure 9-12). The whole-system respiration of Figure 9-12 includes carbon dioxide evolution from soil microorganisms, roots, aboveground decomposers, and the growth plus maintenance respiration of aboveground live material.

Simulated microbial respiration follows a pattern very similar to that of the field measures of respiration, but shows a greater depression early in the season. The early season depression is most evident in the

pattern of simulated microbial plus root respiration (Figure 9-12). There are at least two reasons for this early season disparity between simulated and measured values. The soil temperature employed in the model is that at 5 cm depth. Early in the season field temperatures near the surface permit respiration while simulated temperatures at 5 cm depth are too low to allow significant respiration. Because the lower threshold for root respiration is higher than that for microbes, the disparity between simulated and measured values is more obvious when roots are considered. The release of carbon dioxide trapped during freeze-up is not simulated but will appear in field measures (Benoit, pers. comm.; Coyne, pers. comm.), and this also contributes to the early spring disparity between field and simulated values.

Over the 85-day sample period the accumulated totals of measured respiration and simulated whole system respiration are 159 and 165 g C m⁻² respectively. The difference between measured and simulated values over this period is thus 6 g C m⁻² or 3.7% of the measured values. A disparity of less than 5% is well within the sample error associated with data for root biomass. Thus the simulated dynamics of respiration of microbe, root and other contributing compartments must be assumed realistic within the accuracy of available data. The proportion of simulated total soil respiration that originates with the roots on any given day varies between 33 and 70%, and lies at the lower end of the range of reported values of 50 to 93% (Billings et al. 1978). Errors in different processes might compensate to produce an invalid sense of accuracy. However, the generally realistic behavior of the model for other tundra areas, including Devon Island, Moor House and Abisko (Bunnell and Scoullar 1981), suggests that microbial respiration for specific substrates in the upper 10 cm of soil follows the relationship expressed by the function GRESP. The dynamics of microbial respiration at depth are much less clear and are confused by anaerobic conditions and poorly understood changes in substrate quality with advancing age.

In summary, the concepts of decomposition discussed above appear sufficiently comprehensive to allow laboratory measures to be related effectively to field measures through the vehicle of simulation models. The manner in which microbial respiration responds to temperature, moisture and broad chemical groups predicts not only weight loss but chemical composition of aboveground substrates. Upper limits on decay rates are established by chemical composition, but are modified by abiotic variables. Respiration is most sensitive to temperature and the microflora has responded by extending its capabilities to grow, respire and utilize substrates at low temperatures. Respiration declines with both increasing and decreasing moisture levels. At low moisture levels degradation and loss of chemicals from standing dead vegetation is temporarily suspended; at high moisture levels respiration becomes the province of bac-

teria which cannot degrade compounds of larger molecular weight. Decomposition of such compounds remains poorly understood, but it appears that accumulation of organic matter in tundra is more a product of high moisture levels than of low temperatures.

Microbes and Turnover of Organic Matter and Nutrients

The preceding models concentrate on rates of microbial activity and ignore microbial biomass. The accuracy of the predictions made by these models suggests that concentration on rates of processes is an insightful approach. That in no way obviates attempts to examine the consistency of the measures of microbial biomass with estimated turnover of organic matter. Growth, respiration, production efficiency, and maintenance demands of the microbial biomass in specific substrates can be related to weight loss from that substrate. Using the chemostat model of Marr et al. (1963) it is possible to examine compatibility between field and laboratory data and to evaluate the influence of microbial activities on turnover and accumulation of organic matter. Several workers (Babiuk and Paul 1970, Gray and Williams 1971, Flanagan and Bunnell 1976) have used this approach in attempting to balance budgets of energy or carbon in a variety of ecosystems. The biomass equation of Marr et al. (1963) is expressed as:

$$(dx/dt) + ax = Y(ds/dt)$$

where x = microbial biomass

s = substrate available for microbial growth

Y = yield coefficient, g microbial tissue (g substrate)⁻¹

a = specific maintenance rate—g microbial tissue required to maintain 1.0 g microbial tissue for a specific time, e.g. 1.0 hour.

When the rate of growth is zero, the above can be expressed:

$$ds/dt = ax/Y'$$

The yield coefficient Y' is not identical to Y because at zero growth there is no actual yield. However, material for maintenance is believed to be utilized at very nearly the same level of efficiency as material assimilated for production of new tissue.

Gray and Williams (1971), following the approach of Babiuk and Paul (1970), utilized values for Y' and a of 0.3 g g⁻¹ and 0.001 g g⁻¹ hr⁻¹ respectively. Their values for x and a were derived from field data col-

lected at Meathop Wood in Great Britain. Utilizing these values they found that the annual maintenance demands of the microbial biomass in Meathop Wood were such that no organic matter would be available for microbial growth, or for growth or maintenance of any other soil organism. In commenting on the obvious unreality of the situation, Gray and Williams (1971) suggested a number of possible sources of error: 1) the yield coefficient used was too small, 2) the estimate of maintenance requirements was inflated, 3) microbial biomass was overestimated, and 4) primary productivity was underestimated.

In an analogous study, Flanagan and Bunnell (1976) attempted to minimize the potential errors inherent in the biomass equation by incorporating laboratory determinations of the specific maintenance rates and yield coefficients of major fungal species in the coastal tundra at Barrow. Values for a and Y' were calculated as $0.32 \times 10^{-3} \text{ g g}^{-1} \text{ hr}^{-1}$ and 0.35 g g^{-1} respectively from data on growth and respiration. The value of Y' obtained by Flanagan and Bunnell (1976) is nearly identical to that calculated in studies of organisms from temperate regions, but the value of a is only one-third of that calculated by Marr et al. (1963) in chemostat studies and used by Babiuk and Paul (1970) and Gray and Williams (1971). Using these coefficients Flanagan and Bunnell (1976) estimated that the average standing crop of fungi in the standing dead grew, maintained and renewed itself at a cost of approximately $10 \text{ g substrate m}^{-2} \text{ yr}^{-1}$. This estimate is compatible with the weight loss from standing dead leaves calculated by converting carbon dioxide respired annually by microbes in the tissue to organic matter (Flanagan and Veum 1974).

The following discussion is an attempt to 1) quantify the annual maintenance demands of an average standing crop of microorganisms in a unit area of *Carex-Oncophorus* meadow, 2) estimate the yearly potential for microbial production on the same area, and 3) examine whether microbial potentials for substrate utilization during growth and maintenance are compatible with estimates of the amount of organic matter produced and decomposed each year.

Microbial Maintenance and Production in the Coastal Tundra at Barrow

Direct counts of bacteria from the soils are sparse. Calculations of microbial utilization of substrate are constrained to estimates based primarily upon biomass, maintenance demands and yield coefficients of fungi.

Utilizing the biomass equation and replacing x by 18.1 g m^{-2} (the average standing crop of microbial biomass to 7 cm depth at the *Carex-Oncophorus* meadow), a by $0.32 \times 10^{-3} \text{ g g}^{-1}$, and Y' by 0.35 g g^{-1} , calcu-

TABLE 9-5. *Standing Crops and Annual Weight Loss of Five Organic Matter Pools*

Organic residue	Standing crop (gdw m ⁻²) ¹	Turnover rate (g g ⁻¹ yr ⁻¹)	Weight loss (gdw m ⁻² yr ⁻¹)
Moribund leaves	90	0.300 ²	27.0
Standing dead	50	0.075	4.0
Litter	75	0.100	8.0
Dead roots, 0-7 cm	100	0.025 ³	2.5
Soil organic matter, 0-7 cm	8000	0.020 ³	180.0
Total	8315		221.5

¹Average values from data collected over 4 years at three sites.

²The losses are due primarily to the downward translocation of materials to roots in fall and to leaching in spring by meltwater.

³Estimated from decay rates of roots and cellulose paper in litter bags inserted in the soil, 1972-1977 (inclusive).

lated maintenance demands are 0.0166 g m⁻² hr⁻¹ or approximately 48 g m⁻² for the period of microbial activity, which is about 100 days.

The annual primary productivity of the *Carex-Oncophorus* meadow both above and below ground, including phanerogams and cryptogams, is estimated to be approximately 200 g m⁻². If 48 g of organic matter m⁻² yr⁻¹ is necessary to maintain the average standing crop of microorganisms, 152 g m⁻² yr⁻¹ remains to be removed by microbial and invertebrate activity or organic matter will accumulate.

Litter-bag estimates of annual rates of decomposition for major substrates in the upper 7 cm of soil (Table 9-5) indicate that 222 g m⁻² is decomposed annually. This is approximately one-half the rate for an ungrazed short-grass prairie (Van Dyne et al. 1978). Minimal annual maintenance requirements of microbes (48 g m⁻²) and invertebrates (7 g m⁻², Chapter 11) could be met easily and would leave about 167 g m⁻² annually for production of microbial and invertebrate tissue. Ignoring invertebrates, the potential number of microbial generations possible can be estimated using the equation of Gray and Williams (1971):

$$Y(s + Nx) = Nx$$

where s = total substrate available to microorganisms (total minus maintenance)

N = number of generations of average microbial biomass

Y and x are as in the two previous equations.

Allowance is made for recycling of microbial tissue towards its own pro-

duction at a rate governed also by the yield coefficient Y , in the term $Y(Nx)$. Solving for N , the total number of average microbial standing crops possible per year, gives 5.0 and 4.3 generations based on measures of total decay and primary production respectively. Observed rates of turnover for fungi in *Carex-Oncophorus* meadows were markedly lower, 1.5 to 3.3 times, varying with depth (Table 8-3). In the troughs, however, observed turnover rates were similar to those calculated, 3.6 to 6.2 times, but fungal biomass was significantly lower. Only in the most productive areas do fungi exhibit values comparable to calculations based on laboratory measurements. In these areas the accumulation of organic matter is lowest (Chapter 7). The observation that litter bags in meadows estimate an annual rate of decomposition greater than annual input from primary production may result from overestimation of the decay rates of untested but apparently more recalcitrant material at depth. The observations do suggest that in the most favorable microhabitats decomposition can approximate primary production. Douglas and Tedrow (1959) observed similar variability in rates of decomposition of organic matter from tundra soils. Highest rates of decomposition were observed from the half-bog soil (*Dupontia* meadows and polygon troughs, Table 1-4). Those rates, 190 g m^{-2} , are comparable to the most rapid rates we have estimated and again suggest no accumulation of organic matter in sites most favorable for decomposition.

If all $222 \text{ g m}^{-2} \text{ yr}^{-1}$ of decomposable tissue undergoes dissolution to carbon dioxide, water and minerals through microbial processes, then, based on an average carbon content of 0.45 g g^{-1} organic matter, decomposers should release carbon dioxide to the atmosphere at an average rate of about $152 \text{ mg m}^{-2} \text{ hr}^{-1}$. If annual primary production is matched by decomposition the estimate of average carbon dioxide evolution is $144 \text{ mg m}^{-2} \text{ hr}^{-1}$.

Root and Microbial Respiration

The annual weight loss from belowground substrates plus surface litter is about $190 \text{ g m}^{-2} \text{ yr}^{-1}$ (Table 9-5). If all of this matter, or an equivalent amount minus the average standing crop of microbial biomass below ground ($190 - 17.5 = 172.5 \text{ g m}^{-2} \text{ yr}^{-1}$), is consumed annually by microbial metabolism, maintenance and growth, it is possible to calculate an average release of $\text{CO}_2 \text{ m}^{-2} \text{ hr}^{-1}$ from Barrow soils that does not include the CO_2 emission of roots.

The average carbon concentration of the soil organic matter in the top 10 cm is about 45% so 172.5 g of organic matter could release 78 g C or 286 g CO_2 . The amount of carbon dioxide released annually (100 days) by microbes would be equivalent to an average respiration rate of $119 \text{ mg CO}_2 \text{ m}^{-2} \text{ hr}^{-1}$.

The question concerning root contribution to total soil respiration is partially answered for Barrow tundra soils. Billings et al. (1977) estimated total soil respiration ranging from 75 to 125 mg CO₂ m⁻² hr⁻¹ in mid-June 1972. During the last week in July 1972, total soil respiration as measured by Billings et al. (1977) ranged from 150 to 300 mg CO₂ m⁻² hr⁻¹. The values of Billings et al. are similar to calculations based solely on microbes, and are somewhat lower than actual field measurements made on root-free soils at Barrow (Benoit, unpubl.).

Flanagan and Veum (1974), using respiration data measured in situ in Barrow tundra soils, calculated the average release of CO₂ from these soils to be in the range 147 to 235 mg CO₂ m⁻² hr⁻¹. The calculated rates do not include root respiration. They are about five times less than measurements made on temperate forest floors (Witkamp 1966) and about three times less than the average measurements made in tundra soils of the Taimyr peninsula, USSR (Aristoskaya and Parinkina 1972), which include root respiration. The comparison between the Soviet and U.S. data above suggests that microbes may contribute around 30% of total soil respiration. This speculation is in general agreement with rates of respiration simulated by ABISKO II (Figure 9-12) which indicate that root respiration may contribute from 33 to 70% of total soil respiration on any given day (Bunnell and Scoullar 1975). This range is somewhat lower than the 50 to 93% contribution by root respiration calculated by Billings et al. (1978).

In summary, the observed rates of microbial turnover in the most productive areas very nearly account for the total input of organic matter. Estimated rates of decomposition below ground are compatible with measures of soil respiration, and indicate that some microtopographic units may not be accumulating organic matter. Estimates of carbon dioxide evolution by decomposition above and below ground range from 2.8 to 5.6 g CO₂ m⁻² day⁻¹ (Flanagan and Veum 1974), in general agreement with estimates of carbon dioxide incorporation by atmospheric flux.

Microorganisms and Mineral Nutrient Cycling

The distribution of nitrogen and phosphorus in various ecosystem components can be calculated using data on nutrient content of live fungal tissues from Flanagan and Van Cleve (1977), and nitrogen and phosphorus content of soils and decaying matter from Chapter 12 and Flint and Gersper (1974). Flint and Gersper estimated that the wet meadow tundra required 6.4 g N m⁻² yr⁻¹ for plant and animal growth. According to the calculations above, gross release of nitrogen by decomposition is about 7.5 g m⁻² yr⁻¹, while the combination of exchangeable and dissolved inorganic nitrogen amounts to 8.0 g m⁻² (Figure 9-13).

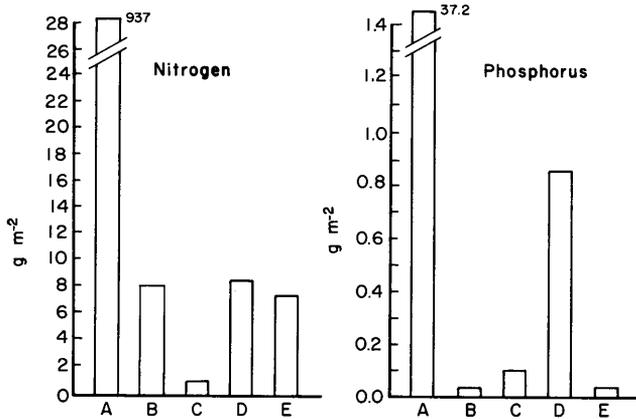


FIGURE 9-13. Total and available pools and potential release rates of nitrogen and phosphorus in the soil calculated for the wet meadow. A) Total amount of nutrient to 20 cm. B) Amount available including dissolved and exchangeable (resin-extractable) phosphorus (Flint and Gersper 1974, Barèl and Barsdate 1978). C) Amount of nutrient in an average standing crop of microbial tissue to 7 cm. D) Potential annual release from tissue assuming 18.1 g m^{-2} microbial biomass, 5.0 generations, and no internal microbial mineral recycling. E) Potential annual release calculated from the nutrient content of the material undergoing decay.

Without including annual input to the system from rain and nitrogen fixation (Chapter 7) there appears to be more than adequate nitrogen for plant growth in the coastal tundra at Barrow. The amount of nitrogen immobilized by the average standing crop of microorganisms (0.8 g m^{-2}) is almost insignificant in terms of available nitrogen plus that generated by decomposition.

The situation is quite different, however, in the case of phosphorus. The average amount of available phosphorus is small, as is the amount of phosphorus released annually in decay processes. The phosphorus immobilized in an average standing crop of microbial tissue is greater than the sum of labile pool plus the annual input via decay (Figure 9-13), suggesting a profound influence of microorganisms on availability of phosphorus in the system. Because tundra microorganisms, except for their resistant propagules, die off each year, they 1) release a relatively large quantity of phosphorus to the soil annually, and 2) are taking phosphorus from the system at levels that are greater than the normal size of

the available pool. These observations indicate a pool of available phosphorus which turns over very rapidly and/or possible limitation to plant metabolism by microbial competition for and immobilization of soil phosphorus.

SUMMARY

Field and laboratory measures have been combined to provide an overall picture of decomposition. The ability of the tundra microflora to utilize substrates varies spatially, with aerobic decomposers showing a marked increase in capacity to degrade cellulose and phenols in the soil, as compared to the phyllosphere. This gradient in potential utilization is accompanied by an increase in anaerobes, and a marked decrease in both zymogenous forms and general microbial biomass. Fungi are better able to utilize cellulose and phenolic substrates than are bacteria. Unfortunately, the enzyme capabilities of the anaerobic microflora remain unknown, but no anaerobic decomposers of aromatic compounds are known from other areas.

Respiration rates of the microflora are governed in a predictable fashion by temperature, moisture, and substrate chemistry. Respiration rates are shown to be the dominant influence on weight loss from substrates. Substrate chemistry establishes a potential maximum rate which is modified by abiotic variables. Ethanol-soluble compounds generally are respired 5 to 7 times more rapidly than non-ethanol-soluble compounds, but some substrates (e.g. *Dryas* leaves) apparently contain substances inhibitory to microbial respiration.

Both bacteria and fungi show adaptations to cold. Microbial respiration continues to -7.5°C and fungal growth is still positive at 0°C , indicating greater levels of activity at low temperatures than are observed in vascular plants. Many microorganisms in colder strata of the environment show linear rather than exponential responses with increasing temperature, suggesting adaptation to cold through more rapid response to small increases in temperature. Cold-adapted microorganisms, especially fungi, increase in numbers from the phyllosphere into soils, while in the upper regions of the soil microbial populations display a wider range of temperature optima and mesophilic forms are more prominent. Among the fungi, psychrophiles, thermotolerant psychrophiles and cold-tolerant mesophiles retain the capacity to utilize structural plant carbohydrates at temperatures below 0°C , while aerobic bacteria are largely restricted to non-structural plant components at 0°C . As bacteria can use the products of fungal decomposition of large molecules, it is possible that co-evolution has permitted the development of different enzymatic responses to low temperatures.

Moisture levels above 20% dry weight are necessary to initiate microbial metabolism, while levels much above 400% dry weight attenuate microbial activity. Oxygen, carbon dioxide, and temperature relations interact with moisture levels to obscure definition of optimal moisture levels for decomposition. Shifting bacterial:fungal ratios along oxygen gradients indicate that oxygen availability and/or moisture alters the numbers and character of participants in decomposition. Large numbers of facultative anaerobic bacteria in litter and soil reflect a commonly occurring niche. Although present, obligate anaerobes are major contributors to decomposition only in heated soils.

Perhaps because of microbial adaptations to low temperatures, organic matter does not appear to be accumulating in some microtopographic units. Only the fungi are capable of degrading the larger compounds, particularly at low temperatures. The fungi, however, are restricted by high levels of moisture to the upper 7 to 10 cm of soil, and organic matter may accumulate at depth. The nutrient dynamics within the soil also suggest that phosphorus, but not nitrogen, immobilized within the standing crop of microbial tissue may be a factor limiting nutrient availability to vascular plants.