AN ABSTRACT OF THE THESIS OF

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Title: SOLUBLE CARBON AND RESPIRATION OF FOREST HUMUS

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Humus is one of the important factors controlling the soil formation process. The nutrients released from it during the decomposition process also affect the growth and reproduction of the forest. The type of humus formed is influenced by the nature of the forest litter and the environment in which it is decomposed.

The whole complex of processes by which plant residues are transformed and finally converted into humus is the result of the combined activity of associations of microbes exhibiting diverse biochemical functions. The respiratory activity in the forest floor decreases with progressive stages of decomposition and humification. This reflects the chemical composition and availability of the remaining carbon compounds as energy source material. It appeared that the content of total soluble carbon might serve as an index of the stage of decomposition and humification.

As a mild oxidizing reagent, potassium persulfate oxidizes

only the water soluble materials in the temperature range of 70° C to 75° C. A water extraction-potassium persulfate oxidation technique was used for the estimation of total soluble carbon content of forest floor materials. Extraction time and the efficiency of the persulfate oxidation of the extract were also investigated.

Continuous aeration and electrolytic respirometer techniques were used for the respiration study and for comparison with the persulfate oxidation technique.

A variety of representative forest floor materials from different forest types in Eastern North America and the Coast Range of Oregon were studied both for respiratory activity and for water soluble carbon content. A highly significant positive correlation was found between levels of water soluble carbon and CO_2 evolution in these samples.

In the areas sampled in the eastern United States and Canada, a majority of the well humified layers (H) gave respiratory carbon/soluble carbon ratios of 1. Most of the less humified samples showed ratios near 1.4. Materials from Douglas-fir forests having low soluble carbon levels had considerably greater respiratory carbon/soluble carbon ratios than the low soluble carbon materials from eastern forests.

The advantages of the persulfate oxidation method over the respiration method are that it is less time consuming, few materials

are required and better control can be exercised. Since the water soluble carbon as determined by the persulfate oxidation test may be expressed in terms of respiration, where good correlations are established, it appears that either the soluble carbon value itself or the correlated respiratory activity may be used as an indicator of the stage of humification. Thus a much more rapid, less tedious means of evaluating the status of forest floor materials is available.

Soluble Carbon and Respiration of Forest Humus

by

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SOLUBLE CARBON AND RESPIRATION OF FOREST HUMUS

INTRODUCTION

Forest litter exerts a marked effect upon all processes taking place in the soil. Forest soils are characterized by large amounts of organic matter decomposing on the forest floor. As decomposition proceeds colloidal organic compounds are synthesized. The distribution, transformation, and accumulation of these compounds determine the nature of the forest humus layers and influence soil formation. The properties of this humus markedly influence the amount of nutrients available for the growth and reproduction of the forest. Differences in humus type have been regarded as indicative of differences in site productivity (Ovington, 1954 and Kornev, 1962).

Variations in the character of the humus layer usually have been associated with the rate of decomposition (Marten and Pohlman, 1942). There is no doubt that microbial activity is one of the most important factors in the process of humus formation. A whole complex of processes by which plant residues are transformed and finally converted into humus are the results of the combined activity of associations of soil organisms exhibiting diverse biochemical functions and enzymatic and chemical reactions.

The carbon content of forest litter is over 50 percent. Organic

carbon is the main energy source for the dominant heterotrophic microorganisms and since most of this is oxidized to obtain energy, CO_2 is a common metabolic waste product of their activity. Various intermediate products may be formed, but these are later attacked by other microorganisms and sooner or later are completely oxidized. Waksman (1952) concluded that about 85 percent of the total carbon dioxide liberated from the soil is due to the activity of microorganisms. Thus, the evolution of CO_2 is not only an index of the activities of the microorganisms of the soil but also of the availability of the soil organic matter.

The "respiratory power of the soil", which reflects the condition and decomposition of the organic matter in the soil, is governed by many chemical and physical factors which influence the activity of microorganisms. However, other factors being favorable the amount and nature of the readily available organic matter, or energy source, is believed to be the dominant controlling factor.

Early in this century, Stoklasa (1912) pointed out that the production of CO_2 was in direct proportion not to total carbon content, but to the available organic matter in the soil. Stotzky and Mortensen (1957) found that N was not a factor limiting decomposition of an Ohio muck, but a readily available carbon source was. Gooding and McCalla (1945) found that the amount of readily available energy material determined the amount of CO_2 evolution from crop residues.

Broadfoot and Pierre (1939) showed that a high correlation existed between the water soluble organic matter and decomposition during the early stage of humification of forest litter. Irrespective of the type of flora, the early decomposition involved principally the water soluble portions. It is possible for the level of the water soluble portions to remain nearly constant as a result of being continually produced during the break-down of more complex constituents. It is understandable now that regardless of the structural peculiarities of the starting material, the carbon in the substrate will ultimately be metabolized through the same final steps and via the same intermediates. The main difference is probably in the solubilizing process by various extracellular enzymes.

The objectives of this study were to determine

1. If there is any correlation between respiration and the levels of water soluble carbon in forest floor materials.
2. If soluble carbon values can serve as an index of respiratory levels and stage of decomposition and humus development.

LITERATURE REVIEW

Soil Organic Matter

Forest Floor

The organic fraction of the soil consists of a complex group of substances and exists in a dynamic state. It is subject to continual changes during the processes of decomposition and resynthesis.

In forests, the principal sources of organic matter are the stems, branches, roots, bark, fruits, seeds, and leaves of trees. The shrubby and herbaceous understory contribute varying amounts depending on the nature of the forest stand. As a result of the interaction of climate, soil conditions, and vegetation, the end products of biological decomposition and resynthesis are distributed in the profile giving rise to a number of characteristic humus types. Forest humus consists not only of the humified organic matter, but also of the surface materials in varying stages of decomposition. Based on the stage of decomposition three separate layers are recognized (Lutz and Chandler, 1947).

1. Litter (L) layer--freshly fallen material.
2. Fermentation (F) layer--material that is undergoing decomposition but is still recognizable as to source, i. e., leaves, twigs, cones, etc.

3. Humus (H) layer--humified, amorphous organic matter.

Based on the morphology and distribution of these layers, forest humus has been classified into three main groups (Hoover and Lunt 1952):

1. Mull: forest floor consists of the L and F layers with the H layer being incorporated into the mineral soil as an Al horizon. The transition from the F layer to the mineral soil is not sharp.
2. Mor: forest floor consists of the L, F and H layers. The boundary between the H layer and the mineral soil is sharp. The H layer is usually matted or compact.
3. Duff-mull: This is a transitional type with the forest floor consisting of the L, F and H layers but with some of the humified material also being incorporated in the mineral soil to form an A1 horizon.

Mull humus is generally associated with the hardwood forests or coniferous forests growing in relatively mild climatic zones, e. g., Douglas-fir. Mor humus generally develops under coniferous forests in cool humid climates. Mor humus is generally more acid than mull.

Hardwood litter is usually higher in nitrogen and lime than coniferous litter; thus, there is a higher number of bacteria and lower number of fungi in hardwood litter than in coniferous litter

(Witkamp, 1963).

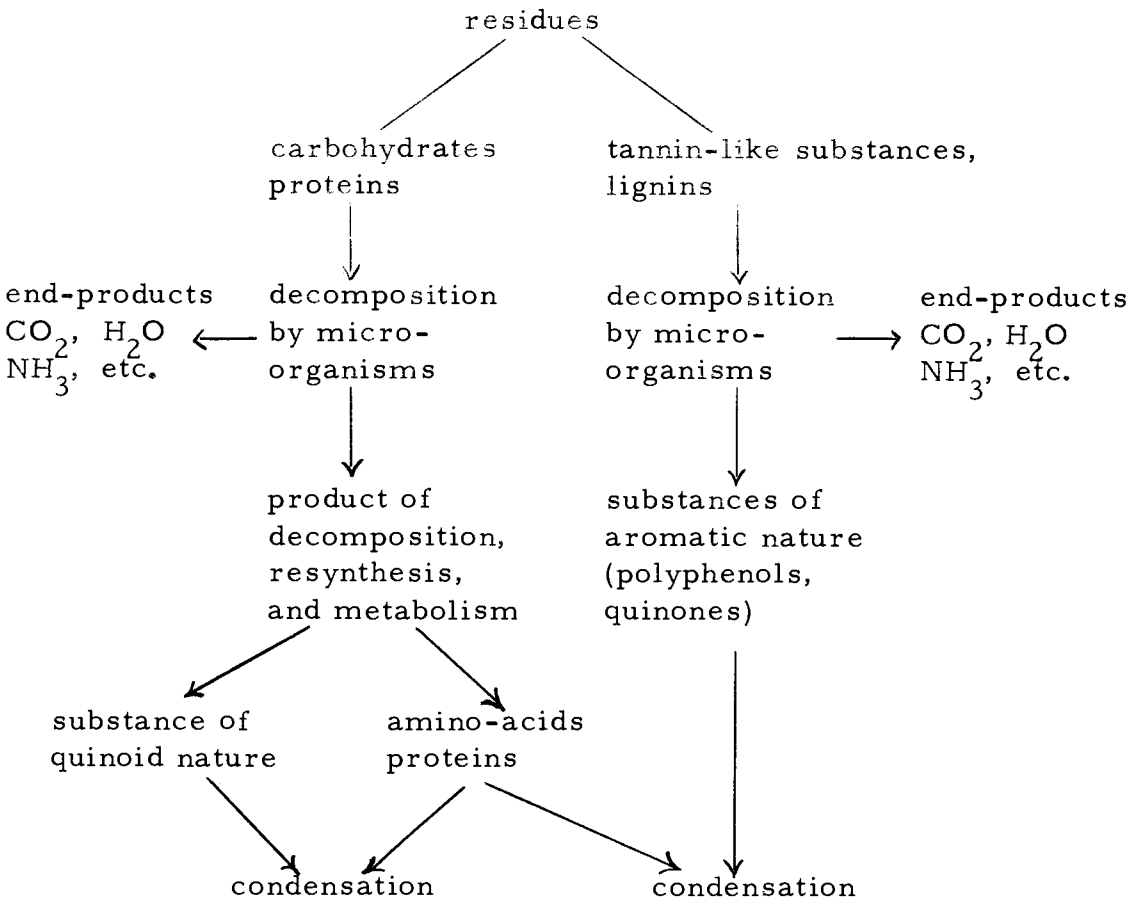
Pearsall (1952) pointed out that a striking feature of mor in Britain was the usual absence of nitrate because of a very low rate of nitrification. Ivarson and Sowden (1959) also noted that the nitrification process occurred in deciduous litter but did not occur in conifer litter. After an exhaustive review of humus development, Handley (1954) concluded that mor humus contained greater quantities of cellulose than mull, its nitrogen exhibited a higher degree of resistance to mobilization, and it was more likely to form in acid habitats. He concluded that the main difference between mull and mor formation was in the type of decomposition and resynthesis, rather than in the rate of decomposition of litter. Handley (1961) found that a leaf protein precipitating material was an important factor influencing the process leading to mor formation.

Biochemistry of Humus Formation

The organic material in soil is continuously being replenished by the addition of plant and animal residues; and its transformations are achieved primarily through action of biological factors. Therefore, in humus there are components of organic residues undergoing decomposition, and metabolic products of microorganisms or products of secondary synthesis in the form of microbial tissues.

A schematic outline of the process of humus formation given

by Kononova (1966) is presented below:



Function of Humus

Upon incorporation with mineral soil, humus serves physically as a cementing agent improving soil structure, porosity, permeability, aeration and water-holding capacity; chemically, it holds phosphorous and other elements in more soluble forms and improves the buffering capacity of the soil; biologically, it serves as a storehouse of plant nutrients. Under appropriate conditions, the slow but

gradual decomposition of the organic matter by microorganisms results in the liberation of a continuous supply of carbon dioxide, of available nitrogen as ammonia, which may soon be changed to nitrate, of phosphorous, and of other elements essential for plant growth. It also provides a favorable medium for the growth of microorganisms thus enhancing the biological weathering of nutrient bearing minerals. In addition, the biochemical processes involving humus produce specific organic compounds which are beneficial to the growth of higher plants. These growth regulating substance known as auxins are produced by microorganisms in the course of decomposition of plant remains.

Respiration

Organic residues can be broken down by either physical forces, as from rainfall, wind, and soil cultivation; chemical forces, as from a strong alkaline solution, or weak and strong acids; or residual plant cell enzymes; or condensation; or polymerization. However, it is generally believed that none of these factors individually, or in combination, can bring about humification in the absence of the activity of microorganisms and animals. Microorganisms function not only in the decomposition of original organic residues but also in the synthesis of organic compounds with the formation of high molecular weight humus substances of specific nature.

Corbit (1934) found that the evolution of CO_2 was proportional to the numbers of microorganisms present when the population was increasing. On the other hand, as population decreased, the relationship between number of microorganisms and CO_2 production was weak. This might be due to a low level of activity by all organisms or by inactivation on the part of some groups of organisms. Ivarson and Sowden (1959) observed that the type of microbial population was not as important as the type of litter or other factors in determining the decomposition rate. Alexander (1964) also reported that considering the diversity of microbial types and the variety of carbon sources, a poor relation between number and CO_2 formation was not surprising.

Witkamp (1963) has suggested that in order to obtain a valid evaluation of the relationship between numbers of organisms and litter decomposition by microbial count techniques, samples must be taken periodically throughout the whole season.

Several techniques have been developed to measure decomposition rates. These include:

1. Measurement of CO_2 evolution or O_2 uptake.
2. Determination of the decrease in organic matter either chemically or by weight loss.
3. Observation of the disappearance of specific constituents such as lignin.

Indicators of Respiration

CO_2 Evolution. Wollny (1897) was the first to show that the CO_2 content of the soil rises and falls with the amount of organic matter present in the soil. Stoklasa (1926), who did some of the first fundamental work in soil respiration, calculated that certain bacteria produce 2 to 2.5 grams CO_2 per 100 grams cell substance per hour. Van Suchtelen (1910) noted that the intensity of CO_2 production was greatest at the beginning of an experiment and rapidly decreased after a short time. He also pointed out that the measurement of CO_2 evolved from different soils furnished a better means for estimating the microbiological activities in the soil than did the number of bacteria. Since autotrophic microorganisms make up only a small portion of the total number of soil microbes, Starkey (1924) concluded that the CO_2 produced from soil gives a reliable although not an absolute index of the decomposition of organic matter. He also noted that for most types of organic matter, different soils showed essentially the same decomposition trend.

O_2 Uptake. Russell (1905) measured the actual amount of oxygen absorbed by the soil as an index of soil oxidation. The amount of oxygen absorbed measures the total action of microorganisms, which are responsible for the decomposition process in the soil. In the natural soil system, a considerable amount of carbon is directly

incorporated into cell substance and thereby does not undergo complete oxidation. Thus Bunt and Rovira (1955) and Katznelson, et al. (1956) all concluded that the Warburg method for the determination of oxygen uptake gave an accurate measure of respiratory activity in soil. Drobnik (1960) demonstrated that the oxidation process consists of two principal parts: (1) primary oxidation which occurs while the substrate is still present and (2) secondary oxidation after the disappearance of the substrates. The primary oxidation is brought about by two different components: (1) the oxidative component represents the potential of enzyme activity in the soil, and (2) the assimilative components built up during the decomposition process by synthesis of microbial enzymes. The size of the oxidative component is a measure of an actual activity of the microflora.

Soluble-Carbon. The rate of decomposition of various plant and animal residues in the soil is controlled in part by the structure and composition of the organic compounds which influence their availability as energy sources. Stoklasa (1912) and Gehring (1922) have shown that the formation of CO_2 in the soil depends not only on the absolute carbon content of the soil, but on the ease of its decomposition. Birch (1959) observed that the flush of decomposition that followed the moistening of a dry soil was due to more organic material being brought into solution and made available to soil microbes.

Under certain laboratory conditions a chemical reaction can be

controlled so that a weak oxidizing reagent such as potassium persulfate will oxidize only the soluble substances in water (Osburn and Werkman, 1932). With the development of combustion flasks (Katz, Abraham and Baker, 1954) and their further modification by Gilmour et al. (1961), the persulfate oxidation procedure can be used for accurate determination of soluble carbon in a wide variety of water soluble compounds including carbohydrates, fatty acids, alcohols and amino acids.

Factors Influencing Soil Respiration

Under comparable temperature and moisture conditions, the amount and composition of organic matter, soil texture and carbon-nitrogen ratio are three main factors influencing respiration (Bollen, 1941). Due to the heterogeneous nature of the carbon sources, it is commonly believed that the composition of humus varies considerably. Other factors held to influence humus composition are mineral parent material, topography, soil properties, climate, ground water conditions, and soil microflora and fauna. Increases in respiration result from adding a source of energy and of nutrients for microorganisms. As a general rule, the richer in nutrient materials plant remains are, the more readily they decompose. Additions of nitrogen fertilizer or nitrogen-rich green manures reportedly promote the decomposition of native soil organic matter (Broadbent and Norman, 1946;

Chapman and Liebig, 1946). The significance of the C/N ratio is related to the nutritional requirements of organisms active in the decomposition. A high nitrogen content favors rapid decomposition. Since nitrogen is the limiting factor, it is necessary to add nitrogen to materials with wide C/N ratios. Using C^{14}, Bingeman, Varner and Martin (1953) showed that addition of the insoluble fraction of alfalfa causes a larger breakdown of native organic matter than addition of the soluble fraction alone or the addition of complete alfafa. Overrein (1967), using N^{15}, observed a positive correlation between incubation temperature and overall nitrogen turnover in raw humus after nitrate application and a negative correlation between incubation temperature and net accumulation of nitrite and nitrate-nitrogen after addition of urea. No significant amount of nitrite or nitrate was detected in the humus after ammonia application. At lower temperatures, nitrogen added as ammonia was used more rapidly than that added as nitrate in supplying the needs of the microorganisms decomposing raw humus. Compared with the ammonia and nitrate treatments, the preferential utilization of nitrogen added as urea generally increased with increasing incubation time and temperature.

In the field, temperature and moisture are two of the most important ecological factors in soil life. In East Africa, Birch (1956) noticed that the amounts of organic matter and nitrogen in the soil were fairly high. He attributed this to high rainfall. Moisture content

is not as limiting a factor in humus accumulation at lower temperature as at higher temperature.

Relation to Ecology

Nutrients stored in various components of the forest floor are intimately related to the maintenance of soil fertility. The rate at which nutrients, especially nitrogen, are released to plants is an important ecological factor which considerably influences the type of plant association. Although nitrification is not an essential factor, it does enhance the production of nursery stock and regeneration of forest.

Ovington (1954) showed that the surface accumulation of organic matter is, in general, greatest where percentage carbon is high and pH, percentage nitrogen and ash are low. Mull humus is advanced in the process of decomposition and contains more nitrate and less carbon than the mor type. Mor humus usually contains only traces of available nitrogen but considerable quantities of combined nitrogen. Liming and cultivation increases nitrate production in mor humus (Waksman, Tenney, and Stevens, 1928).

As previously mentioned, successive dryings accelerated respiration. Any cultural practice that enhances soil drying such as burning, exposure of bare surfaces following ploughing should hasten the loss of soil carbon. Kornev (1962) found that a dense undergrowth

associated with a forest stand, increased the biochemical activity of the litter. Preliminary studies of forest floor materials from Douglas-fir stands revealed considerable variation in CO_2 evolution and nitrogen mobilization from samples from stands with different understory species composition.[1]

Fenton (1958) showed that a greater amount of nitrogen was released from soil to which birch litter had been added than from soil to which pine litter had been added. Voigt (1965) concluded that although considerable variation in availability of nitrogen to Douglas-fir seedlings existed in soil cultures where nitrogen originated from decomposing leaf tissue or from humus samples, a 60-90 percent recovery of original nitrogen was obtained.

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[1] Personal communication with Dr. C. T. Youngberg, Department of Soils, Oregon State University, Corvallis.

MATERIALS AND METHODS

Sampling Procedures

Forest floor samples were collected in Douglas-fir stands in the Coast Range of Oregon and in a wide variety of forest stands in Eastern North America. In each stand six one-square-foot samples were collected down to the mineral soil. In the Douglas-fir stands this consisted of the combined L and F layers, with the F material making up the bulk of the sample. The Douglas-fir samples were collected by Mr. Charles Tarnocai from four stands of each of the following understory vegetation types: ocean spray-salal, salal, vine maple-salal, salal-sword fern, vine maple-sword fern, sword fern, salmonberry-sword fern and sword fern-oxalis. Samples were also collected in a dense Douglas-fir stand without understory vegetation.

The samples from forests in eastern North America were collected by Dr. C. T. Youngberg while he was on a sabbatical leave. In many of the stands sampled it was possible to separate the L, F and H layers. Where possible this was done. In some hardwood stands there was no H layer development and in these a combined L and F layer sample was taken. Information on stand location, forest type, and kinds of samples taken is presented in Appendix Table 1.

Samples were dried in circulating air oven at 70°C for 48 hours and ground in a Wiley mill to pass a 20-mesh screen. Depending on the amount of material all six sub-samples from each stand were composited or sub-samples 1-3 and 3-6 were combined for two composite samples. If the original samples were large they were not combined. Prepared samples were stored in wax lined bags that were stapled shut to minimize absorption of moisture.

Chemical Analysis

Total N was determined using a micro-Kjeldahl method. Analysis for percentage of other elements was determined on 1 g of material which was digested in nitric and perchloric acids. The digested material was diluted, filtered and made up to a volume of 100 ml with distilled water. Aliquots of this solution were used for analysis. Potassium was determined by flame photometry. Phosphorus was determined with a vanadomolybdophosphoric yellow color method in which nitric acid was used in place of sulfuric acid (Jackson, 1958). Calcium and magnesium were determined on the Perkin-Elmer Atomic Absorption Spectrophotometer Model 303. To prevent the tying up of either Ca or Mg with phosphate or sulfate, 1,500 ppm Sr were added to the diluted aliquot of the digest. Volatile matter was determined by igniting a ground sample at 600°C for one hour in muffle furnace.

Experimental Procedure

Prior to running the CO_2 evolution, O_2 uptake and soluble carbon experiments, the moisture content and saturation capacity were determined by standard methods for all samples used.

CO_2 Evolution

In the first experiment, 25 g samples were used and in all subsequent experiments 15 g samples were used. Sample weights were on a water-free basis.

Duplicate samples were placed in 250 ml Erlenmeyer flasks and adjusted to 50 percent of saturation capacity. To facilitate uniform wetting the samples were shaken on a rotary shaker for five minutes.

A continuous aeration apparatus (Bollen, 1941) was used. Air was passed through a series of alkaline and acid solutions (ten percent NaOH, ten percent H_2SO_4, ten percent $Ba(OH)_2$ and distilled water) to remove CO_2 and to prevent the samples from drying out. The CO_2 free, moist air was passed over the moist samples and the CO_2 evolved was absorbed in 8 ml of N NaOH contained in 3/4" x 6" collection tubes which were changed every three days at the beginning of the experiment and weekly after two weeks. The first experiment was run for 63 days. Subsequent runs were 30 days. Determination

of absorbed CO_2 was made by double titration (Cooper, 1941) using a Beckman model K automatic titrimeter. Results were expressed as cumulative carbon evolved as CO_2 in mg per g of forest floor material.

O_2 Uptake

A modified electrolytic respirometer (McGarity, Gilmour and Bollen, 1958) was used for O_2 uptake studies. An eight percent Na_2SO_4 sclution was the electrolyte used for the generation of oxygen and a small vessel containing ten percent KOH solution was placed in the respiration vessel for the adsorption of evolved CO_2. Fifteen gram samples of forest floor material were used and adjusted to 50 percent moisture content. The volume of oxygen consumed equalled half the volume of hydrogen collected in the gas burette. Carbon dioxide determination was by the double titration method (Cooper, 1941) using Beckman automatic titrimeter.

Soluble Carbon

Duplicate 10 g samples were placed in 250 ml Erlenmeyer flasks. An excess of 100 ml of distilled water over saturation capacity was added for extraction of soluble carbon. The samples were shaken on a reciprocating shaker. Different lengths of shaking time were compared. After shaking, the samples were filtered

through a Büchner funnel.

For combustion, a wet persulfate oxidation technique was used (Gilmour, et al., 1961). A 50 ml Erlenmeyer type flask is fitted with a center well, large enough to receive a glass vial for carbon dioxide absorption. The vial has a built-in prong to facilitate removal by either metal or glass tongs. A rubber serum cap completes the flask assembly.

Duplicate aliquots of each sample extract were pipetted into the flask, the volume adjusted to 5 to 10 ml with distilled water and 0.3 ml of 5 N H_2SO_4 added. The addition of acid liberates any free carbonate or bicarbonate. Then, after swirling the flask gently, 1.0 ml of four percent $AgNO_3$ was added both to precipitate free chlorides and to act as a catalyst for the oxidation process. Approximately 1.5 to 2 mg of potassium persulfate were then added and the flask swirled to distribute the persulfate. About 2 ml of 5 N NaOH were added to the center well vial and the vial placed in the center well by means of the tongs. The serum cap was wetted and tightly fitted at the neck of the flask. A rubber band was also used to improve sealing. The vessel was evacuated by inserting a 20-gauge hypodermic needle through the rubber stopper. This step effects removal of any dissolved carbon dioxide and promotes the efficiency of the NaOH solution for the absorption of CO_2. The flask was then placed in an oven at 70° to 75° C for two hours. The flasks

required little attention below 75° C. Above 75° C, the evolution of CO_2 becomes too vigorous and forces the cap out. After cooling, the serum cap was removed and the contents of the center-well vial washed into a 50 ml Erlenmeyer flask. Again, CO_2 was determined by double titration with Beckman autotitrimeter. The reaction of the forest floor extract was determined using a Beckman zeromatic pH meter. This determination was made no later than two days after extraction.

In order to determine the completeness of oxidation from soluble organic carbon to carbon dioxide the following steps were taken.

1. Different volumes of sample extract were oxidized by the same quantity of reagent.
2. Reoxidation was made on the same sample extract immediately after the first oxidation to ensure the completion of oxidation.

RESULTS AND DISCUSSION

CO_2 Evolution

Moisture is one of the environmental factors controlling development of microorganisms. Moisture deficiencies result in reduced rates of moisture diffusion and microbial growth and ultimately the organisms go into a dormant or spore stage. The length of the dormant stage is influenced by environmental conditions such as moisture, temperature, pH and other factors. As a result of moisture excess the physiology of organisms will be affected chiefly by the resultant effects on free oxygen supply. The moisture capacity of soils varies not only with texture, but also with structure and organic matter content. For general soil microbial activity, the optimum moisture content is commonly considered to be approximately 50 percent of saturation capacity (Waksman and Starkey, 1924). Since the CO_2 evolved in soil respiration results from the combined activities of all microbes present, anaerobes as well as aerobes, and autotrophs as well as heterotrophs, and since each kind possesses characteristic respiratory powers, it is evident that the optimum moisture for this general microbial function is determined by a complexity of interrelationships. Although such definite functions as ammonification, nitrification and nitrogen fixation apparently have definite moisture optima, an optimum range rather than an

optimum point would seem more likely to apply to CO_2 evolution (Bollen, 1941). Within this range, a change in moisture content might increase respiratory action of some species while decreasing that of others. Saturation capacity data for the samples in this study are summarized in Appendix Table 2.

Respiration was studied on samples from a wide variety of stands and representing different stages of decomposition and humification. CO_2 evolution curves from selected samples are presented in Figures 1-8; the remainder of the data are summarized in Appendix Table 3.

The first experiment, using 25 g samples was continued for a period of two months. The curves in Figure 1 indicate a sustained though diminishing evolution of CO_2 with time. After one month, the data already revealed differences in respiration among samples. Although the trend of differences in CO_2 evolution continued for the remainder of the experimental time, the differences were well established in the first four weeks. This phenomenon agrees in general with the statement that under uniform conditions in the laboratory the most extensive changes take place during the first few weeks; after prolonged incubation an equilibrium condition is attained (Potter et al., 1916 and Waksman et al., 1924). Thus it appeared that a 28 days period would be adequate for the remainder of the experiments. CO_2 evolution curves for the remainder of the

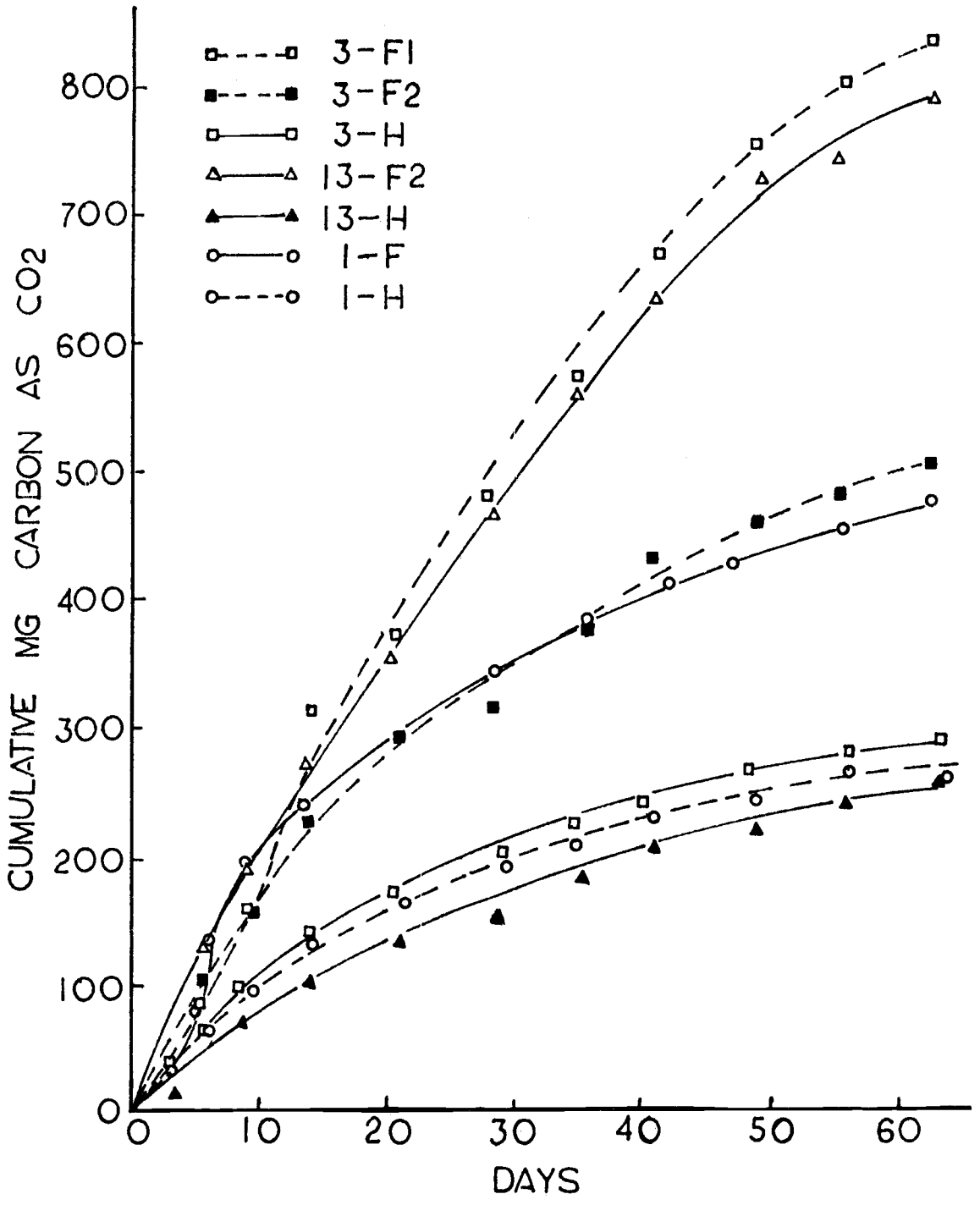

Figure 1. CO_2 evolution from forest humus layers from Eastern North American Forests. (For sample identification see Appendix Table 1.)

samples from eastern forest samples are given in Figures 2 to 7.

Although sustained evolution of CO_2 occurs with prolonged incubation, the order of respiratory power of the different forest floor materials varies little during the course of incubation. Materials which are high or low during the initial period are also high or low at the end of the incubation period. Under similar temperature and equivalent moisture conditions, the respiratory properties of forest humus tends to be affected mainly by the stage of humification. Samples from the litter layer (L), which are composed of freshly fallen materials, respire at a higher rate than those from partially humified F layer and from thoroughly humified H layer. F layer materials also have a higher respiration rate than those from H layers. The data presented in Figures 1 through 7 indicate the following rates of CO_2 evolution: L > F > H and LF > F1 > F2. It is evident from these data that the biochemical activity in the forest floor decreases with progressive stages of decomposition and humification. This reflects the chemical composition and availability of the carbon source in the materials. Both Waksman (1952) and Kononova (1966) have pointed out that microbes play an essential role in the decomposition of organic matter. It is reasonable to believe that the difference in CO_2 evolution ability is due mainly to the use of the most available forms of organic substances by microorganisms and to the accumulation of the forms that are of low availability. Freshly

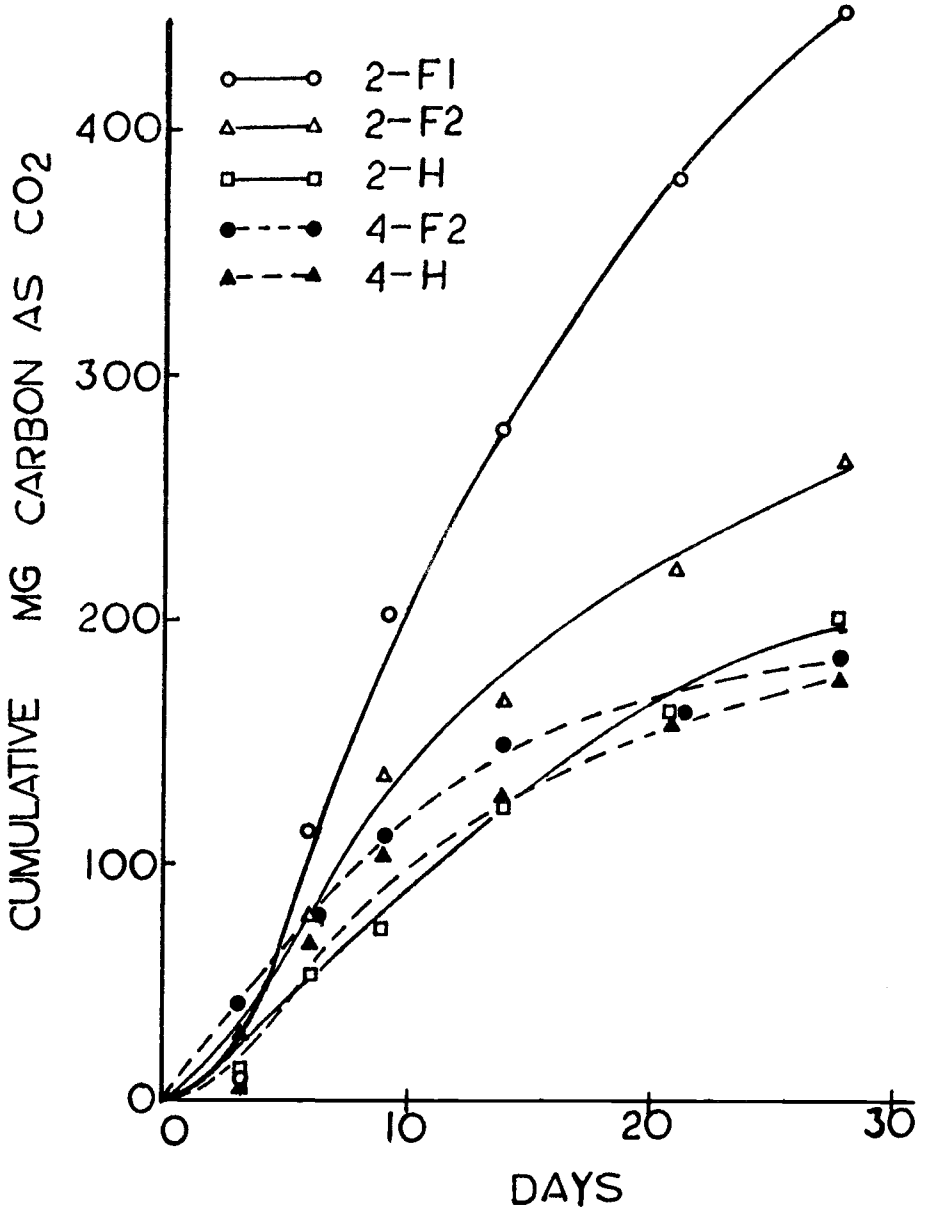

Figure 2. CO_2 evolution from forest humus layers from Eastern North American Forests.

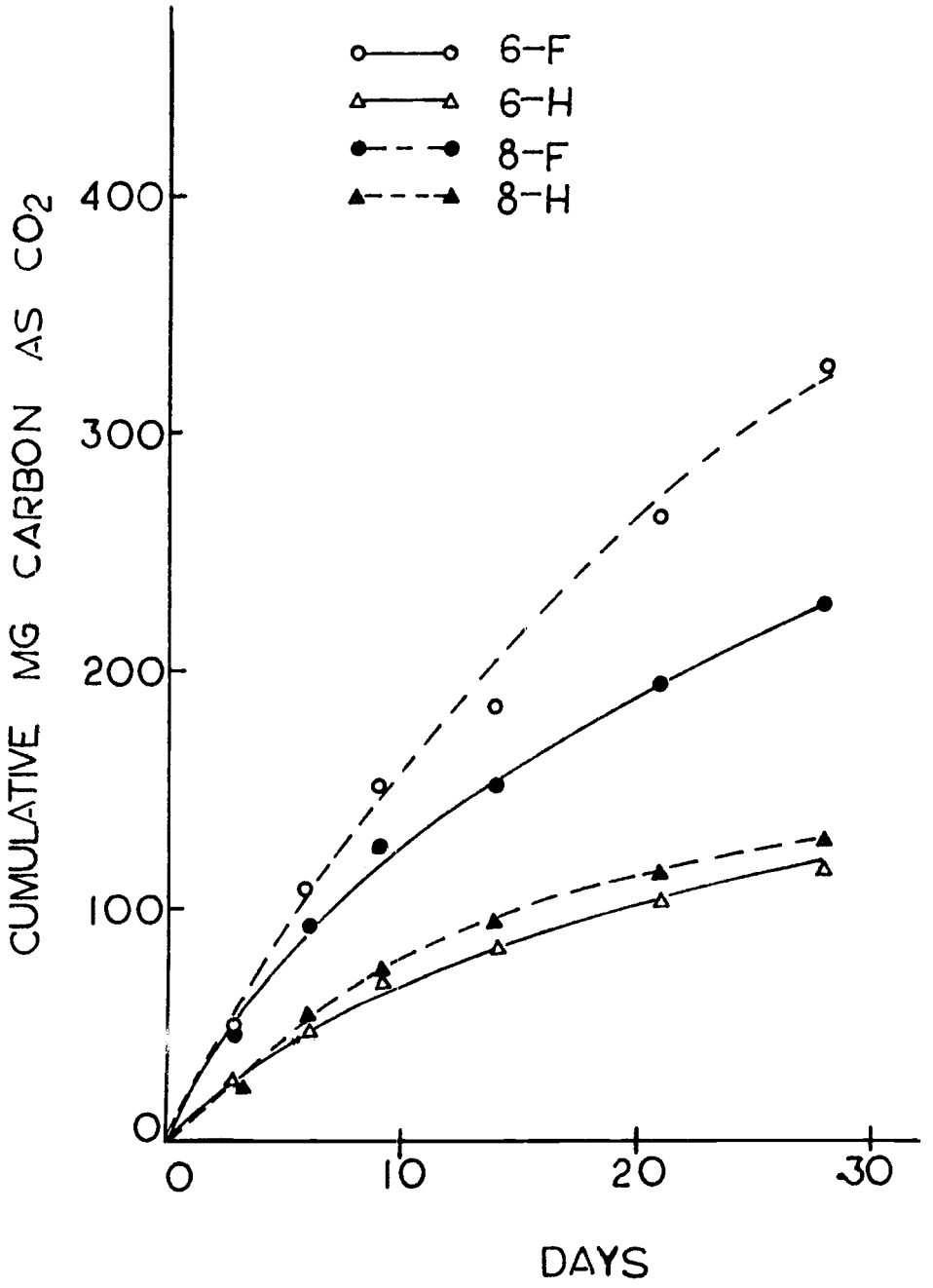

Figure 3. CO_2 evolution from forest humus layers from Eastern North American Forests.

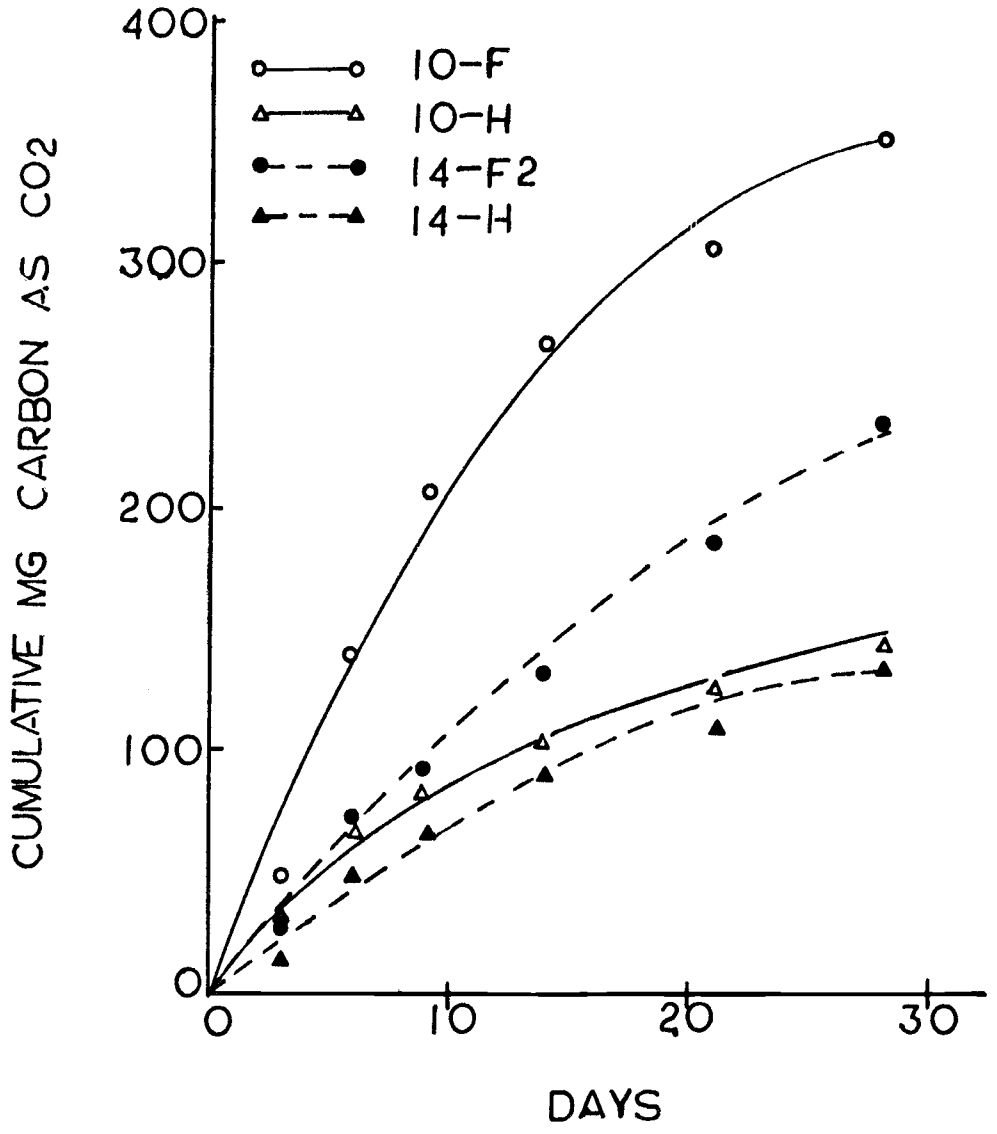

Figure 4. CO_2 evolution from forest humus layers from Eastern North American Forest.

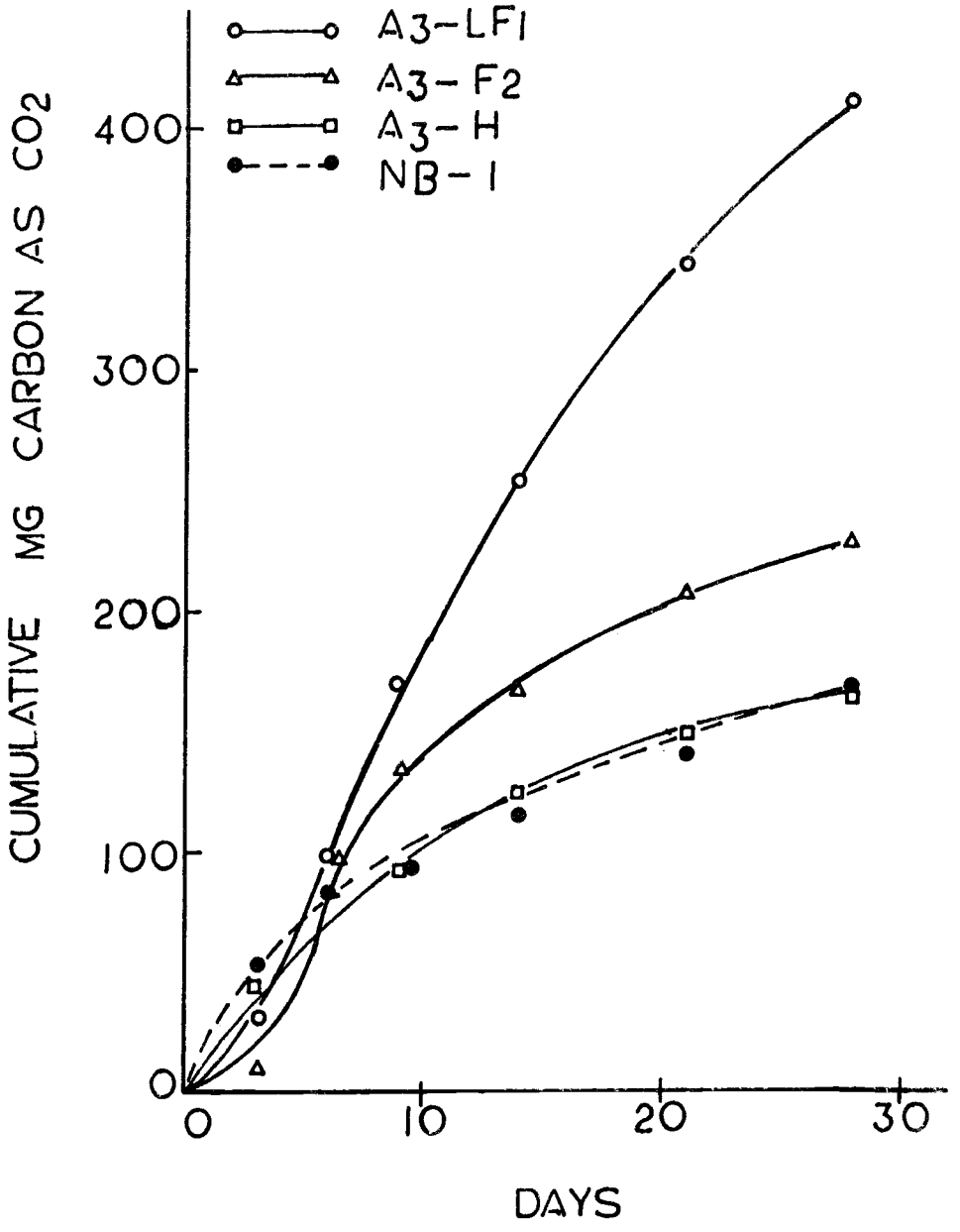

Figure 5. CO_2 evolution from forest humus layers from Eastern North American Forests.

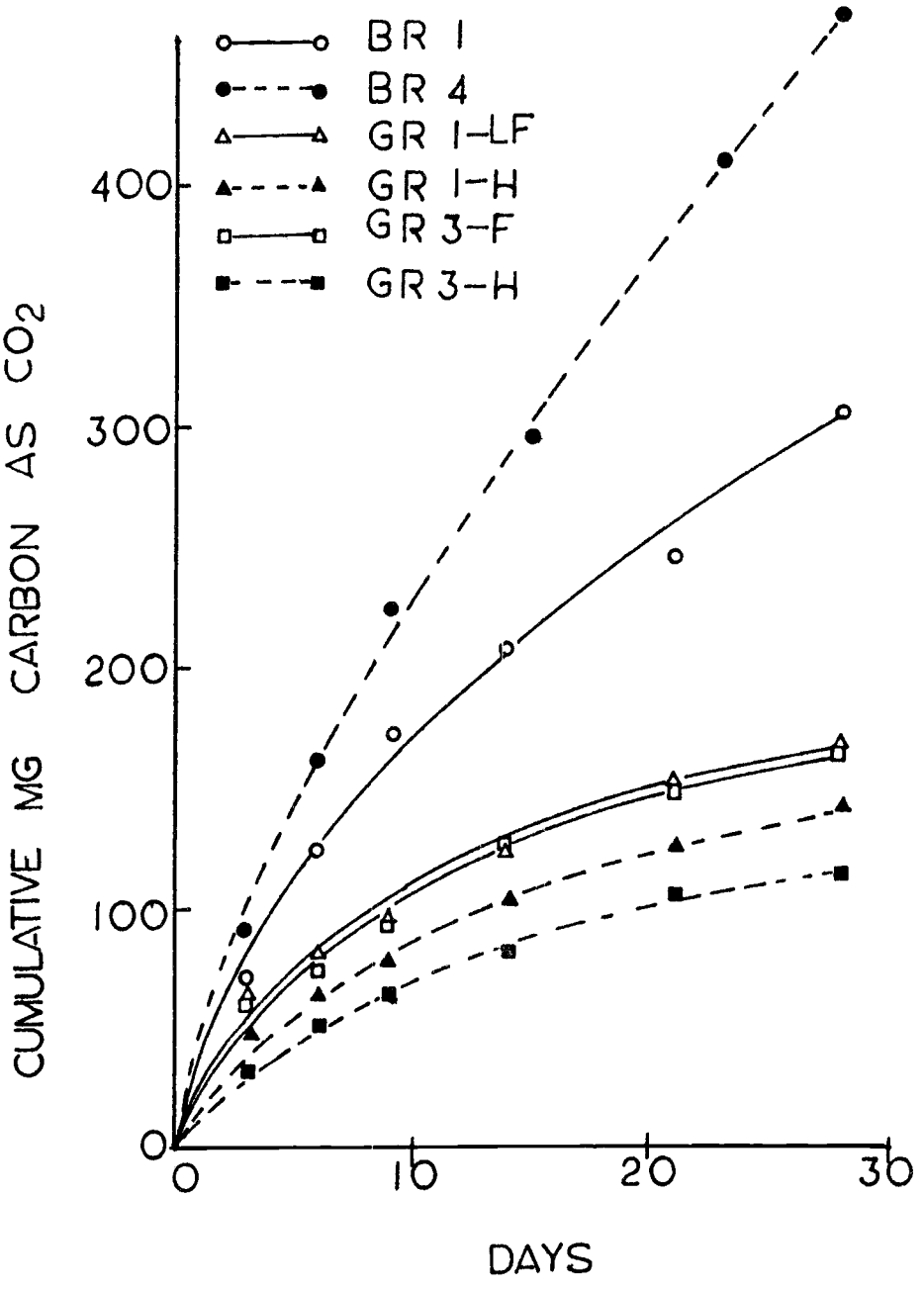

Figure 6. CO_2 evolution from forest humus layers from Eastern North American Forests.

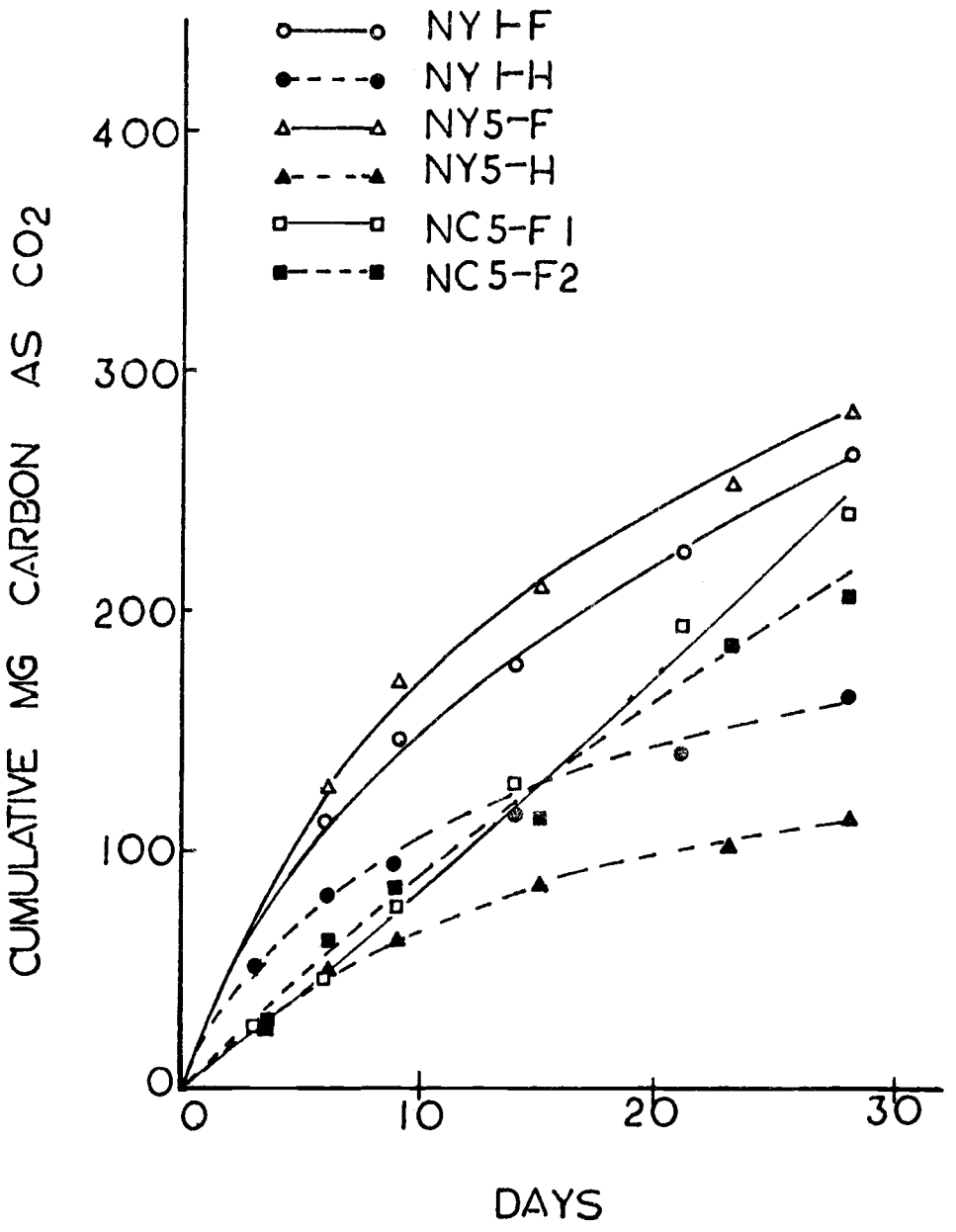

Figure 7. CO_2 evolution from forest humus layers from Eastern North American Forests.

fallen materials contain much more ready-to-use organic matter. As humification progresses the amounts of simple available materials decrease significantly and the amounts of high molecular weight complex materials, such as lignin and cellulose increase. It would appear then that CO_2 evolution values resulting from controlled incubation tests could serve as an index of the stage of decomposition and humification.

On materials having an ample source of readily available carbon, microbes, predominantly molds, begin to show up early in the incubation period. A longer time is needed for the growth of microbes on samples that are more humified. The predominance of molds can be explained by the acidic environments (Table 5).

The chemical analysis data for the forest floor materials are summarized in Appendix Table 4. As humification progresses, the total concentration of basic cations decreases. Carbon is oxidized and evolved in the decomposition and humification process. Since total carbon content decreases, the ash content increases. The high ash content in many of the H samples is due to the mixing of mineral soil in the H layer. In the decomposition process the nitrogen content generally increases. The lower concentration in some H samples is related to the higher ash content.

The C/N ratio of organic matter controls, to a great degree, the rate of mineralization and liberation of plant nutrients. When the

nitrogen concentration is higher than required by the microorganisms active in the decomposition, the excess amount will be liberated as ammonia and under certain circumstances, nitrate will be formed. For plant remains a ratio of 10:1 or less indicates an advanced stage of decomposition; such residual material is resistant and is subject to attack only by the autochthonous microflora, which is physiologically adapted to its utilization, and further decomposition is slow.

A wide C/N ratio is characteristic of forest litter, thus, much of the nitrogen is utilized by the microorganisms active in the decomposition processes with a minimum amount being mobilized to other plants.

Since nitrification is an autotrophic transformation, consuming rather than liberating CO_2 in primary metabolism, and since it represents only a small portion of the total soil microbial activity, it can exert, per se, only a negligible influence on soil respiration (Bollen, 1941).

Ivarson and Sowden (1959) found that liberation of nitrogen in the form of ammonia occurred somewhat more rapidly in decomposing deciduous litter than in decomposing coniferous litter. Litter of mixed species composition should possess different respiratory and nitrogen release properties. The influence of individual species can be quite marked. The influence of understory vegetation on the nature and properties of the forest floor should be reflected in the CO_2

evolution from the different forest floor types. The respiration data for forest floor material from Douglas-fir stands with different understory vegetation are presented in Figure 8. Also given is the CO_2 evolution curve for forest floor material composed of pure Douglas-fir litter. These data reveal that the material from the more mesic stands (sword fern, salmonberry-sword fern and sword fern-oxalis) have lower respiratory rates than material from the drier sites (ocean spray-salal, salal and vine maple-salal). This would seem to indicate a more advanced stage of humification in the more mesic stands.

O_2 Uptake

Oxygen uptake data are plotted in Figure 9. The volume of oxygen consumed increases with incubation time. The trend of O_2 uptake parallels the trend for CO_2 evolution from the same samples as shown in Figure 1. As was the case with CO_2 evolution, the F layers had higher rates of oxygen uptake than the H layers.

As a rule, for the heterotrophic and aerobic utilization of organic carbon, one mole of O_2 is required for the production of one mole of CO_2. The data in Table 1 reveal that O_2 consumption values are higher than the values of CO_2 produced. The CO_2 produced during the O_2 uptake study was also greater than amount produced in a similar period of time in the CO_2 evolution experiment. There are

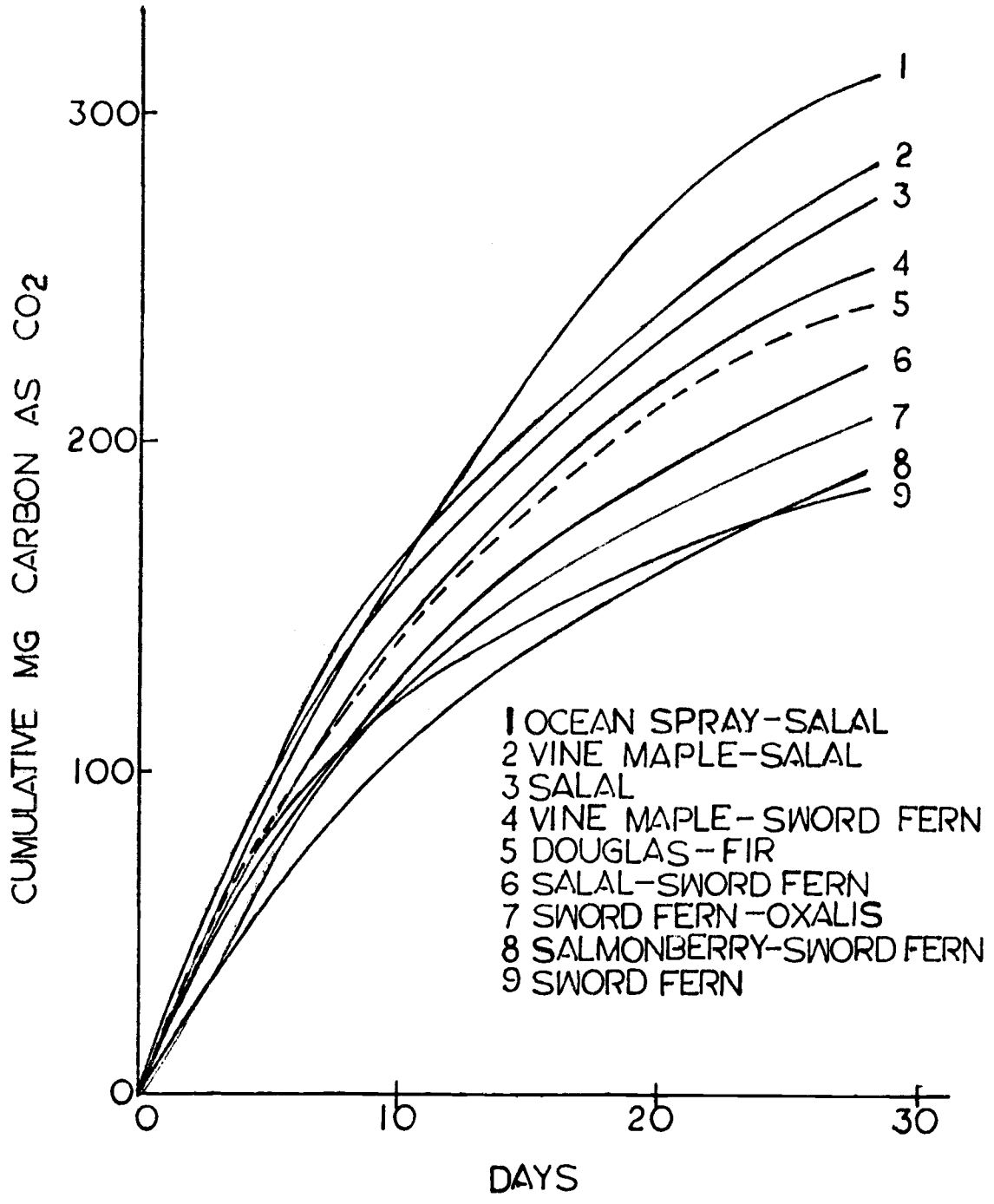

Figure 8. CO_2 evolution from forest floors from Douglas-fir stands with different understory vegetation.

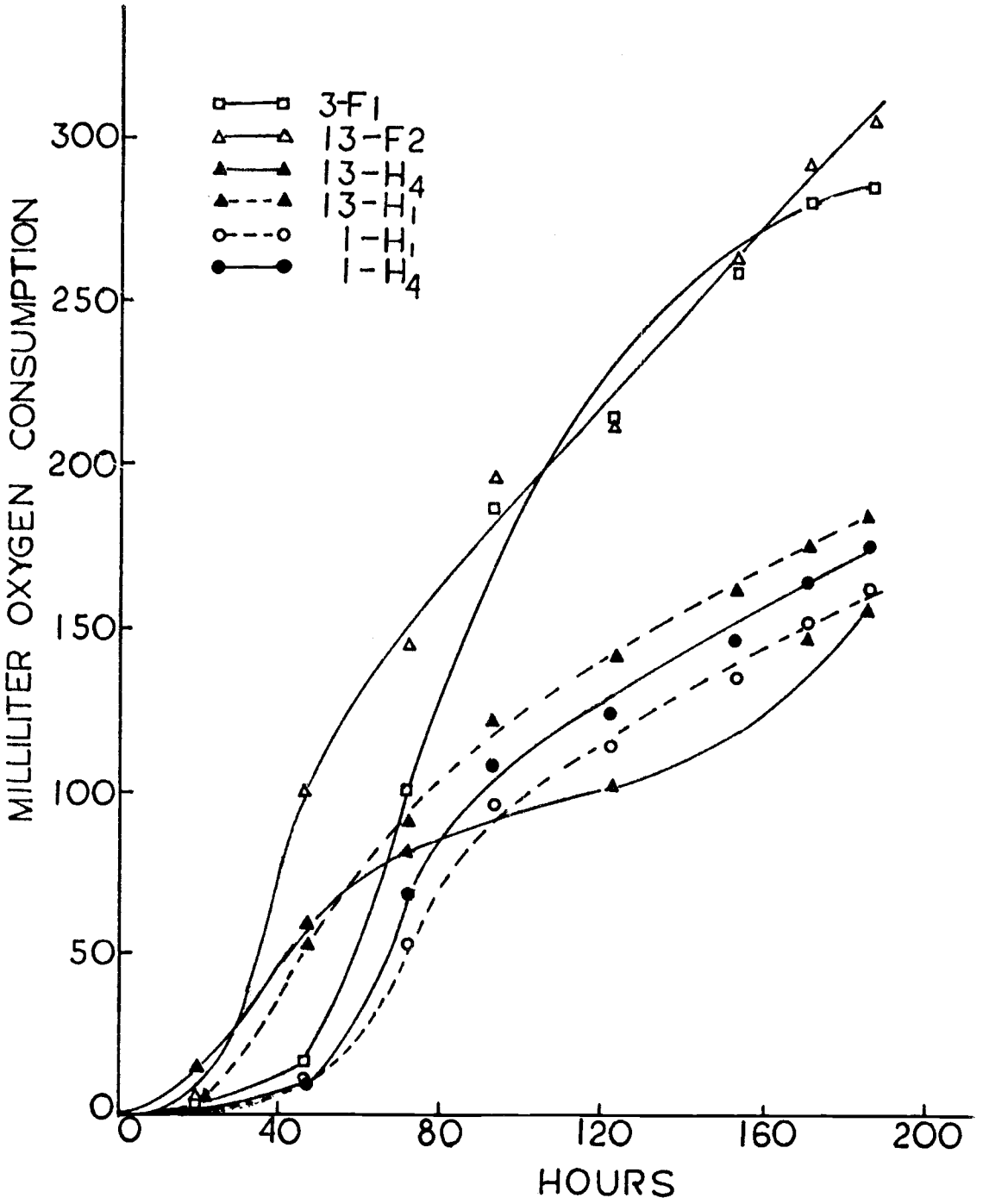

Figure 9. Oxygen uptake by microbes in native organic matter.

several reasons for this phenomenon. First, CO_2 is not the only product formed from the carbon of the organic matter in the process of decomposition. The autotrophic microorganisms reassimilate some of the CO_2, while all heterotrophic organisms reassimilate some of the carbon during the process of growth and reproduction. In these situations the fungi reassimilate much more carbon than the bacteria per unit of organic matter decomposed; second, in a closed system such as the electrolytic respirometer and in the presence of a continuous supply of oxygen, microbes are induced to respire at a much higher rate than those in the CO_2 collection respirometer, in which a somewhat more natural environment is provided. The reproducibility of O_2 uptake data for duplicate samples proves the absence of leakage loss of gases.

Table 1. Comparison between data for O_2 uptake and CO_2 evolution.

	O_2 uptake per g sample		CO_2 evolution per g sample in 9 days incubation
	O_2 used mg	CO_2 produced mg	CO_2 produced mg
3-F1	27.3	10.50	6.06
13-F2	29.3	11.60	7.71
13-H(1)*	17.7	6.08	3.78
13-H(4)*	15.0	5.23	2.95
1-H_1	15.3	5.22	3.82
1-H_4	16.7	5.24	4.10

*Composite of three subsamples.

Plate counts made on the respirometer samples using standard media and techniques indicated that there was no relationship between microbial population and respiration.

Soluble Carbon

Potassium persulfate acts as a mild oxidizing agent according to the following reaction:

$$K_2S_2O_8 + H_2O \longrightarrow 2\ KHSO_4 + [O]$$

Accordingly it is possible to oxidize selectively the water soluble carbon (Osburn and Werkman, 1932) to the end product of carbon dioxide. As soon as the oxidation reaction starts, the content of the main well darkens and gas evolution commences. The reaction proceeds smoothly at 70° C to 75° C and is usually completed within 30-minutes. At the end of this period, the dark color has disappeared and the solution is water clear.

From the above mentioned reaction equation, it can be seen that the solution becomes acid during the process and consequently there is no difficulty in driving all the CO_2 out of the solution. Solubility of potassium persulfate is approximately 5 g per 100 ml of water. If the reagent is not in solution, the liberation of nascent oxygen occurs at the solid surface and the oxidizing efficiency is low.

For the extraction of total soluble carbon, it is supposed that

the soluble substances are homogeneously distributed in the clear extract, after the sample solution is filtered. Concentration of soluble materials presented in each portion of the extract will be the same; from this value of concentration and the amount of total water added, the amount of total soluble materials can be calculated. Because of the satisfaction of saturation capacity, all samples are compared on the same physical basis.

Differences in the length of shaking period before filtration may affect the extraction of total soluble carbon. Seven different kinds of forest floor materials were used to evaluate the effect of shaking time on the amount of soluble carbon extracted. The data are summarized in Table 2. The data indicate that there was an influence of increased shaking time on the soluble carbon extracted. For samples of high respiratory activity, some increases of total soluble carbon extracted occurred with the prolonging of the shaking period, however, the data are not consistent and it appears that the most of the soluble carbon is extracted following the initial period of shaking. It appears that even for materials in different stages of decomposition and humification, the maximum extraction of total soluble carbon can be achieved in a short time.

Another advantage of a shorter shaking period is the decrease in the chance of microorganisms increasing during a longer shaking period and using the soluble carbon as an energy source. Such an

increase in the activity of microorganisms would result in an underestimate of soluble carbon. Although a uniform shaking time for all types of samples might result in a slight underestimation for non-humified materials (L and F) in contrast to a maximum extraction efficiency for humified materials (H), the advantage of better reproducibility would seem to outweigh any disadvantage. The data in Table 2 indicate that a 12-hour extraction period results in maximum extraction for humified materials (A2-H, A4-H and GR4-H). Further, they show that most of the soluble carbon from the less humified materials (ocean spray-salal, NY5-F, A2-F and A4-F) was also extracted during the 12-hour shaking period. In view of these findings, a 12-hour shaking period was used for the remainder of the studies.

In order to evaluate the oxidizing efficiency of the persulfate reagent, equal amounts of the reagent were compared using different volumes of the sample extract.

Approximately 2 g of potassium persulfate were used to oxidize two different volumes of the same sample extract. The fairly close coincidence of total soluble carbon recovery from the two extracts reveals the steady oxidizing power of potassium persulfate (Table 3). When the amount of total soluble carbon recovered per flask exceeds 10 mg, e. g., sample 8-L, the determination should be rerun with a smaller sample.

Table 2. Effect of shaking time on the extraction of total soluble carbon.

Sample	Recovery mg C as CO_2 per g sample						
	Length of shaking period before extraction (hours)						
	6	12	24	36	48	72	96
Ocean-spray Salal	14.48	15.68	14.56	---*	15.12	16.00	14.07
NY5-F	---	16.05	16.69	16.61	18.15	16.91	---
A4-F	11.18	11.92	11.65	12.22	11.69	13.65	---
A2-F	18.35	19.20	18.81	20.17	20.20	19.20	---
A2-H	11.01	11.89	9.89	11.59	11.80	---	---
A4-H	6.19	6.4	4.89	5.27	5.27	7.32	---
GR4-H	---	11.39	9.89	10.28	11.09	9.74	---

*Incomplete

Table 3. Oxidizing power of $K_2S_2O_8$*.

Sample	ml of extracts used		Recovery of mg C as CO_2 per flask		Total recovery of mg C as CO_2 per g sample	
	A	B	A	B	A	B
1-H	2	5	1.30	3.36	8.71	9.08
3-F1	2	5	1.91	4.19	12.80	11.32
Ocean spray Salal	5	10	5.09	10.45	13.52	14.01
1-L	3	5	4.63	6.64	21.90	18.85
7-L	3	5	5.85	9.39	28.70	27.81
8-L	3	5	10.47	13.42	47.90	36.50
13-LF	3	5	4.51	6.86	23.79	21.99

*Two spoon-end-spatulas (≒ 1.5 to 2.0 gm) of $K_2S_2O_8$ were used.

Immediately following the removal of the center cell vial, the solution contained in the main well was reoxidized in the same flask and via the same steps to see if complete oxidation had occurred in the initial run. The data given in Table 4 demonstrates that complete oxidation is essentially achieved in the first run.

Table 4. Degree of completion of wet combusion.

Sample	Oxidation	Recovery of mg C as CO_2 per flask	Total recovery of mg C as CO_2 per g sample
3-Fl	1st	5.20*	24.35
	2nd	0.26	---
1-H	1st	1.96	8.15
	2nd	0.24	---

*0.42 mg C as CO_2 were present in blank flasks.

The agreement obtained among replicate (4) determinations indicates that leakage loss through gas exchange is not a serious factor affecting the precision of the method.

For comparative purposes the data for soluble carbon and for CO_2 evolution are presented in Table 5. These data are for forest floor samples from different forest types in eastern United States and Canada. They also represent different stages of decomposition and humification. A definite relationship does exist between the amount of soluble carbon in the material and its respiratory activity. As humification increases, the respiratory activity of forest floor

decreases, as does the amount of soluble carbon. A regression analysis (Draper and Smith, 1967) was made of the relationship between CO_2 evolution and soluble carbon. The correlation between these two parameters are presented in Figure 10. The significance of this regression relationship was tested by Student's t-distribution. The positive correlation coefficient is 0.78. A normal distribution pattern is obtained when data from Table 5 for the respiratory carbon/soluble carbon ratios are plotted against the frequency distribution (Figure 11). The data from Table 5 indicate that the higher the degree of humification the nearer the respiratory carbon/soluble carbon ratio is to 1. For the less humified samples the ratio is 1.4. The somewhat higher levels of soluble carbon in the less humified materials result in a build-up of the microorganism population in the initial phase of the respiration process. The larger population attacks some of the more complex carbon compounds resulting in a prolonged steady rate of CO_2 evolution. This can be seen in the initial steep portion of the CO_2 evolution curve for the F materials (Figures 1-7) in contrast period for the more humified H materials. With the more stable or resistant compounds in these materials the ratio between respiratory carbon and soluble carbon is essentially 1.

Table 5. Summary of soluble carbon, extract reaction and respiratory carbon/soluble carbon ratio for forest floor materials from Eastern North American Forests.

Sample	pH	mg soluble carbon per g sample	mg C as CO_2 evolved per g sample	Respiratory carbon to soluble carbon ratio
1-L	3.4	18.85	---	---
-F	3.31	14.91	13.17	0.88
-H	3.27	9.75	7.72	0.79
2-L	4.08	56.40	---	---
-F1	3.86	16.09	30.18	1.87
-F2	3.50	14.75	17.67	1.20
-H	3.54	7.59	8.45	1.11
3-L	4.0	60.60	---	---
-F1	4.32	13.05	19.10	1.46
-F2	4.19	14.58	12.70	0.83
-H	3.51	10.74	11.62	1.08
4-L	3.87	56.80	---	---
-F1	4.0	23.41	---	---
-F2	3.72	14.80	12.54	0.85
-H	3.52	7.83	9.35	1.19
5-L	3.90	69.60	---	---
-F	3.60	28.00	---	---
-H	2.70	8.96	9.49	1.06
6-L	3.87	33.5	---	---
-F	3.69	15.1	15.08	0.99
-H	3.49	7.45	7.78	1.04
7-L	4.00	25.39	---	---
-F	3.71	20.88	---	---
-H	3.78	9.73	---	---
8-L	3.90	36.50	---	---

Table 5. Continued.

Sample	pH	mg soluble carbon per g sample	mg C as CO_2 evolved per g sample	Respiratory carbon to soluble carbon ratio
-F	3.81	14.48	22.29	1.54
-H	3.80	8.05	8.49	1.06
9-L	3.96	45.81	---	---
-F	3.80	15.01	22.03	1.47
10-L	3.82	35.90	---	---
-F	4.16	17.79	23.60	1.32
-H	3.81	7.39	9.27	1.25
11-L	3.65	32.99	---	---
-F	3.70	17.81	17.18	0.96
-H	3.42	4.98	9.77	1.96
13-LF	4.10	23.79	---	---
-F2	4.1	11.09	13.80	1.25
-H	3.7	5.84	6.85	1.17
14-LF	4.0	19.40	---	---
-F2	4.0	9.94	15.90	1.60
-H	4.0	4.46	8.85	1.98
A2-F	4.71	19.20	23.97	1.25
-H	4.10	11.89	11.34	0.95
A3-L	3.80	20.46	27.20	1.33
-F	3.40	14.31	14.48	1.01
-H	3.20	11.91	12.25	1.03
A4-F	5.51	11.92	19.38	1.63
-H	5.06	6.40	7.21	1.12
A5-F	4.56	14.14	22.47	1.59
-H	4.46	4.08	6.04	1.48
NB-1	3.60	7.60	10.51	1.39
BR-1	5.72	16.60	23.28	1.40

Table 5. Continued.

Sample	pH	mg soluble carbon per g sample	mg C as CO_2 evolved per g sample	Respiratory carbon to soluble carbon ratio
BR-2	4.50	17.10	20.54	1.20
-4	4.02	15.80	28.77	1.81
GR1-LF	4.20	13.35	11.27	0.84
-H	3.73	11.72	9.95	0.85
GR4-F	4.10	10.46	10.84	1.03
-H	3.50	9.35	10.51	1.12
NY1-F2	4.01	12.85	17.75	1.38
-H	3.65	7.01	11.10	1.58
NY-2	5.50	16.05	27.20	1.70
NY-3	5.20	16.68	25.06	1.54
NY5-F	4.40	14.69	19.11	1.30
NY5-H	4.09	6.07	7.10	1.17
NC-1	5.62	12.22	28.76	2.19
NC5-F1	3.96	16.70	19.18	1.15
-F2	3.86	8.14	13.81	1.70

* Incomplete

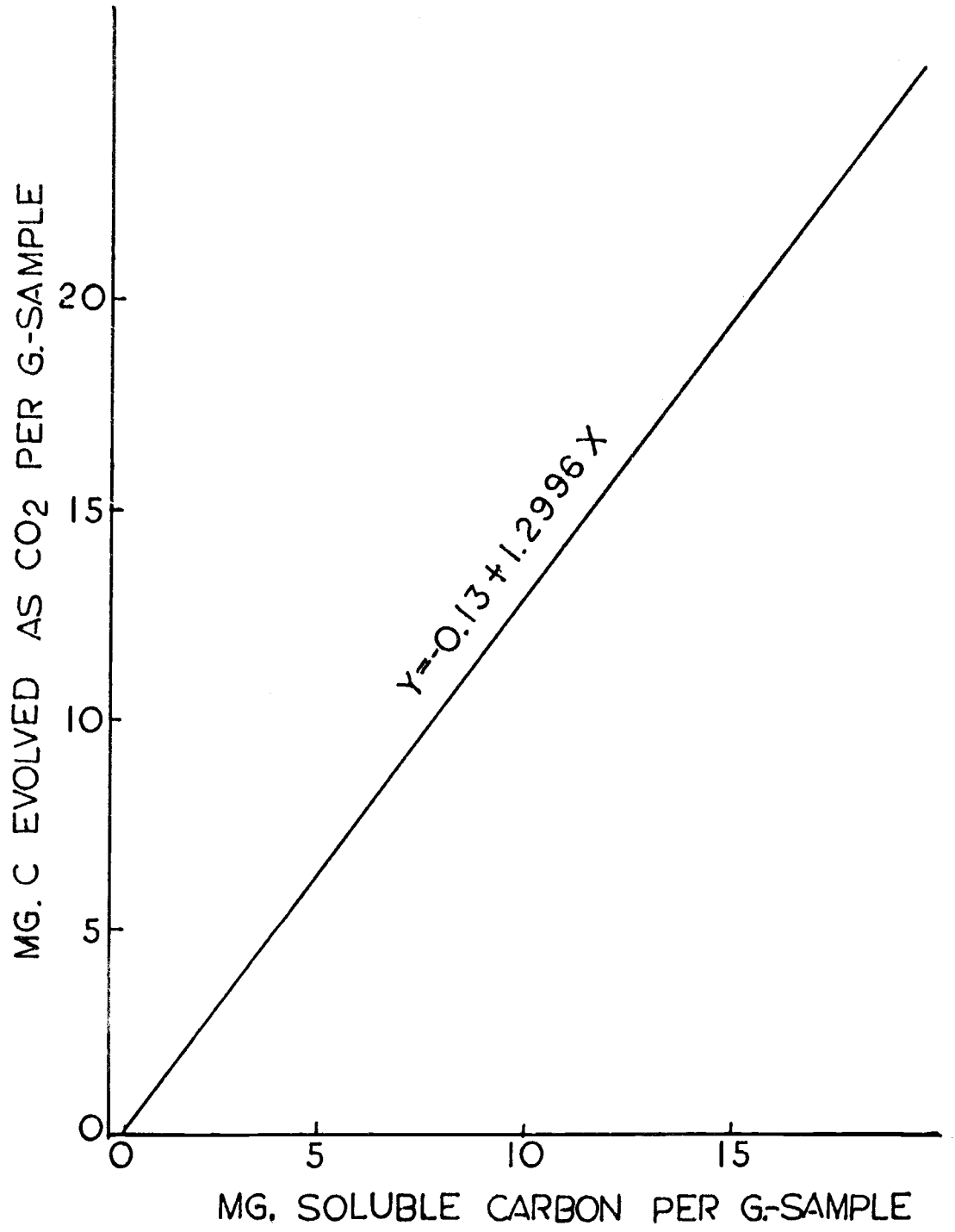

Figure 10. Regression coefficient line for soluble carbon and respiration $t_{byx} = 25.5 > t\,(^{v=48}_{0.01}) = 2.690$; $r = 0.781$; $n = 50$.

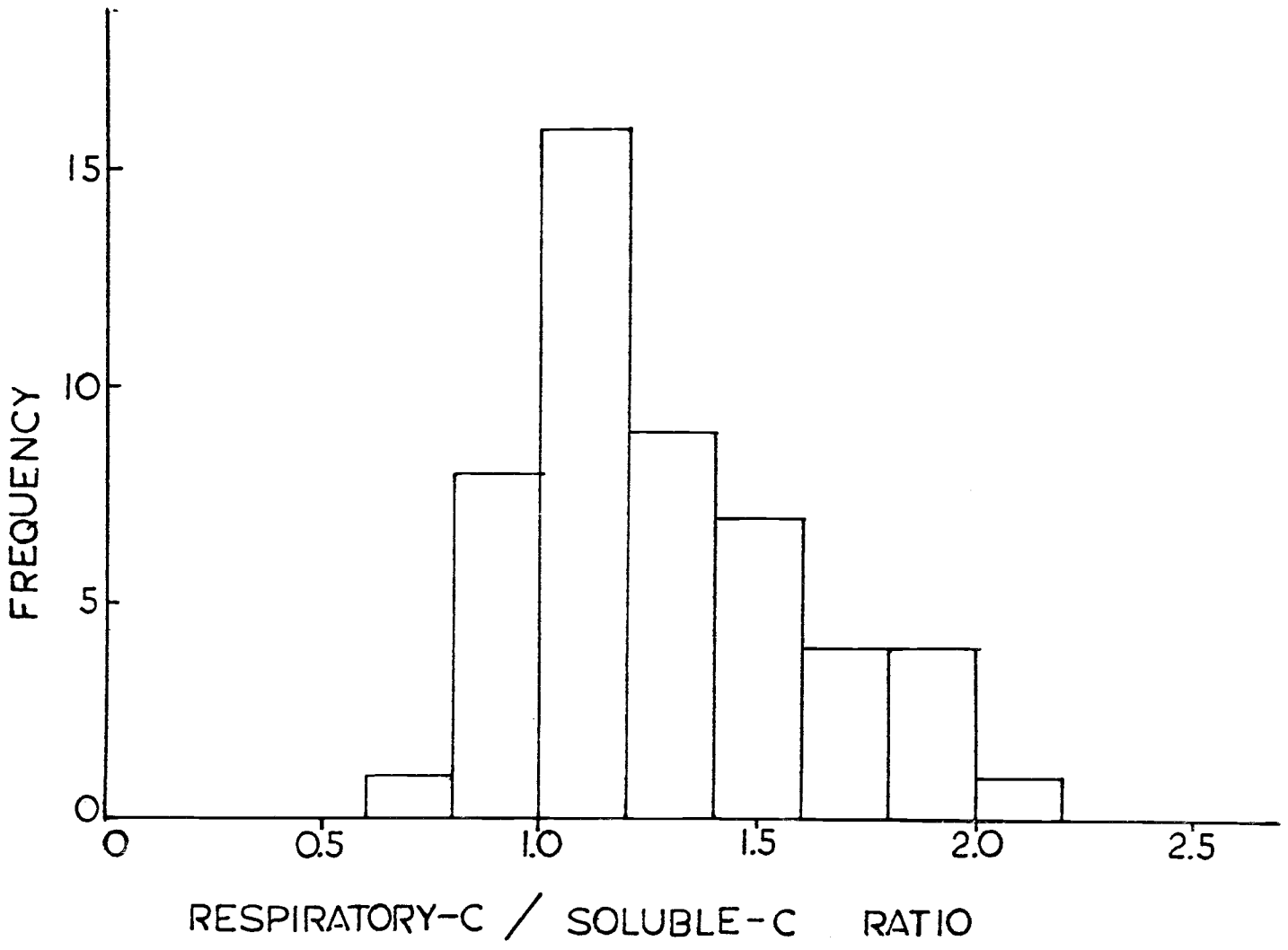

Figure 11. Frequency distribution of respiratory carbon/soluble carbon ratios.

The data in Table 5 show that the more humified materials are generally more acid than the less humified materials. This is due to the production of various organic acids, as intermediates or end-products by microorganisms in the course of decomposition of organic matter. Materials with a higher content of basic cations (Appendix Table 3) generally produce less acid end products. Difference in chemical composition may determine the type of decomposition and kind of humus that will be formed. A general decrease is noted in the total content of basic cations as humification proceeds (Appendix Table 3).

In a forest stand, the nature of understory vegetation will affect the chemical composition of forest floor and thus influence decomposition processes. This will be reflected in differences in respiration of the forest floor materials. The data presented in Table 6 (plotted in Figure 12) show that the salmonberry-sword fern and the sword fern type have the lowest levels of soluble carbon. These two types also have the lowest CO_2 evolution rates (Figure 8). On the other hand, the ocean spray-salal, salal, and vine maple-salal types have higher soluble carbon and respiratory rates. It would appear from a comparison of the salmonberry-sword fern and the sword fern types that soluble carbon rather than nitrogen content is the limiting factor in the respiratory activity of forest floor materials.

Table 6. Summary of soluble carbon, extract reaction, total nitrogen and respiratory carbon/soluble carbon ratio for forest floor materials from Douglas-fir stands with different understory vegetation.

Understory communities	pH	Total N %	mg soluble carbon per g sample	mg C as CO_2 evolved per g sample	Respiratory carbon to soluble carbon ratio
Salal	5.11	0.88	14.53	20.77	1.43
Ocean spray-Salal	5.35	0.71	13.83	20.62	1.49
Vine maple-Salal	5.62	0.74	11.91	20.47	1.72
Salal-sword fern	5.04	1.02	10.28	15.58	1.51
Douglas-fir*	5.92	0.87	8.96	16.03	1.79
Sword fern-Oxalis	4.70	0.75	8.54	13.74	1.61
Vine maple-sword fern	5.89	1.07	7.06	17.12	2.42
Salmonberry-sword fern	4.96	1.52	6.12	12.72	2.08
Sword fern	4.92	0.88	5.87	13.74	2.34

*Dense growth without understory covering.

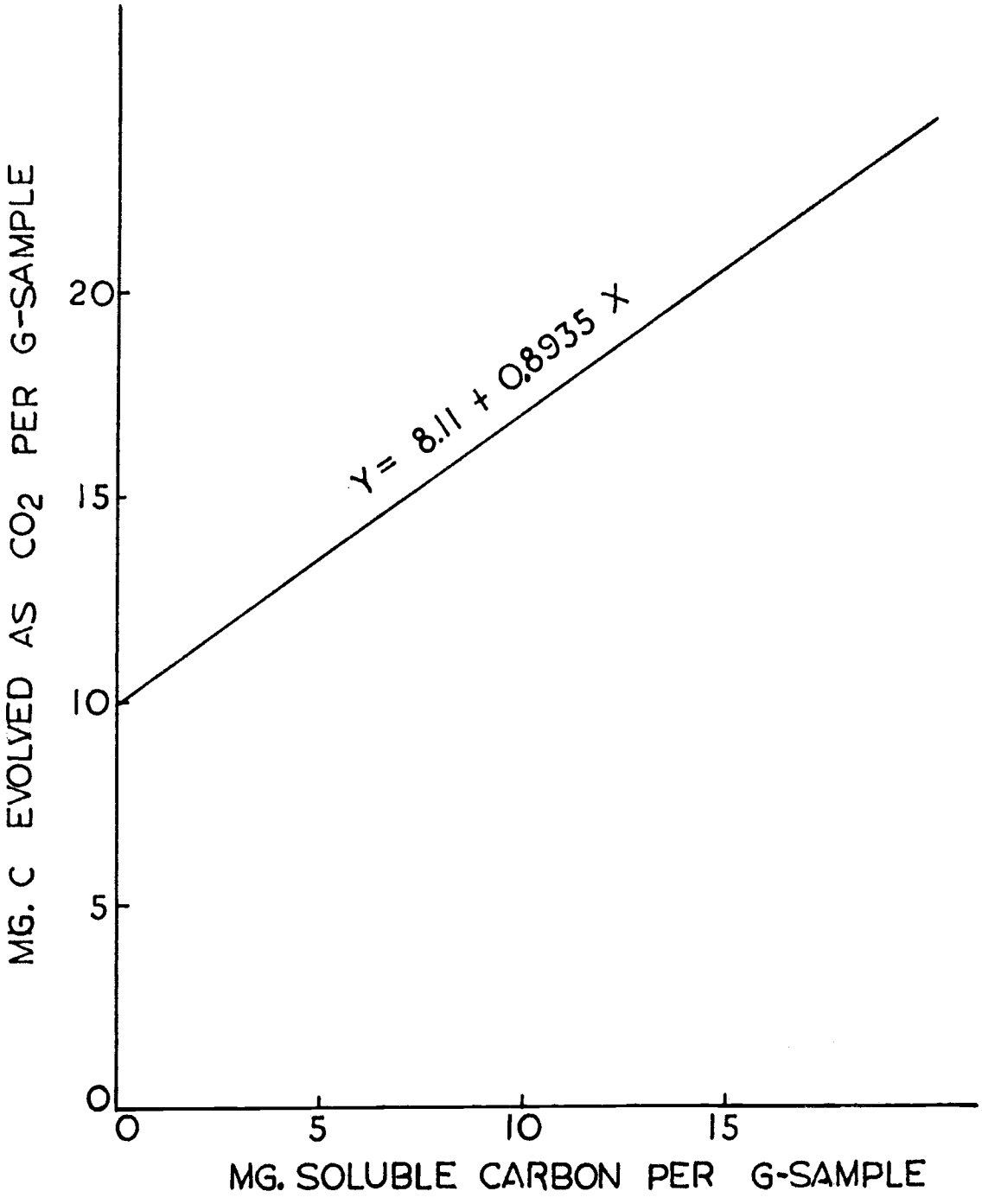

Figure 12. Regression coefficient line for soluble carbon and respiration tbyx = 4.68 > $t(^{v=7}_{0.01})$ = 3.499; r = 0.8501; n = 9.

As pointed out in the literature review, the flush of decomposition depends on the percent carbon in the soil and the length of drying (Birch, 1959). Alternate drying and wetting brings more organic material into solution and increases the availability of carbon. It is evident that the soluble carbon plays an important role in respiration. It is also evident that ratio of respiratory carbon to soluble carbon varies with the stage of humification (Table 5).

It is generally recognized that the most reliable measure of the organic matter content of the soil is the amount of organic carbon present. The conversion factor of organic carbon to organic matter is 1.89 for the freshly fallen leaves (L), 1.85 for the decomposing fermentation layers (F), and 1.80 for the structureless humus (H) (Lunt, 1930). Although it is possible to evaluate the stage of decomposition of the forest floor on the basis of morphology, the soluble carbon technique will serve as a more precise method of determining the stage of humification.

The advantages of the persulfate oxidation method over the respiration method are that it is less time consuming, fewer materials are required and better control can be exercised. Since the soluble carbon recovered by the persulfate oxidation test may be expressed in terms of respiration, it appears likely that either the soluble carbon value itself or the related respiratory activity may be used for the distinguishing of the stage of humification.

A comparison of the data from Tables 5 and 6 shows that respiratory carbon/soluble carbon ratios for materials having low soluble carbon levels in the eastern forest types (H) are closer to 1 than those from low soluble carbon level materials from Douglas-fir types (sword fern and salmonberry-sword fern). This is probably related to the differences in the decomposition processes and humus development resulting under the different climatic conditions in the two regions. Mor type of humus development is characteristic of the northeastern U. S. (New England and New York) and New Brunswick. The strongly acid reaction of the extracts (Table 5) is characteristic of this type of humus development. Mull humus formation is more characteristic in the Douglas-fir forests of western Oregon. The extracts are less acid (Table 6) and the humus layers developed lack the H layer typical of the mor type. As humification proceeds the amorphous (H) material is incorporated into the mineral soil. This process is generally characteristic of the less acid environments in contrast to the accumulation of an unincorporated layer of amorphous material (H) on the surface in more acid environments. Forest floor decomposition proceeds quite rapidly in Douglas-fir forests and the development of distinct layers such as the L, F, and H does not normally occur. As mentioned in the sampling section the forest floor in these kind of stands are dominantly F type of materials.

It appears from the results of this study that soluble carbon

analyses can be used for evaluating the development of forest humus within comparable forest regions (within the Northeastern U. S. or the Pacific Northwest) but not between contrasting regions (Northeastern U. S. vs. Pacific Northwest).

According to the regression equation $Y = -0.13 + 1.2996x$, it is possible to calculate expected respiratory values from soluble carbon values. Calculated respiratory values for some eastern U. S. forest humus samples are given in Appendix Table 5.

SUMMARY AND CONCLUSION

A satisfactory technique for the measurement of total soluble carbon content of forest floor materials was developed.

The amount of total soluble carbon was estimated on the basis of equal moisture level, which was accomplished by adding to each sample an excess of 100 ml of distilled water over saturation capacity.

The effect of length of shaking period on extraction efficiency was studied. Twelve hours of rotatory shaking was selected as optimum on the basis of better reproducibility with samples with high and low soluble carbon contents. Another advantage was that no carbon loss through the growth of microorganisms was detected during this short period. Complete oxidation in the combustion flasks has also been demonstrated. The reproducibility of results both for duplicate combustion flasks and for duplicate samples indicated the absence of leakage loss.

The continuous aeration respirometer as well as the elctrolytic respirometer was used to study the respiratory activity of forest floor materials. Electrolytic respirometer data indicate a higher level of activity than the CO_2 collection respirometer.

Respiratory activity and soluble carbon content were determined for a variety of representative forest floor materials from

different forest types in Eastern North America and in the Coast Range of Oregon. A highly significant positive correlation was found between levels of soluble carbon and respiration.

Respiratory activity of forest floor materials decreases with an increase in the stage of humification. The persulfate oxidizable soluble carbon content appears to be a more reliable index of the stage of humus development than the total nitrogen content. The more humified materials are also generally more acid than the less humified materials.

In the areas sampled in the eastern United States and Canada, the majority of the well humified layers (H) had respiratory carbon/soluble carbon ratios of 1. The majority of the less humified materials had ratios of 1.4. Forest floor materials from Douglas-fir forests that had low soluble carbon levels had much higher respiratory carbon/soluble carbon ratios than materials with low soluble carbon contents from eastern forests.

Because of its simple, precise and time saving features, the persulfate oxidation technique for determining soluble carbon serves better as a means of determining the state of decomposition and humification of forest floor materials than the more time consuming respiration method.

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APPENDIX

Appendix Table 1. Summary of stand location and type and kinds of samples from Eastern North America Forests.

Location	Forest Type	Sample Types	Sample Numbers	Humus Type
Harvard Forest	Hemlock-red maple	L, F, H	1L, 1F, 1H	Mor
Massachusetts	Red oak-red maple -white pine	L, F1, F2, H	2L, 2F1, 2F2, 2H	Duff mull
"	Red oak-red maple	L, F1, F2, H	3L, 3F1, 3F2, 3H	"
"	Hemlock-red oak -yellow birch	L, F1, F2, H	4L, 4F1, 4F2, 4H	Mor
"	Hemlock-hard maple -red oak	L, F1, F2, H	5L, 5F1, 5F2, 5H	Duff mull
"	Red pine	L, F, H	6L, 6F, 6H	
"	White pine-white spruce	L, F, H	7L, 7F, 7H	Duff mull
"	White pine-red oak- red maple-hemlock	L, F, H	8L, 8F, 8H	Duff mull
"	White pine	L, F1, F2	9L, 9F1, 9F2	"
"	Norway spruce	L, F1, F2, H	10L, 10F1, 10F2, 10H	Mor
"	Red pine	L, F1, F2, H	11L, 11F1, 11F2, 11H	Duff mull
"	Red oak-red maple -white pine (pit)[1]	LF, F2, H	13LF, 13F2, 13H	"
"	Red oak-red maple- white pine (mound)[2]	LF, F2, H	14LF, 14F2, 14H	"
Black Rock Forest	Red oak-hard maple			
Cornwall, N. Y.	-white ash-white oak -yellow poplar	LF	BR1	Mull
"	Red oak-hard maple	LF	BR2	"
"	Red oak-red maple -chestnut oak	LF	BR4	"
Adirondack Mt. NY	Red spruce-yellow birch	F, H	NY1-F, NY1-H	Mor

Appendix Table 1. Continuted.

Location	Forest Type	Sample Types	Sample Numbers	Humus Type
Adirondack Mt. NY	Hard maple-basswood -Hemlock-yellow birch-beech	LF	NY2	Mull
"	Beech-hard maple	LF	NY3	Mull
"	Hemlock-yellow birch	L, F, H	NY5-F, NY5-H,	Mor
Vermont	Hard maple-beech-yellow birch	LF	V1	Mull
Hubbard Brook Exp. Forest-New Hampshire	Hard maple-beech -yellow birch-red maple	L, F, H	NH1-L, NH1-F, NH1-H	Mor
Bartlett Exp. Forest New Hampshire	Hard maple-yellow birch beech-red maple	L, F, H	NH2-L, NH2-F, NH2-H	Mor
Acadian Exp. Forest New Brunswick	Red maple-grey birch -white birch-balsam fir -yellow birch	L, F, H	A2-L, A2-F, A2-H	Mor
	Red spruce-white pine-Balsam fir	LF, F2, H	A3-LF, A3-F2, A3-H	Mor
"	Red maple-grey birch -white birch-balsam fir-yellow birch (pit)[1]	F, H	A4-F, A4-H	Mor
"	Red maple-grey birch--white birch-balsam fir-yellow birch(mound)[2]	F, H	A5-F, A5-H	Mor
Gasperean Forks New Brunswick	Black spruce-jack pine	Moor[3]	NB-1	Mor
Green River Exp. Forest New Brunswick	White spruce-yellow birch	LF, H	GR1-LF, GR1-H	Mor

Appendix Table I. Continued.

Location	Forest Type	Sample Types	Sample Numbers	Humus Type
Green River Exp.	Black spruce-balsam fir	M[4], F, H	GR3-M, GR3-F, GR3-H	Mor
Forest	" " " "	M, F, H	GR4-M, GR4-F, GR4-H	Mor
New Brunswick				
Duke Forest N. C.	Loblolly pine (12 yrs)[5]	L, F1, F2	NC3-L, NC3-F1, NC3-F2	Mull
"	" " (26 yrs)	L, F, F2	NC4-L, NC4-F1, NC4-F2	Mull
Bent Creek Exp.	Yellow poplar-red oak			
Forest, N. C.	-chestnut oak-red maple	LF	NC1	Mull
"	Loblolly pine (34 yrs)	L, F1, F2	NC5-L, NC5-F1, NC5-F2	Mull
de la Howe Forest				
South Carolina	Short leaf pine	L, F, H	SC1-L, SC1-F, SC1-H	Duff mull
Calhoun Exp. Forest				
South Carolina	Loblolly pine (24 yrs)	L, F1, F2, F3	SC3-L, SC3-F1, SC3-F2	
			SC3-F3	Mull

[1]Sampled in pit on area of mound and pit microrelief

[2]Sampled on mound on area of mound and pit microrelief

[3]Upland moor formed under ericaceous vegetation. Sampled whole organic mat instead of by layers.

[4]Moss layer

[5]Age of plantation

Appendix Table 2. Saturation capacity of forest floor materials.

Sample	% Saturation capacity on oven dry basis	Sample	% Saturation capacity on oven dry basis
1-L	418.6	13-LF	610.0
-F	350.5	-F2	481.6
-H	236.7	-H	259.3
2-L	518.9	14-LF	476.5
-F1	435.7	BR-1	424.2
-F2	406.2	-2	409.3
3-L	447.8	-4	452.8
-F1	491.4	A3-LF	468.9
-H	298.5	-F2	433.7
4-L	541.1	-H	384.5
-F1	514.0	A4-F	560.7
-F2	360.0	-H	361.8
5-L	393.1	A5-F	491.9
-F1	348.9	-H	187.7
-F2	359.3	GR1-LF	358.2
-H	228.9	-H	300.4
6-L	407.3	GR3-F	436.3
-F	390.5	-H	330.8
-H	229.9	GR4-F	337.3
7-L	453.6	-H	360.2
-F	389.4	NB-6	307.3
-H	315.8	NC1	472.3
8-L	354.3	NC5-F	417.5
-F	361.3	NY1-F2	459.1
-H	189.2	-H	444.6
9-L	429.1	NY-2	488.0
-F1	451.0	NY-3	523.1
-F2	383.8	NY5-F	415.7
10-L	476.6	-H	373.9
-F1	373.9		
-F2	435.1		
-H	196.5		
11-L	454.6		
-F1	370.8		
-F2	377.7		
-H	271.0		

Appendix Table 2. Continued.

Sample	% Saturation capacity on oven dry basis
*Douglas-fir	311.5
**Ocean spray-Salal	329.6
**Sword fern-Oxalis	324.4
**Sword fern	359.6
**Vine maple-Sword fern	326.9
**Vine maple-Salal	386.5
**Salmonberry-Sword fern	373.9
**Salal-Sword fern	358.3
**Salal	407.2

*Dense growth without understory growth

**Species of understory vegetation associated with second growth pure Douglas-fir stand.

Appendix Table 3. Summary of CO_2 evolution data from respiration experiments.

Sample	Cumulative mg C as CO_2 (days)						mg C as CO_2 per g sample
	3	6	9	14	21	28	
5-F2	36.35	71.03	133.18	165.49	187.76	219.71	14.64
-H	29.71	10.71	84.72	104.70	131.10	145.89	9.72
9-F1	36.61	124.46	182.12	219.05	283.79	330.42	22.02
-F2	23.43	89.91	123.86	135.63	150.81	176.44	11.45
11-F1	37.99	115.72	171.68	204.81	229.62	257.72	17.18
-F2	16.52	84.75	116.12	137.99	151.87	174.11	11.60
-H	12.15	61.16	82.67	103.16	124.38	141.51	9.43
BR-1	81.28	136.99	200.79	240.59	278.80	349.26	23.28
-2	64.79	120.20	168.87	195.42	229.69	308.11	20.54
A2-F	84.63	144.78	192.46	265.95	332.55	372.65	24.84
-H	22.40	69.79	90.99	117.40	146.00	160.90	10.73
A4-F	70.89	119.64	170.45	221.59	312.69	347.09	23.14
-H	35.40	50.69	64.81	78.71	93.97	106.64	7.11
A5-F	74.16	97.30	175.99	243.18	335.96	388.03	25.87
-H	27.20	37.14	49.24	62.63	80.18	89.49	5.97
GR1-LF	63.65	81.65	98.06	123.66	153.61	170.26	11.35
-H	49.20	64.14	79.59	100.19	124.17	142.57	9.50
GR4-F	45.07	74.59	110.00	125.69	148.89	165.73	11.05
-H	52.34	58.24	71.84	88.04	107.02	120.72	8.05
NY-2	60.70	117.09	160.11	225.44	304.54	340.58	22.71
NY-3	66.00	129.88	175.38	252.63	333.13	374.73	24.98
NC-1	114.80	181.95	232.63	288.54	370.73	431.48	28.76
F1-F	39.54	66.04	96.44	129.32	189.52	224.22	14.95

Appendix Table 4. Summary of chemical analysis of forest floor materials.

Sample	Percent						
	N	P	K	Ca	Mg	Ash	K+Ca+Mg
1-L	0.68	0.055	0.068	0.385	0.015	1.63	0.463
-F	1.49	0.100	0.098	0.215	0.034	6.32	0.347
-H	1.17	0.088	0.060	0.010	0.038	28.41	0.108
2-L	0.60	0.083	0.318	0.430	0.133	3.30	0.881
-F1	1.37	0.100	0.118	0.486	0.076	3.48	0.680
-F2	1.92	0.110	0.118	0.162	0.049	9.22	0.329
-H	1.15	0.093	0.660	--- *	0.045	36.48	---
3-L	0.63	0.048	0.292	0.595	0.122	2.83	1.009
-F1	1.37	0.093	0.108	0.755	0.083	4.39	0.946
-F2	1.73	0.100	0.098	0.375	0.071	14.40	0.544
-H	1.18	0.093	0.060	0.045	0.075	28.04	0.180
4-L	0.77	0.100	0.162	0.770	0.188	4.16	1.120
-F1	1.37	0.115	0.090	0.760	0.057	4.25	0.907
-F2	1.80	0.125	0.118	0.357	0.054	9.75	0.529
-H	1.20	0.093	0.055	0.080	0.049	35.43	0.184
5-L	0.72	0.088	0.278	0.710	0.106	6.18	1.094
-F1	0.67	0.080	0.125	0.637	0.044	4.20	0.806
-F2	1.57	0.115	0.100	0.680	0.080	11.91	0.860
-H	1.10	0.105	0.068	0.180	0.109	38.55	0.357
6-L	0.63	0.120	0.125	0.547	0.061	1.55	0.733
-F	1.43	0.083	0.078	0.267	0.038	5.57	0.383
-H	1.13	0.083	0.078	0.142	0.068	35.07	0.288

Appendix Table 4. Continued.

Sample	Percent						
	N	P	K	Ca	Mg	Ash	K+Ca+Mg
7-L	0.80	0.078	0.162	0.400	0.048	1.93	0.610
-F	1.53	0.108	0.060	0.560	0.053	7.95	0.673
-H	1.33	0.110	0.070	0.270	0.133	29.43	0.473
8-L	0.58	0.065	0.122	0.567	0.087	2.07	0.776
-F	1.46	0.083	0.040	0.443	0.046	7.61	0.529
-H	1.18	0.123	0.068	0.222	0.091	40.84	0.381
9-L	0.81	0.088	0.123	0.448	0.076	1.91	0.647
-F1	1.43	0.103	0.070	0.350	0.053	3.04	0.473
-F2	1.66	0.110	0.065	0.311	0.061	11.80	0.437
10-L	1.10	0.118	0.132	0.640	0.042	4.01	0.814
-F1	1.62	0.160	0.104	0.847	0.050	8.38	1.001
-F2	1.95	0.255	0.075	0.740	0.061	14.92	0.876
-H	1.26	0.348	0.095	0.595	0.088	41.51	0.778
11-L	0.54	0.050	0.132	0.436	0.060	1.93	0.628
-F1	1.05	0.075	0.068	0.442	0.038	2.61	0.548
-F2	1.30	0.075	0.065	0.311	0.038	5.11	0.414
-H	1.31	0.075	0.085	0.250	0.063	22.79	0.398
13-LF	1.01	0.065	0.132	0.655	0.086	3.11	0.873
-F2	1.58	0.105	0.090	0.398	0.061	7.50	0.549
-H	1.00	0.105	0.090	0.065	0.074	20.21	0.229
14-F2	1.46	0.100	0.111	0.290	0.079	15.56	0.480
-H	0.92	0.098	0.085	0.657	0.094	41.45	0.836

Appendix Table 4. Continued.

Sample	Percent						
	N	P	K	Ca	Mg	Ash	K+Ca+Mg
BR-1	1.09	0.078	0.155	---	0.195	16.03	---
-2	1.33	0.100	0.120	0.910	0.128	14.22	1.158
-4	1.47	0.088	0.125	0.742	0.081	8.18	0.948
GR1-LF	2.02	0.143	0.185	0.255	0.107	10.18	0.547
-H	2.10	0.148	0.147	0.132	0.099	15.68	0.378
GR3-M	---	0.115	0.208	0.324	0.057	3.54	0.589
-H	---	0.070	0.060	0.045	0.049	8.18	0.154
GR4-F	1.58	0.093	0.095	0.220	0.033	3.31	0.348
-H	1.04	0.063	0.060	0.165	0.043	4.38	0.268
NB-6	0.93	0.065	0.098	0.030	0.065	29.34	0.193
A2-F	1.77	0.143	0.170	0.805	0.091	8.25	1.066
-H	1.45	0.125	0.155	0.360	0.110	18.49	0.533
A3-L	1.18	0.160	0.162	0.470	0.050	3.38	0.682
-F	1.30	0.100	0.115	0.180	0.050	4.79	0.345
-H	1.12	0.070	0.100	0.060	0.061	13.71	0.221
A4-F	1.27	0.120	0.132	0.842	0.094	6.25	1.068
-H	1.46	0.178	0.155	0.360	0.110	18.49	0.625
A5-F	1.44	0.135	0.147	0.820	0.090	10.52	1.057
-H	1.01	0.120	0.192	0.220	0.106	47.73	0.518
NY1-F2	1.52	0.088	0.085	0.490	0.044	6.81	0.619
-H	1.44	0.060	0.052	0.300	0.034	9.34	0.386

Appendix Table 4. Continued.

Sample	Percent						
	N	P	K	Ca	Mg	Ash	K+Ca+Mg
NY-2	1.63	0.080	0.090	1.700	0.135	10.71	1.870
NY-3	1.72	0.088	0.090	0.922	0.066	8.92	1.100
NY5-F	1.51	0.105	0.078	0.885	0.066	7.74	1.029
-H	2.07	0.078	0.052	0.635	0.068	17.54	0.755
NC-1	0.52	0.070	0.162	1.025	0.433	31.78	1.620
NC3-L	0.73	0.073	0.059	0.385	0.077	2.66	0.517
-F1	0.82	0.073	0.046	0.385	0.060	3.86	0.491
-F2	0.91	0.078	0.063	0.330	0.056	16.07	0.449
NC4-L	0.59	0.065	0.062	0.257	0.061	3.05	0.380
-F1	0.67	0.070	0.046	0.285	0.059	4.58	0.390
-F2	0.87	0.075	0.052	0.232	0.048	17.76	0.332
NC5-F1	2.03	0.070	0.052	0.320	0.078	4.15	0.450
-F2	0.88	0.065	0.052	0.215	0.039	17.91	0.306
SC1-L	0.57	0.028	0.058	0.522	0.114	4.03	0.694
-F	0.94	0.055	0.062	0.447	0.079	14.85	0.588
-H	0.52	0.050	0.090	0.311	0.076	52.09	0.477
SC3-F1	0.51	0.048	0.033	0.320	0.074	2.98	0.427
-F2	0.55	0.055	0.038	0.322	0.061	5.03	0.421
-F3	0.72	0.055	0.040	0.310	0.063	23.78	0.413
NH1-L	1.23	0.088	0.110	0.915	0.083	5.70	1.113
-F	1.69	0.118	0.120	0.835	0.094	9.09	1.049
-H	1.43	0.108	0.108	0.230	0.050	23.30	0.388

Appendix Table 4. Continued.

Sample	Percent						
	N	P	K	Ca	Mg	Ash	K+Ca+Mg
NH2-L	1.29	0.105	0.095	0.847	0.049	6.95	0.991
-F	1.60	0.105	0.085	0.642	0.051	16.17	0.778
-H	1.19	0.093	0.071	0.200	0.050	43.22	0.321
Douglas-fir	0.87	0.221	0.275	0.875	0.334	--- *	1.484
Ocean spray-Salal	0.71	0.089	0.130	1.050	0.275	---	1.455
Salal	0.88	0.138	0.232	0.875	0.207	---	1.314
Vine maple-Salal	0.74	0.137	0.132	0.875	0.315	---	1.322
Salal-Sword fern	1.02	0.141	0.115	0.838	0.246	---	1.199
Vine maple-Sword fern	1.07	0.145	0.183	0.900	0.413	---	1.496
Salmonberry-Sword fern	1.52	0.139	0.198	0.412	0.236	---	0.846
Sword fern	0.88	0.147	0.118	0.625	0.157	---	0.900
Sword fern-Oxalis	0.75	0.118	0.115	0.325	0.197	---	0.637

* Incomplete

Appendix Table 5. Some expected values of respiratory ability.

Sample	mg soluble C per g sample	Calculated respiratory ability for 28 day incubation in mg C per g sample
NH-1-L	15.3	19.75
-1-F	12.7	16.37
-1-H	5.37	6.84
NH-2-L	14.10	18.19
-2-F	10.73	13.81
-2-H	4.59	5.83
SC1-F1	10.42	13.41
-F2	14.09	18.18
-H	4.10	5.19
SC3-F1	13.15	16.95
-F2	8.71	11.18
-F3	5.29	6.74
NC3-L	17.90	23.13
-F1	12.73	16.41
-F2	7.56	9.69
NC4-L	18.60	24.04
-F1	14.30	18.45
-F2	5.49	7.00

Regression equation: $Y = -0.13 + 1.2996x$