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Respiratory rates were measured, in situ, for the litter, the soil, and the litter-soil subsystems of a Pseudotsuga menziesii forest as a function of type of understory vegetation. The major objectives were to demonstrate the utility of the litter layer as a distinct subsystem of this forest ecosystem, to demonstrate the existence of respiratory patterns in the litter subsystem related to type of understory vegetation, to determine if moisture and/or temperature were important factors in creating these patterns, and to generate an estimate of annual rate of respiration of the litter subsystem of a Pseudotsuga menziesii forest.

Six understory types (Holodiscus discolor, Acer circinatum, Gaultheria shallon, Tsuga heterophylla, Castanopsis chrysophylla, and Polystichum munitum) were sampled. All differences in annual respiratory rates for all subsystems were significant at $F_{0.05}$, however the range of differences between types in the respiratory rates of the litter

subsystems, normalized to a per gram of litter basis, were higher by an average factor of six and exhibited a hierarchy of magnitudes different from those of the unnormalized litter, the soil, or the litter-soil subsystems. The litter subsystem was found to be a useful and meaningful division of the forest ecosystem.

Due to suspected methodology related errors associated with lateral movements of carbon dioxide into the sample areas from without, the soil and the litter-soil measurements were probably in error, possibly quite large. Error in absolute rate of respiration for the litter subsystem is also suspected but probably to a smaller degree and not affecting the hierarchy related to type.

The litter subsystems for two of the types were found to have moisture contents different by a relatively large percentage from that of the litter subsystems of the other types. It appeared, however, that moisture difference was not the major cause of the hierarchy by type of respiratory rates of the litter subsystem. Temperature was not a significant factor in the observed hierarchy. The annual respiration yields based on the litter subsystem, as a probable result of the specific methodology used, appeared to yield more reasonable estimates for rates of decomposition of organic matter in a forest floor than do previously published studies based on the litter-soil subsystem. It appears that Pseudotsuga menziesii forests compared to other temperate coniferous forests have a rapid turnover rate for organic matter entering the litter subsystem.

# Patterns of Energy Utilization in the Litter Subsystem of a Douglas-Fir Forest

by

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# PATTERNS OF ENERGY UTILIZATION IN THE LITTER SUBSYSTEM OF A DOUGLAS-FIR FOREST

## INTRODUCTION

Of all terrestrial communities, forests are probably the most complex and massive and forest ecologists have long attempted to restrict their research to whatever features they felt were of greatest importance or could be recorded most readily (Ovington, 1962). Many divisions of the forest have thus been made in order to explain the whole, but probably the most promising start with the concept of an ecosystem, a term first introduced by Tansley (1935). Conceptually, the ecosystem is viewed as a functional unit with recognizable boundaries and an internal homogeneity (Smith, 1970). Synecologists (Daubenmire, 1968; Dansereau, 1957) have devised a number of classification schemes for delimiting plant communities and these form the most used bases for recognizing particular terrestrial ecosystems.

Much of our knowledge of the structure and functioning of ecosystems is qualitative and one of the major goals of ecologists is to find ways of quantitatively analyzing ecosystems (Bourlière and Hadley, 1970). Energy flow measurements have been utilized by many ecologists (Odum, 1957; Teal, 1962; Olson, 1963; Wiegert, 1964; Phillipson, 1966; Ellenberg, 1971) as a quantitative method for studying ecosystems. Wiegert, Coleman, and Odum (1970) consider energy

flow to be a vital part of any ecosystem analysis because energy drives the complex cycles of materials that are the form, function, and diversity of life.

In a forest ecosystem, energy flow via the detritus pathway is the major site of heterotroph activity and may be considered a heterotrophic subsystem of the forest (Reiners, 1968). It is estimated that as high as 80 to 90 percent or more of the net primary productivity of a forest is decomposed in the litter-soil subsystem (Ovington, 1961; Bray and Gorham, 1964). The energy relations within the litter-soil subsystem have attracted considerable attention from ecologists, but this subsystem is extremely complex and it will be a long time before the energy flow of very many of its inhabitants is well understood (Macfadyen, 1963; Reiners, 1968). As Clark (1967) points out, the biggest problem is that most of the inhabitants of this subsystem are microscopic and traditional approaches involving numbers and detailed analyses of individual species are difficult to accomplish and even more difficult to interpret.

It is possible to measure total respiration of the litter-soil subsystem as a unit and use this as an estimate of heterotrophic activity and numerous such studies have been made utilizing a variety of techniques (Macfadyen, 1970; Parkinson, Gray and Williams, 1971; Froment, 1972). Three major approaches for field measurements have been developed (Macfadyen, 1970; Macfadyen, 1971) and each

have their particular advantages and disadvantages. All involve enclosure either completely or partially, for at least the time of measurement, of a representative sample(s) of the forest floor with some degree of disturbance to the subsystem. Dobbs and Hinson (1966) point out that almost any disturbance promotes microbal activity. Proper choice of containers, care in putting the containers in place, and a long time interval after the initial disturbance before initiating measurements should control much of this effect (Macfadyen, 1971).

The most recent developed method (Macfadyen, 1970) utilizes continuous circulation of air through the enclosure by means of a pump with the $CO_2$ content in the air-stream determined variously. This method, when an infrared gas analyzer is used for $CO_2$ determinations, is probably the most sensitive and yields the best estimate of total respiration available, although presently errors of an unknown magnitude are caused by the continuous modification of the natural gas relationships of the subsystems by the air-stream. In addition, of the three methods, this involves by far the most expensive field equipment and is also the most difficult to maintain operational in the field.

The other methods are estimation of the carbon dioxide increase in the air content of the enclosure by extraction of periodic small samples, and continuous absorption of $CO_2$ in alkali during enclosure with determination of the $CO_2$ content of the alkali done in the lab. The first does not have the moving air stream problem, but raises the

serious problem of the effect of $CO_2$ buildup in the container on the heterotrophs in the subsystem (Alexander, 1961) and is very time consuming in the field. The latter method has been extensively used, is by far the cheapest method utilizing the simplest equipment in the field, and allows a large number of samples to be taken during the same time interval, over variable time periods, and with acceptable field work loads. In addition, the equipment can be left in place indefinitely without problems due to exposure to the weather. According to Macfadyen (1970), the inverted box variation of this method, first developed by Witkamp (1966a) probably yields the most reasonable data although it appears to underestimate the actual $CO_2$ rates.

Recently, much attention has been given to the problem of errors inherent in and limitations of these three methods when used to determine the respiration rates of the litter-soil subsystems, and each of them appear to cause serious deviations from normal conditions for heterotroph metabolism and to yield inaccurate estimates of total respiration rates (Ballard, 1968; Woodwell and Botkin, 1970; Odum et al., 1970; Macfadyen, 1971; Parkinson, Gray and Williams, 1971). However, as Reiners (1968) points out, carbon dioxide evolution is the most convenient method for studying this subsystem. If absolute values are unreliable, at least such data are our most useful estimates for comparing rates of biological activity under various conditions and can be used as diagnostic parameters of ecosystem types and for

describing energy-flow and clarifying the factors which control rates of decay and nutrient release in the litter-soil subsystem.

Which method to use depends upon the information needed. If the most accurate estimate of $CO_2$ yields for short time periods is desired and the expense is justifiable, then the continuous air stream with infrared $CO_2$ analyzer is the system to utilize. If a large number of samples with long measurement periods is needed and the accuracy of the absolute values is not so critical, then some variation of Witkamp's (1966a) method is appropriate.

Besides the problems of reliability and reality of the methods available for measuring the $CO_2$, there exists the problem of lack of internal homogeneity in the litter-soil subsystem. While the litter respiration is predominantly the result of heterotroph activity, the soil portion includes such activities plus root respiration (Macfadyen, 1970). Some researchers estimate the root fraction to be as high as 50 percent of the total respiration in this subsystem (Bray and Gorham, 1964; Wiant, 1967). Since root respiration is directly coupled with the activity of the producers, it is likely influenced by different factors, and/or the same factors differently than is the respiration of the decomposers.

Methods have been devised to attempt to accurately account for the root fraction in litter-soil respiration but they have met with limited success, are often very time consuming, and involve

considerable disturbance of the subsystem (Head, 1970; Odum, et al., 1970; Head, 1971). Since the majority of the decomposition of the detritus in many forest ecosystems occurs in the litter fraction (meaning here that portion of the subsystem above the mineral soil surface and including a humus layer if present), an alternate approach is to redefine the subsystem to exclude the soil portion and consider the litter as a separate subsystem (Attiwill, 1968).

In some forests this presents a problem when a humus layer grades into the mineral soil making boundaries difficult to delimit but in many forests, including the Douglas-fir ecosystem used in this investigation, a distinct litter subsystem, easily separable from the soil, exists. Witkamp (1963) was apparently the first to measure $CO_2$ in the field in isolated litter subsystems, although many investigators had previously used gravimetric methods to estimate decomposition rates in the litter subsystem (Bobcock and Gilbert, 1957; Witkamp and Drift, 1961; Crossley and Hoglund, 1962; Drift, 1963).

Defining the litter as a subsystem distinct from the soil offers greater homogeneity for investigations into factors influencing the activity of the heterotrophs. However, the activity in the litter subsystem is not, unlike the activity of the litter-soil subsystem, a measure of all the detritus not exported from the ecosystem which could be significant if one were interested in nutrient cycling. In addition, the uncertainty of the absolute values obtained may be increased

due to the increased manipulation of the litter necessary for measuring it separately. However, in forests with easily recognized litter-soil boundaries and with proper care in the handling, this factor can probably be kept insignificant. For studies involving factors affecting major heterotrophic activity in forest detritus pathways, the homogeneity of the litter subsystem in these very complex pathways can be valuable, particularly in permitting smaller sample sizes.

Numerous studies have been made of the factors affecting respiration rates in the litter-soil subsystem. Temperature and moisture have been found to be strongly correlated with respiration and thus climate is an important factor (Witkamp, 1966b). Witkamp (1969) reports that daily cycles of $CO_2$ evolution from the litter and soil are prominent. "Soil" flushes which appear to be due at least in part to temperature differences between the soil and the air immediately above it are common. Witkamp (1969) suggests that for comparisons of $CO_2$ rates from different sites and for estimation of mean decomposition rates over various time periods, it is necessary to determine the $CO_2$ evolution rates for 24-hour periods in order to account for the effect of daily cycles. Reiners (1968) discusses the importance of wetting-drying cycles on litter-soil respiration and considers that systems, in which such cycles are frequent, may be maintained in an immature state with less diversity, less complexity and higher energy flow per unit biomass than those in more mature systems.

The quantity of litter received per unit area and per specific location on the forest floor is an obvious factor and Bray and Gorham (1964) give an extensive summary of data on litter-fall. Less obvious is the influence of the temporal pattern of the distribution of detritus to the litter-soil subsystem (Hopkins, 1966). The relationship between the type of overstory vegetation and the respiration rates in the litter-soil subsystem has been extensively studied. Woodwell and Marples (1968), Duvigneaud and Denaeyer-De Smet (1970), Fortescue and Martin (1970), Ulrich, Ahrens, and Ulrich (1971), and Reiners (1972) serve as a good introduction to the vast amount of information accumulated and include extensive reference lists.

Many studies have been made, often with laboratory microcosms, attempting to correlate either decomposition rates (variously estimated) with the presence of certain mineral nutrients and/or their quantities and to a lesser degree with a variety of organic compounds. Edwards, Reichle, and Crossley (1970) give a good summary of the substances studied and the types of relationships considered important. Carbon-nitrogen ratios are apparently the most common chemical property showing good correlation with litter decomposition rates, although Witkamp (1963) found this to be of only limited value to characterize suitability of different leaf types for microbial attack.

Most of the attention has been directed at chemicals known or suspected to act as fertilizers and/or at the energy values of the most

abundantly produced organic substances, but other effects are possible. Rennerfelt (1948) demonstrated that thujaplicins, phenol-related substances extracted from Thuja plicata, strongly inhibited spore germination and growth of fungi and bacteria in concentrations as low as 10 ppm. Florence (1965) reports that Lithocarpus densiflorus litter stimulates microbial activity of humus in Sequoia sempervirens forests. Li et al. (1971) report that Alnus rubra litter has a high content of phenolic compounds some of which are inhibitory to micro-organisms.

The physical structure of the litter as related to decomposition rates has not been frequently studied although Kucera (1959) discussed the role of the leaf texture, Malone and Swartout (1969) the role of organic particle size, and Old (1969) the role of contact with the soil as related to the vegetation producing the litter.

The effect need not be directly on the decomposers. The soil fauna long have been believed important in determining the rate of litter decomposition (Birch and Clark, 1953). Studies have shown that even though their total respiration constitutes a small portion of the total litter-soil respiration, the fauna are significant factors in the decomposition of the litter through their "processing" of it (e.g. by fragmenting, increasing surface area, and in some cases chemically altering the litter, and by aeration of the subsystem) (Witkamp, 1961; Nielsen, 1962; Witkamp and Crossley, 1966; Macfadyen, 1967;

Satchell and Lowe, 1967; Edwards et al., 1970). Thus, changes in litter decomposition rates could be effected by factors affecting the fauna.

Forests often have extensive understory vegetation consisting of a variety of species. The importance of understory vegetation in forest ecosystems has been stressed by several investigators particularly Scott (1955) and Ovington (1962). Many understory plants have a high nutrient content (Scott, 1955). Hughes (1970) considers the measurement of the contribution of the ground vegetation to forest litter to be important, even though the preponderance of litter produced originates in the overstory.

Bray and Gorham (1964) have summarized much of the data available on understory litter production and cite a maximum figure of 28 percent of the total litter produced in a forest. This maximum is for a very young stand of Robinia (Auten, 1941) and excepting such immature stands, Hughes (1970) estimates an average of nine percent as the mean total understory contribution to the litter subsystem for major forest types. Some of the figures Hughes uses to compute the average include small trees that are not part of the overstory.

Many litter production studies are currently underway, many of these as part of International Biological Program (IBP) studies of various ecosystems. Numerous studies have been made of litter-fall and nutrient cycling in Douglas-fir forests (Abee and Lavender, 1972)

but with the exception of Tarrant, Isaac, and Chandler (1951) and Abee and Lavender (1972) these have all been on relatively young stands. Abee and Lavender (1972) report that in a mature Douglas-fir forest, approximately six percent by weight of the total litter produced per year is due to the understory species.

Thus, in terms of biomass the contribution of the understory to the litter subsystem is usually small, however, its effect on decomposition rates and movements of materials is not necessarily insignificant. Witkamp and Frank (1967) note that groundcover can be a significant factor in the retention of cesium-137 and thus of mineral cycling in general. Minderman (1968) concludes that after a relatively short time, e.g. 10 years, the accumulation of organic material in the litter is mainly determined by those components of the litter that are more or less unassailable, even if originally they were added in only small quantities. Such components are, for example, condensed or polymerized polyphenols and perhaps other components with equally long decomposition times produced by heterotrophic organisms (Minderman, 1968).

Thus, it is possible that despite their small organic contribution, certain components of certain understory species may have an important influence on decomposition in the litter-soil subsystem. This can be by fertilizing, inhibiting, or otherwise affecting the accessibility of the litter to decomposition, either through the

decomposers directly or by affecting the distribution and activity of certain litter and soil fauna.

Since forest litter subsystems are often very heterogenous, influenced by physical, chemical, and biotic factors interacting, a study designed to determine heterotroph activity in the subsystem needs to account for as many of these factors as needed to enable focusing on the factor(s) of interest and accomplish this without introducing significant variables into the system. Lab approaches, while very attractive in terms of equipment available, accuracy of measurements possible, easing of logistics, and the potential for isolating single factors, present very difficult problems in determining their reality. The potential unreality of the lab situation in contrast to the field in complex terrestrial ecosystems like forests has been noted by several researchers (Engelmann, 1966; Macfadyen . 1967; Parkinson et al., 1971). The duplication of realistic moisture and temperature regimes, the disturbance due to handling, the movement of fauna and materials into and out of the subsystem (including those leached from the living plants), the maintenance of the physical structure and gas exchange conditions of the subsystem are problems very difficult to resolve in laboratory microcosms. The relationship to natural ecosystems of studies in which subsystems are constructed in labs using isolated organisms, litter-soil extracts or of decomposition studies that are

made on litter that has been variously collected, dried, ground, and rewetted is even harder to ascertain.

For these reasons there exist a real need for field measurements which despite the present limitations of the methods available can provide much information about the nature of ecosystems.

## Objectives

The major purpose of this investigation was to demonstrate and quantify the effect of some selected understory species on the energy utilization rates in the litter subsystem of a major forest type as measured by rates of $CO_2$ evolution. The specific objectives were fourfold:

1. To measure the annual carbon dioxide production rate of the litter subsystem of a Douglas-fir forest as a function of understory type.

2. To test the hypothesis that the litter subsystem in a Douglas-fir forest is a useful subsystem for quantitatively studying heterotrophic utilization of energy.

3. To estimate the annual $CO_2$ production rate of the forest stand studied, on a unit area basis for comparison with existing data for other forest types.

4. To determine if moisture and temperature were major factors in the relationship between understory type and respiration rate of the litter layer.

# AREA OF STUDY AND METHODOLOGY

## Study Area

A forest with Douglas-fir (Pseudotsuga menziesii) as the sole dominant was the ecosystem chosen for this study for several reasons. According to Franklin and Dyrness (1969), Douglas-fir is frequently the sole dominant in the Tsuga heterophylla zone. This vegetation zone is the most extensive and in terms of timber production, the most important in western Washington and Oregon. The choice of a forest dominated by one overstory species eliminates one source of confounding variability, that of the overstory litter being contributed by more than one species. The common occurrence of overstories consisting of similar-aged trees decreases the variability of the litter input due to age as a confounding factor. Finally, this is an esthetically pleasing forest type to this researcher and was a pleasure to work in.

Field measurements and collections of litter were made during the litter respiration season of August 31, 1971 to July 3, 1972 on a mature Douglas-fir forest stand located in the Corvallis City Watershed on a ridge on the eastern slopes of Mary's Peak at an elevation of approximately 460 meters. The stand occupies a flat, bench-like rectangular area 450 meters long by 150 meters wide, just north of U. S. Forest Road no. 1242 which in this area runs just north of the ridge top. Within this area, four sample areas, each of 2500 square

meters, were laid out contiguous except between areas 2 and 3 where a gap was made to avoid a site where several trees had been previously cut. The northern boundaries of the areas were placed 60 meters in from the edge of the road which was the southern boundary for salvage logging performed north of the road in the 1960's. Map location of the four areas was determined by using a tape measure with the south edge of road 1242 at the intersection with road 1242F as a bench mark (Figure 1). The area designations of 1-4 on Figure 1 are the ones used throughout this report.

The particular stand used in this study was selected for several reasons. At 460 meters elevation it is below the altitude where snow is common in winter months and this minimizes the problem of snow cover over 2 cm, a depth which makes sampling infeasible with the methods used. It is easily accessible from road 1242 which is an all-weather road maintained free of obstructions throughout the year. It had a variety of understory species associated with the pure Douglas-fir overstory. The choice of a flat area minimizes the effect of topography on the litter respiration. The apparently even-aged overstory and the lack of unavoidable visible disturbance should have helped minimize the effect of overstory variation on litter input to the litter subsystem. The watershed is closed to the general public and this allowed the permanent placement of field equipment without fear of disturbance. The areas were close enough to my residence to

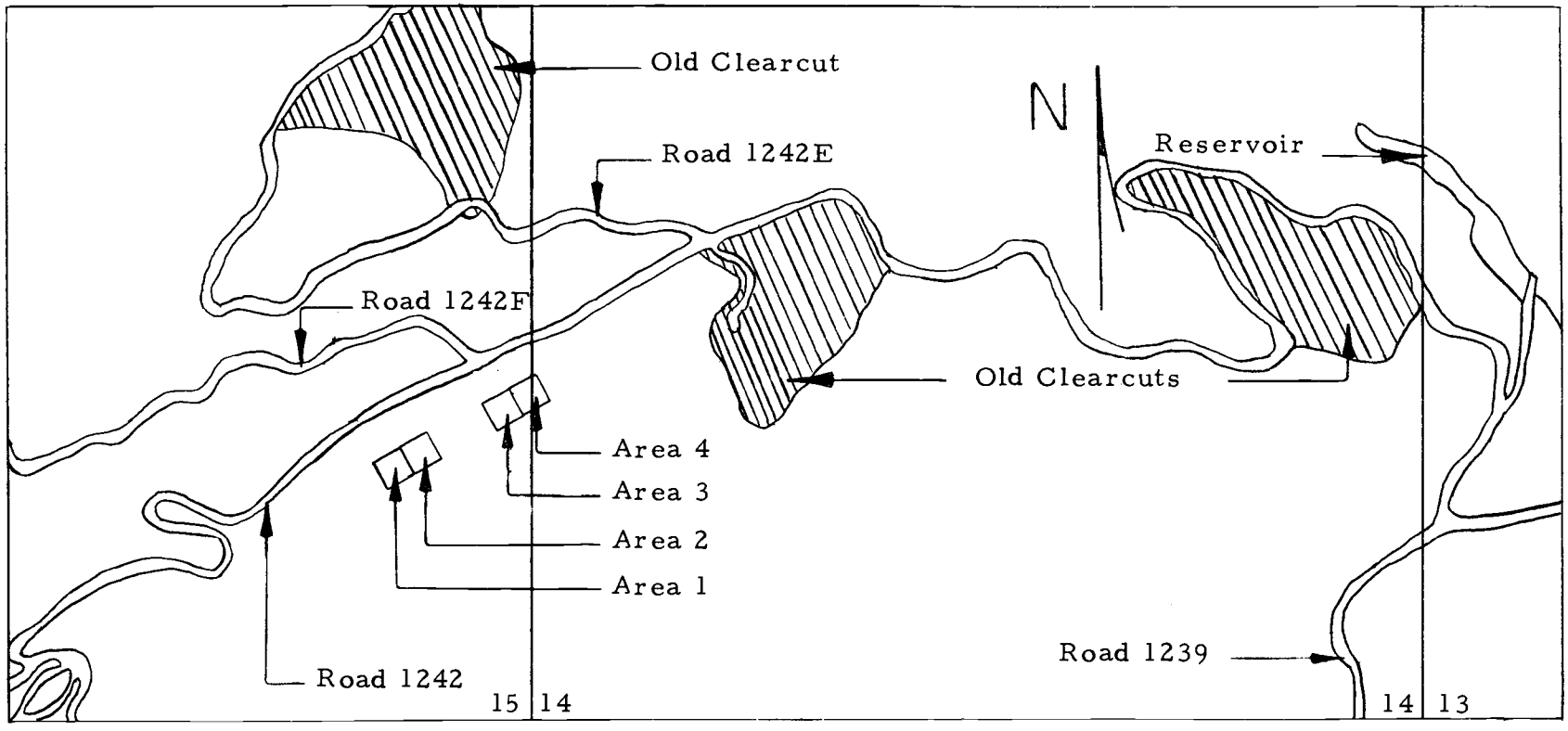



Figure 1. Map of location of sample areas. Adapted from U. S. Forest Service Timber Sale Map for Marys Peak Ranger District, Siuslaw National Forest.

allow frequent sampling with an acceptable expenditure of time and money.

## Selection of Understory Types

Six distinct understory types were chosen:

1. Salal (Gaultheria shallon)
2. Creambush oceanspray (Holodiscus discolor)
3. Vine maple (Acer circinatum)
4. Western hemlock (Tsuga heterophylla)
5. Golden chinkapin (Castanopsis chrysophylla)
6. Sword fern (Polystichum munitum)

These type names refer only to the tallest understory species associated with the type and do not preclude the existence of smaller species beneath them.

The criteria for selection for use as an understory type were that in all four areas the type was found free of apparent, man-related disturbances and covering a sufficient area to permit sampling unconfounded with the other understory types. This does not necessarily mean individuals of one species isolated, as for example, oceanspray was invariably found associated with salal beneath it, but means that a salal type could be recognized as distinct from the salal associated with the oceanspray..

Sufficient area was determined by the area needed for location of the respiration sampling devices and the taking of periodic moisture content determinations with a minimal effect upon each other and of avoiding sampling in areas in which types intergrade. This was estimated to be at about 10 $m^2$. Only the six types chosen met these criteria, although Berberis nervosa was found in all four areas, sometimes common, it was always too confounded with other types and covered areas too small for recognition as a distinct type. All other understory plants were either not found in all areas or occupied too small an area in at least one of the areas.

A "typical" individual (for oceanspray, chinkapin, and hemlock), or "typical" patch (for sword fern, salal, and vine maple) was located in each area. The criteria for "typical" individual or patch were that the center of the area it covers be at least 3 meters from the base of the nearest overstory tree, that it not be confounded with large fallen limbs or stems, that it appeared healthy, and that it appeared to represent the usual form for the species in the forest. A "typical" chinkapin or hemlock was a small tree, a "typical" sword fern or salal was a large patch of many individuals, a "typical" vine maple was a clump, and a "typical" oceanspray was a single shrub..

Other criteria could have been chosen and several of these species are also found occurring together, especially on the edges of their occurrence, but these criteria are believed to represent the

most common condition in this forest stand. This typing procedure was utilized instead of a completely random selection to minimize the effect of factors which were not central to the major goal of demonstrating the existence of the understory effect and to reduce the sample size necessary for this in order that a single researcher could handle the fieldwork. This does result in decreased accuracy in the estimation of the annual respiration yield for the litter subsystem of this stand. Since the annual yield as designed is a rough estimate meant for comparison with similar rough estimates made on other ecosystems this was considered acceptable.

## Determination of Sample Spot Location

The sample spots to be used for locating the equipment for the collection of carbon dioxide were located randomly in the following manner: A 10 $m^2$ segment of each "typical" individual or patch was mapped on graph paper using one square to represent 100 $cm^2$ of understory type. The 10$m^2$ segments were from the middle of the area covered by the "typical" individual or patch. Two widely spaced points were marked on the ground and on the drawing of each individual or patch, to be used as reference points.

From a table of random numbers (Snedecor and Cochran, 1967) a number from 1-1000 was drawn and marked on the appropriate square on the graph paper. Using the two reference points this square was

then located in the field. Three such points were located on each drawing, sequentially numbered. In cases where a large piece of wood or surface roots made locating the device for the collection of carbon dioxide impossible around the first square chosen, then the next chosen square was used. The location of each device was made around the 100 $cm^2$ as closely as the stems of the understory plants would permit.

## Methodology for Collection of Carbon Dioxide

The devices for collection of $CO_2$ were a modification of Witkamp's (1963) inverted box method. Two open-ended cylinders, 15.65 cm in diameter were sunk 2.5 cm into the mineral soil around the sample spots during the first week of August, 1971. This time was chosen for placing the cylinders because during the summer the litter is dry and easy to handle. The sinking of the cylinders was facilitated by a sharpened edge on the bottom of the cylinder and by cutting with a sharp, thin-bladed knife. Care was taken to minimize the disturbance to the litter and soil and to place the paired cylinders in litter of comparable depth.

The cylinders were made by cutting out the bottoms of acrylic plastic containers. The cylinder thus formed was 8.6 cm tall. This height represents a compromise between the available materials, the need for the cylinders to project far enough above the litter to allow

sealing of the tops, and the desire to minimize the disturbance of the subsystem by keeping the projection above the surface as low as feasible. In practice this projection ranged from 0.8 cm to 4.5 cm depending upon litter depth. Acrylic plastic was chosen because it was cheap, resistant to physical and biological degradation, and its thermal properties more likely parallel those of the litter than metal. Any living herbs or mosses growing in the area circumscribed by the cylinders were carefully removed.

For collection of $CO_2$ the cylinders were closed with modified cannister tops. The tops were modified by cutting out the center and gluing to the remaining rim heavy, polyethylene bags, 30 cm long by 25 cm wide. These tops when sealed (achieving an airtight seal was aided by use of Dow high-vacuum stopcock grease) enclosed a minimum air volume above the litter surface of approximately 3 liters. This volume was desired so that the oxygen in the air enclosed within the containers represented at least four times the maximum expected to be used during a sampling period.

The flexible bags were to allow the enclosed system to adjust to the removal of oxygen by the respiring heterotrophs and to removal of gaseous $CO_2$ by the $CO_2$ traps with minimum change in pressure. This was accomplished by the collapsing of the bag rather than permitting gas pressures to lower. This minimized any possible effect of change of pressure on the activity of the organisms and avoided

inducing gas movements in the litter and/or soil due to a lowering of the pressure at the surface.

Gas exchange is known to take place slowly through polyethylene (Renfrew and Morgan, 1957), however, this is small and was accounted for by the controls. The controls were two cannisters with their bottoms intact. These were placed 7.5 cm deep into the litter-soil subsystem to approximate the temperature condition in the subsystem and were sealed during a sampling period the same way as the open-ended cylinders. The internal volume of the cylinders was adjusted to represent the average depth of the litter by adding an appropriate amount of moistened perlite. The $CO_2$ yield during a sample period for the controls represented the exchange through the polyethylene, the $CO_2$ normally present in the air, and the $CO_2$ due to handling and preparation of the $CO_2$ absorbing materials. A lab control measuring the $CO_2$ due to the handling and preparation of $CO_2$ absorbed, allowed calculation of the background in the containers during a sample period. Subtracting the controls yields from the yields in the open-ended cylinders gives the net $CO_2$ attributed to the heterotrophic activity in the subsystem.

The $CO_2$ traps were small, wide-mouthed glass jars, 4.2 cm by 3.5 cm, which were sealed for transport to and from the field. They were filled with either 20 ml of 0.5 N or 1 N KOH, the normality used depending upon the activity of the heterotrophs. The use of alkali

solutions for absorbing $CO_2$ is described by Conway (1962). The 0.5 N and 1 N KOH stock solutions were prepared once a week using Acculute[1] standard $CO_2$-free volumetric KOH solutions.

The $CO_2$ traps were placed on the litter or soil surface, unsealed, left for the duration of the sample period, resealed, and then returned to the lab. In the lab the containers were allowed to come to lab temperature (approximately 25° C) and then their conductivity measured according to the method of Wollum and Gomez (1969) by a Beckman model RC 16B2 conductivity bridge with a Beckman CEL-G 20 pipette conductivity cell. These conductivities were adjusted for any difference from 25° C of the lab temperature according to the method in the Beckman manual (Instruction Manual, 1967).

The adjusted conductivity readings were converted to milligrams of $CO_2$ by standardizing the conductivity with an appropriate range of 0.5 N KOH and 1 N KOH solutions containing known $CO_2$ concentrations. The standards were prepared according to the method of Wollum and Gomez (1969) and their $CO_2$ content determined using the two-phase titration with HCl as described by Lieth and Ouellette (1962).

## Respiration Measurements of the Subsystems

One of the two open-ended cylinders placed at each sampling spot was used to measure soil and litter respiration as a unit. The other

[1] Tradename of Anachemia Chemical Inc., Champlain, N. Y.

container had its litter carefully removed from the top of the soil and placed in a fiber-glass mesh tray (mesh size 0.16 cm) which was designed to just fit inside of the cylinders. During non-sampling periods this tray with the litter, remained on top of the soil in the cylinder. At the start of a sampling period the tray with litter was removed from the open-ended cylinder and placed in the cylinder with a bottom which was dug into the litter near the open-ended cylinder. Carbon dioxide evolved from the soil subsystem was collected from the cylinder minus the litter. Carbon dioxide evolved from the litter subsystem was collected in the cylinder with a bottom. Carbon dioxide evolved from the litter-soil subsystem was collected from the bottomless cylinder with the litter-soil subsystem intact.

Precipitation and litter-fall during the sampling periods was collected in appropriate sized containers near the cylinders and added to the cylinders at the end of each sampling period.

The sampling periods were 24 hours long and ran from the first adequate light for movement in the forest in the morning to the same clock time the following morning. As the seasons progressed the starting times were changed with the change in time of sunrise. This regime was adopted to minimize diurnal effects. According to Witkamp (1969) an afternoon high followed by a predawn low is the usual pattern of respiration from the litter-soil subsystem and is probably caused by temperature change. Since all the samples cannot

be started and terminated at the same time, accomplishing this during or near the time of lowest respiration rates was used to minimize this variation due to the time of day.

It proved to be too difficult to move rapidly through the forest in the darkness before dawn, even with a light, so the time of first light in the morning was chosen. Rapidity of movement was necessary to minimize the time interval between the first and last sample made in a 24-hour period and by laying out a definite route to follow, it was possible to service the 72 respiration samples and the two controls in an average time of 105 minutes. Following a definite, marked route also served to minimize disturbance to the understory type in the vicinity of the equipment for the collection of carbon dioxide and to pinpoint areas to avoid in the other field sampling carried out in this study. The sampling sequence was always "by the numbers" starting with area 1 and ending in area 4. Since it is possible that a significant effect could occur due to the regular starting and finishing time differences for the sample spots, this effect was checked for, as a phenomena of the areas, in the statistical analyses of the data.

Collection of carbon dioxide was done throughout the litter respiration season. A dry summer period of varying lengths is usual in western Oregon and if the moisture content of the litter falls low enough, measurable respiration in this subsystem ceases. Thus the litter respiration season was defined as starting with the first rains

of late summer or early fall that lead to litter respiration and terminating when the drying in early summer causes cessation of litter respiration.

A 24-hour on, 24-hour off sampling regime was followed, interrupted only by periods of snow greater than 2 cm and occasionally by the press of other duties. This represented a compromise between gaining the maximum amount of information while minimizing the effect of long-term enclosure of the subsystems. This was not only a matter of moisture, but also a matter of maintaining normal $CO_2$ relationships in the subsystem. Macfadyen (1970) recommends the continuous absorption of $CO_2$ method be used only for time intervals of several hours duration because of possible effects on the activity of the microorganisms of the lowered $CO_2$ caused by its removal by the $CO_2$ traps. While this may be true at the surface, the fact that this method appears to underestimate litter respiration (Witkamp, 1966a; Macfadyen, 1971; Froment, 1972) would indicate that, if anything, it should cause a buildup of $CO_2$ in the subsystem.

This is a difficult factor to assess, since it is not known how much or if the $CO_2$ levels are changed in the subsystem, nor how deep into the subsystem the effect might occur during a particular sampling regime. Cochrane (1958), in discussing the effects of $CO_2$ on the growth of fungi in lab experiments, states that high $CO_2$ pressures generally inhibit the growth of fungi but the level at which inhibition

occurs is quite variable. For example, some are inhibited by as low as 23 mm of $CO_2$, others are relatively unaffected by pressures as high as 150 mm or more. He also mentions that soil fungi appear to be stratified by their tolerance to $CO_2$, the deeper, the more tolerant. Since Witkamp (1969) demonstrated very large diurnal fluctuations it seems possible that the fungi are stratified to mean daily $CO_2$ levels while experiencing widely ranging levels during a typical day.

In addition, the published data indicated that the inhibition effect, if any, on soil fungi is only at high concentrations (Burges and Fenton, 1952; Walsh and Stewart, 1971) and in at least one case (Buston, Moss and Tyrrell, 1966) $CO_2$ was actually shown to promote the growth of fungi. Thus it was felt that the demonstrable advantages of a 24-hour period with a regular pattern of non-closure to help minimize such disturbances as the $CO_2$ changes might cause outweighed the possible advantage of very short term measurements.

Normalization of the litter-respiration to $CO_2$ yield per gram of litter in the cylinder was used to allow direct comparison of the respiration rates between types, unconfounded by the differential litter depths in the litter trays. The weights for normalization were determined by bringing the litter in the trays into the lab at the end of the litter respiration season and determining their oven-dry weights gravimetrically. The procedure for drying is discussed in the litter-weight section.

## Litter Temperature

The temperature of the litter subsystem at or near the soil surface and the air temperature immediately above the litter subsystem surface at each sample spot were taken with a thermister. This was usually done once every six days immediately following the termination of a 24-hour respiration sample. The litter temperature was taken by inserting the thermister probe 1.6 centimeters into the litter of the litter and soil subsystem sample at each of the 26 individual sample spots. The 1.6 cm depth represented the minimum depth of litter found at the sample spots.

Daily temperature data for use as the covariant in covariant analysis of the litter respiration were obtained from measurements taken by the plant staff outside the Rock Creek Water Treatment Plant of the city of Corvallis. This plant is located approximately two air miles southeast of and 310 meters lower than the study area. Absolute values would tend to differ from those of the site but for the covariant analysis, all that is needed is that the sequence of the changes be the same. The temperature data available consisted of maximum, minimum, and 0800 daily temperatures. A mean temperature computed as the average of the 0800 temperature at the start of a sample period, the 0800 temperature at the termination of a sample period, and the maximum and minimum during a sample period was taken

to be the best estimate available of the 24-hour temperature pattern during a sample period at the study site.

## Litter Moisture

Moisture content of random samples of the litter subsystem beneath the six understory types was determined. The moisture content of the litter was measured as percent moisture determined from the difference between the wet weights and the oven-dry weights of the samples. Moisture samples were taken weekly in the early fall and in the spring when moisture conditions were believed to be changing and were not taken during the late fall and during the winter when it became obvious that the almost daily rains were resulting in an approximately steady-state moisture content in the litter.

The random samples were restricted to areas beneath the "typical" individuals or patches. Randomization was achieved using the method used for location of the $CO_2$ collection devices. No samples were taken closer than 50 cm to a $CO_2$ collection container to minimize disturbance of the gas relations in the soil and litter in these areas.

Grier and McColl (1971) report that the water storage capacity is relatively consistent in a forest floor regardless of type and give a table for estimating sample size needed to estimate moisture content with a sampling error of 10 percent or less at 95 percent probability.

Extrapolating from this table I estimated that three small (in area) samples from each "typical" individual or patch would suffice for the purposes of my study.

Using the general methods of Wallwork (1959) litter samples were carefully punched from the litter subsystem with a metal cylinder the end of which had a surface area of 9.62 $cm^2$. These samples were placed in labeled polyethylene bags, transported to the lab and their wet weights determined. From the literature there appears to be no standard method accepted by most researchers for drying litter samples in preparation for dry-weight determinations. Bray and Gorham (1964) discuss the problems of loss of volatile materials using different temperatures and time regimes and conclude that no one method appears clearly best. I used the method that appeared to be most commonly used, that of placing the wet litter in an 105° C oven until a constant weight was found (Capstick, 1952; Hurd, 1971).

## Litter Weight

Litter weights of random samples were taken and oven-dried using the same cylindrical device and temperature treatments as were used for the moisture samples. In each of the four areas, for each of the six types, 50 random samples were taken in December, 1971. The random spots for samples were determined by roughly type-mapping each of the areas as to the six understory types and then locating

randomly, with a north-south orientation, map lines through each distinct patch of understory type to a minimum of 50 meters total length. Then, by the decimeter, using a table of random numbers, (Snedecor and Cochran, 1967), 50 points were chosen and located in the field.

The oven-dry weights were used to calculate an estimation of the mean dry weight of litter/unit area/understory type. Grier and McColl (1971) on a study in a second growth Douglas-fir forest state that good estimates of forest floor weights can be obtained by similar samples and give a table of sample sizes necessary to estimate means to a plus or minus 10 percent with 95 percent confidence. The sample size of 50/area/type is a calculated guess based on their data and on the accuracy I felt sufficient for the objectives of this study.

No samples were taken from beneath the 10 $m^2$ area of the "typical" individuals or patches to avoid undue disturbance to the vegetation and the forest floor in these areas. No samples were taken immediately next to logs or large branches on the floor as they represent a special case of very large amounts of woody material.

Since channeling of materials down the boles of trees is known to cause greater litter depths to occur immediately next to the tree (Gersper and Holowaychuk, 1971) these areas represent a situation different from that under the rest of the canopy. Accordingly, a distance 1 meter around each overstory tree was considered out of the

areas to be sampled. This distance was chosen because Bollen, Chen, Lu, and Tarrant (1967) and Gersper and Holowaychuk (1971) and others had found that the effect was confined mostly within 30-50 cm of the bole of the tree.

## Percent Douglas-Fir Needles

In 20 percent (10 out of each 50) of the oven-dry litter weight samples, the Douglas-fir needles and needle fragments that were recognizable as such, were separated from the rest of the litter and weighed. Expressed as grams of Douglas-fir needles/gram of litter, this was used as a measure of the variability of the detritus contribution of the overstory to the litter subsystem beneath the various understory types. The separation was done with needle-pointed forceps with confirmation of doubtful fragments by comparison with knowns under the low-power of a dissection scope.

## Estimation of Mean Annual Rate of Respiration of the Litter Subsystem

Line intercepts (Canfield, 1941) were used to estimate the area covered by the understory types. Fifty intercepts, 1 meter apart and 50 meters long, were made parallel to the eastern boundaries of each area. The northern boundary of each area was used as the baseline. A meter tape was laid out and the interception of the understory types

was measured to the nearest decimeter. Douglas-fir trees and any understory species covering an area larger than one $m^2$ in area were also recorded. While a random distribution of the lines likely would have yielded more accurate estimates (Cain and Castro, 1959) I felt that for the purposes of this study the extra work in randomizing was not justifiable.

The relationship, percent of total area covered by an understory type times the mean weight of litter/$m^2$ of that type times the mean annual respiration/$m^2$/unit weight of litter of that type summed for the six types, was used to estimate the mean annual respiration/$m^2$ of the litter subsystem. This estimate was for that portion of an average $m^2$ in the stand occupied by the six understory types.

## Methods of Analysis

The following statistical methods were used:

1. For all respiration data, two-way analysis of covariance with temperature as the covariate and understory types and sampling areas as factors.

2. For normalized litter respiration and for soil respiration compartmentalized into three seasons, three-way analysis of covariance with temperature as the covariate and understory types, sampling areas, and the three seasons as factors.

3. For soil and litter temperatures, two-way analysis of covariance with air temperature as covariate and understory types and sampling areas as factors.

4. For litter weights, two-way analysis of variance with understory types and sampling areas as factors.

5. For percent Douglas-fir needles, two-way analysis of variance with understory types and sampling areas as factors.

6. For moisture, two-way analysis of variance with understory types and sampling areas as factors.

7. For testing correlations between air temperatures at site and 0800 air temperatures at weather station, analysis of covariance with air temperature at site and 0800 air temperature at weather station as covariants.

8. For overall significance of factors in 1-6 F-test.

9. For linear comparisons for significance of specific effects within factors (e.g. difference between two types) in 1-6, Scheffe's test.

10. For determining the degree of correlation in 3 and 7 the following relationship:

$$\rho = \frac{\text{Cov } (xy)}{Sx \cdot Sy}$$ (Snedecor and Cochran, 1967).

# RESULTS

Rates of respiration for the litter, the soil and the litter-soil subsystems under the six understory types were measured as change in the conductivity in KOH solutions for 126, twenty-four hour periods. These periods were always separated by at least a 24-hour period of non-sampling. All measurements were made in the litter respiration season of August 31, 1971 to July 1, 1972. Conversion of the conductivity readings to mg $CO_2$ was done using a set of known standards.

Thirty-nine days were lost to snow accumulations greater than 2 cm in the sampling area. A summary of the weather for the litter respiration season is given in Table 1. As can be seen overcast, often rainy days predominate for much of the litter respiration season. The precipitation totals are probably underestimates of the precipitation received by the forest in the sampling areas because the data was gathered at a lower elevation and rainfall generally seemed to increase with increase in elevation on this mountain.

Litter plus soil rates of respiration were calculated by summing the litter and soil measurements at each sample spot. All rates of respiration were converted to a per hour per $m^2$ basis except for normalized rates of respiration for the litter subsystem. Normalized rates of respiration for the litter subsystem were calculated to minimize the effect of differential litter depths in the samples to allow

Table 1. Summary of weather for Corvallis Watershed for litter respiration season August 31, 1971-July 1, 1972.[1]

| Month | Moisture days | Overcast[2] days | Clear days | Snow[3] days | Precipitation total cm water |
|---|---|---|---|---|---|
| Aug. 31 | 1 | 1 | 0 | 0 | 2.74 |
| Sept. | 14 | 14 | 16 | 0 | 11.34 |
| Oct. | 10 | 12 | 19 | 0 | 13.37 |
| Nov. | 22 | 26 | 4 | 0 | 33.63 |
| Dec. | 26 | 28 | 3 | 16 | 40.59 |
| Jan. | 18 | 19 | 12 | 11 | 42.00 |
| Feb. | 22 | 26 | 3 | 6 | 24.59 |
| Mar. | 21 | 24 | 7 | 0 | 25.02 |
| Apr. | 15 | 15 | 15 | 6 | 16.58 |
| May | 11 | 15 | 16 | 0 | 10.13 |
| June | 8 | 14 | 16 | 0 | 5.18 |
| July 1 | 0 | 0 | 1 | 0 | 0 |

[1] From daily records of City of Corvallis Water Treatment Plant except for snow days which were determined on site

[2] Includes partly cloudy and fog

[3] Defined as days when snow on ground in morning exceeded 2 cm in the sample areas

comparison of mean rates to test for the effect of different vegetation types and/or different areas. Normalization was achieved by dividing the rates of respiration of the litter subsystem by the oven-dry weight in grams of the litter from the appropriate litter tray (Table 2). The respiration rates which were normalized to a per gram of litter basis were converted to a per kilogram litter basis. The kilogram figure is the closest base 10 number to the average litter weight per $m^2$ in the stand (Figure 2) and was chosen to enhance the visualization of the differences when comparing subsystems. Figures 2-50 are on pages 52-100 respectively. These figures were grouped for convenience and the reader is to remember that whenever Figures 2-50 are mentioned they will be found on pages 52-100.

Table 2. Oven-dry weight of litter in litter trays (grams).

| Vegetation type | Areas 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| *Holodiscus discolor* | 13.572 | 10.262 | 14.727 | 11.608 |
| *Acer circinatum* | 6.274 | 15.849 | 11.168 | 16.583 |
| *Gaultheria shallon* | 10.690 | 16.048 | 8.772 | 10.884 |
| *Tsuga heterophylla* | 9.490 | 16.127 | 14.593 | 20.585 |
| *Castanopsis chrysophylla* | 20.168 | 24.111 | 15.637 | 17.879 |
| *Polystichum munitum* | 30.038 | 27.423 | 31.509 | 18.095 |

All mean respiration values unless otherwise specified are the mean of the four 24-hour samples taken for each vegetation type during each sampling period. The statistical analyses utilized are given in the section on methodology and the major statistical quantities generated, that are pertinent, are given in the Appendix. The mean litter respiration season rates for all subsystems (including here the normalized rates of respiration of the litter subsystem and the litter plus soil rates of respiration) are all significant at $F_{0.05}$ for type and for area. Within factor differences (i. e. between types or areas) are also all significant for rates of respiration as tested by Scheffé's Test at 0.05 significance level.

Figures 3-12 illustrate the distinct patterns found in the relationship between the normalized rates of respiration of the litter subsystem and the vegetation types during the litter respiration season. The mean annual normalized litter respiration by type, for comparisons, are given in Figures 13-15 and in Table 5. They range from a high of 125.9 mg $CO_2$/hr/kg litter for the Holodiscus discolor type to a low of 60.1 mg $CO_2$/hr/kg litter for the Polystichum munitum type.

The data represented in Figures 13-15 also show the relatively smaller differences found between types for the other subsystems and the lack of apparent relationship between the pattern of differences found in the normalized rates of respiration for the litter subsystem and the patterns found in the other subsystems. Comparison of the

litter-soil subsystem rates of respiration with the litter plus soil subsystem rates of respiration given in Figure 15 indicate a consistent magnitude difference, the latter being larger for all types. Figure 15 also indicates that there is a similar hierarchy of rates of respiration by types for both the litter-soil and litter plus soil subsystems.

Figures 16-45 give the daily means for the litter, the soil, the litter-soil, and the litter plus soil subsystems and allow visualizing the similarities and differences in these subsystems throughout the litter respiration season. In particular can be seen the differences in the litter and the soil subsystems with respect to vegetation type and to date (and presumably thus to weather and physiological state of the producers).

Figure 2 illustrates the generally inverse relationship found between normalized litter rates of respiration and mean litter weight per $m^2$ for the vegetation types. The type difference in weight is significant at $F_{0.05}$, the area is not. The weight differences between types are all significant as tested by Scheffé's Test at 0.05 level of significance. Comparison of Table 3 with figures 2 and 13 indicates that, based on measurable percent Pseudotsuga menziesii needles per unit total weight of litter in the subsystem sample, there is no apparent significant relationship between the detritus contribution of the over-story and the magnitude and direction of the differences in rates of respiration between types or with the differences in litter weights

between types for the litter subsystem. The type difference for needle percentage is significant at $F_{0.05}$ but the area difference is not. All individual differences between types for needle percentage are significant as tested by Scheffé's Test at 0.05 level of significance.

Litter and soil temperatures were taken on 47 separate days at an average interval of six days throughout the litter respiration season except for snow days when no measurements were made. The correlation between litter and soil temperatures was 0.79. Table 4 gives the mean litter respiration season temperatures for the types and the areas. No significant difference ($F_{0.05}$) was observed for temperature by type or area.

The correlation between mean air temperature and the corresponding 0800 temperature reading at the water treatment plant was 0.84. This is a measure of correlation of the temperature changes in the sample areas with the temperatures at the treatment plant and is of interest because the treatment plant temperature values were used as the covariate in the analysis of covariance of the respiration data to reduce the variability in the samples due to temperature for statistical analysis.

Mean moisture of the litter for each vegetation type was determined from 12 samples per type taken during each of 22 days during the litter respiration season (Table 5). Type difference was significant at $F_{0.05}$ but area difference was not. As tested by Scheffé's Test for

Table 3. Douglas-fir needle weight expressed as percent of oven-dry weight of litter.

| Vegetation type | Percentage | Area | Percentage |
|---|---|---|---|
| Holodiscus discolor | 25.3 | 1 | 27.4 |
| Acer circinatum | 24.2 | 2 | 27.8 |
| Gaultheria shallon | 30.4 | 3 | 27.5 |
| Tsuga heterophylla | 28.0 | 4 | 26.9 |
| Castanopsis chrysophylla | 26.4 | | |
| Polystichum munitum | 29.9 | | |

Table 4. Mean litter subsystem temperatures in degrees centigrade for litter respiration season 1971-1972.

| Vegetation type | Mean temperature | Area | Mean temperature |
|---|---|---|---|
| Holodiscus discolor | 8.5 | 1 | 8.4 |
| Acer circinatum | 8.4 | 2 | 8.4 |
| Gaultheria shallon | 8.4 | 3 | 8.4 |
| Tsuga heterophylla | 8.4 | 4 | 8.4 |
| Castanopsis chrysophylla | 8.4 | | |
| Polystichum munitum | 8.4 | | |

Table 5. Comparison of mean[1] percent moisture of the litter with mean annual rate of respiration of the litter subsystem.

| Vegetation type | Percent moisture | mg $CO_2$/hr/kg of litter |
|---|---|---|
| Holodiscus discolor | 96.6 | 125.9 |
| Acer circinatum | 96.2 | 124.4 |
| Gaultheria shallon | 107.8 | 120.0 |
| Tsuga heterophylla | 124.2 | 99.4 |
| Castanopsis chrysophylla | 106.2 | 86.0 |
| Polystichum munitum | 129.7 | 60.1 |

[1] Mean based on the 22 sample periods, is biased towards Fall and Spring and is thus not to be taken as an estimation of mean annual moisture.

the significance at 0.05 of the differences between types, the differences between the Holodiscus discolor type and the Acer circinatum type and the difference between Gaultheria shallon type and Castanopsis chysophylla type are not significant. All other differences between types for moisture are significant.

The first nine moisture sampling periods were at an average 6-10 day interval from September 1 to October 28, 1971. At this point (Figure 46) it appeared that the frequent rains and high humidity had caused stabilized moisture conditions in the litter and only one more set of moisture samples was taken in 1971, that of November 15. Moisture sampling was resumed on April 25 when it appeared that moisture conditions might be changing in the area. Sampling was then conducted at approximately six-day intervals until July 3, 1972.

Based on the moisture data (Figures 46-47) and the respiration data (Figures 3-12 and 16-45) a distinct change in the subsystems occurred on, or about October 15, 1971. This change from the previous conditions was typified by stabilized moisture in the litter and a sharp decrease in rates of respiration. A similar, but less distinct change in the opposite direction occurred on about April 18-25, 1972. These changes were considered as representing the onset of distinct seasons and the moisture data and normalized rates of respiration of the litter subsystem were compartmentalized into 3 seasons called Fall, Wet, and Spring. Wet rather than winter was chosen as the appropriate name because of the time and the weather encompassed by this period. Figures 48-50 illustrate the results of this compartmentalization. No clearcut major relationship between litter moisture by type and rates of respiration of the litter subsystem by type is apparent for any of the three seasons.

Table 6 gives the mean normalized rate of respiration of the litter subsystem for each season. Type difference is significant at $F_{0.05}$ and the differences between types are all significant as tested by Scheffé's Test at 0.05 level of significance. Comparison of the respiration rates in Table 6 with the mean normalized rates of respiration for the litter subsystem for the entire litter respiration season in Table 5 reveals that there are seasonal differences in rate

magnitudes but there are no large departures from the hierarchy of the mean rates, revealed by compartmentalization.

As the data in Table 6 suggest there are also no significant differences $F_{0.05}$ for the temperature between types revealed by compartmentalization.

Table 6. Seasonal mean respiration rates in mg $CO_2$/kg of litter and seasonal litter temperature means in degrees centigrade.

| Vegetation type | Fall[1] mg $CO_2$ | $^oC$ | Wet[2] mg $CO_2$ | $^oC$ | Spring[3] mg $CO_2$ | $^oC$ |
|---|---|---|---|---|---|---|
| *Holodiscus discolor* | 214.5 | 12.2 | 72.8 | 5.6 | 176.2 | 11.9 |
| *Acer circinatum* | 210.5 | 12.3 | 71.6 | 5.6 | 177.8 | 11.9 |
| *Gaultheria shallon* | 203.5 | 12.2 | 67.7 | 5.6 | 175.0 | 11.9 |
| *Tsuga heterophylla* | 158.6 | 12.3 | 57.3 | 5.6 | 147.8 | 11.9 |
| *Castanopsis chrysophylla* | 144.5 | 12.3 | 50.3 | 5.6 | 122.0 | 11.9 |
| *Polystichum munitum* | 98.4 | 12.3 | 35.3 | 5.6 | 86.4 | 11.9 |

[1]Fall (August 31, 1971 - October 14, 1971)

[2]Wet (October 14, 1971 - April 30, 1972)

[3]Spring (May 1, 1972 - July 1, 1972)

Table 7 gives the rates of respiration for the subsystems by areas. The area difference is significant at $F_{0.05}$. Between area

differences are all significant as tested by Scheffé's Test at 0.05 level of significance.

Table 7. Comparison between subsystems by areas of rates of respiration in mg $CO_2$/hr for the litter respiration season, 1971-1972.

| Respiration source[1] | Areas | | | |
|---|---|---|---|---|
| | 1 | 2 | 3 | 4 |
| Normalized litter respiration | 0.106 | 0.097 | 0.104 | 0.098 |
| Litter respiration | 73.10 | 88.44 | 78.02 | 78.82 |
| Soil respiration | 75.51 | 87.45 | 81.21 | 85.47 |
| Litter-soil respiration | 135.92 | 163.25 | 146.05 | 151.91 |
| Litter plus soil respiration | 148.51 | 175.40 | 159.90 | 163.60 |

[1] Normalized rates based on mg $CO_2$/hr/gm oven-dry litter, all other rates mg/$CO_2$/$m^2$

A comparison of Table 7 with Figures 13-15 illustrates that the relative magnitude of differences in rates of respiration between areas is similar to the relative magnitude of differences in rates of respiration between types for all subsystems except for the differences in the normalized rates of respiration for the litter subsystems which are much greater between types than between areas. Apparently compartmentalization of the stand by areas will yield differences as significant as those by type for all but the normalized litter subsystem.

An estimation (Table 9) of mean daily and mean annual rate of respiration for the litter layer of the Pseudotsuga menziesii stand represented by the four areas was calculated utilizing the following relationships:

1. $EMR_T = NR_T(MW_T)\ (MA_T)/100$

Where:

$EMR_T$ = Estimated mean rate of respiration per hour per type per $M_T^2$

$M_T^2$ = fraction of average $m^2$ in stand occupied by the type

$NR_T$ = Mean normalized litter rate of respiration per hour per type per gram litter (Table 5)

$MW_T$ = mean litter weight in grams per type per $m^2$ (Table 10)

$MA_T$ = Mean percent of total area per type (Table 8).

2. $EMR_y = (\Sigma\ EMR_T)\ (N_d)$

$EMR_y$ = estimated total annual respiration for the litter respiration year 1971-1972 for the fraction of the stand (Table 9) that is represented by the six vegetation types.

$N_d$ = number of days between September 1 and July 1 except for snow days (Table 1) which are assumed as days of zero respiration ($N_d = 263$)

These estimates do not represent those areas not sampled according to the criteria for exclusion from the sample areas as given

Table 8. Percent of total area covered by vegetation types.

| Vegetation type | Sample Areas 1 | 2 | 3 | 4 | Mean |
|---|---|---|---|---|---|
| Gaultheria shallon | 68.16 | 61.10 | 44.37 | 58.34 | 57.99 |
| Acer circinatum | 12.72 | 18.30 | 33.13 | 12.01 | 19.04 |
| Polystichum munitum | 5.10 | 11.70 | 9.12 | 10.63 | 9.14 |
| Holodiscus discolor | 5.96 | 2.71 | 5.34 | 8.49 | 5.63 |
| Tsuga heterophylla | 3.24 | 3.66 | 5.29 | 7.47 | 4.92 |
| Castanopsis chrysophylla | 1.34 | 1.58 | 1.32 | 2.06 | 1.58 |
| Cornus nuttallii | 2.68 | -- | -- | -- | 0.75 |
| Taxus brevifolia | -- | -- | 0.52 | -- | |
| Pseudotsuga menziesii[1] | 0.78 | 0.93 | 0.88 | 0.97 | 0.89 |

[1] Basal area

Table 9. Estimated mean rates of respiration for an "average" square meter for the four sample areas. [1]

| Vegetation type | Mean Respiration: mg $CO_2$ per hour | Mean Respiration: g $CO_2$ per year |
|---|---|---|
| Gaultheria shallon | 63.92 | 403.44 |
| Acer circinatum | 20.69 | 130.60 |
| Polystichum munitum | 9.12 | 57.53 |
| Holodiscus discolor | 5.54 | 34.96 |
| Tsuga heterophylla | 5.20 | 32.81 |
| Castanopsis chrysophylla | 1.83 | 11.53 |
| Total | 106.29 mg $CO_2/hr/m^2$ | 670.87 g $CO_2/yr/m^2$ |

[1] Assumes no respiration for the 1.64 percent of the total area that is not covered by the six types. "Average" refers to weighting of the respiration by average percent of total stand covered by type.

in the methodology section of this thesis. Tables 8 and 9 can also be viewed as measures of the relative importance of the various understory types in this stand.

A check on the reality of the magnitude of the litter respiration rates that were calculated using the normalized litter respiration rates was made by estimating the per $m^2$ rates of respiration for the average litter subsystem for each type and comparing them to the litter respiration rates that were measured (Figure 8). The following relationship was used to calculate these estimated values:

$$ER = NR_T (W_T)$$

Where:

ER = estimated mean rate of respiration per hour per $m^2$

$NR_T$ = rate of respiration for each type normalized to a per gram basis by dividing by weight of litter in litter tray (Table 5 respiration figures divided by $10^3$)

$W_T$ = mean weight in grams of litter per type (Table 10)

The results are given in Table 11 and the consistently larger values for the estimated rates indicate that either the litter weights used for normalization (Table 2) are biased (possibly causing an overestimation of the mean annual respiration rates for the samples) and/or the mean weights determined from the samples taken in December, 1971 (Table 10) are biased (possibly overestimating the mean annual litter weights for the stand).

Table 10. Mean weight in grams of litter in litter subsystem by vegetation types.

| Vegetation type | Litter weight $g/m^2$ |
|---|---|
| Holodiscus discolor | 782.22 |
| Acer circinatum | 873.49 |
| Gaultheria shallon | 916.19 |
| Tsuga heterophylla | 1,064.45 |
| Castanopsis chrysophylla | 1,348.44 |
| Polystichum munitum | 1,661.02 |

Table 11. Comparison of measured rates of litter respiration with estimated rates of litter respiration in mg $CO_2/m^2/hr$.

| Vegetation type | Measured | Estimated |
|---|---|---|
| Holodiscus discolor | 82.12 | 98.46 |
| Acer circinatum | 76.52 | 108.67 |
| Gaultheria shallon | 71.99 | 110.22 |
| Tsuga heterophylla | 77.00 | 105.77 |
| Castanopsis chrysophylla | 87.28 | 115.97 |
| Polystichum munitum | 82.71 | 99.79 |

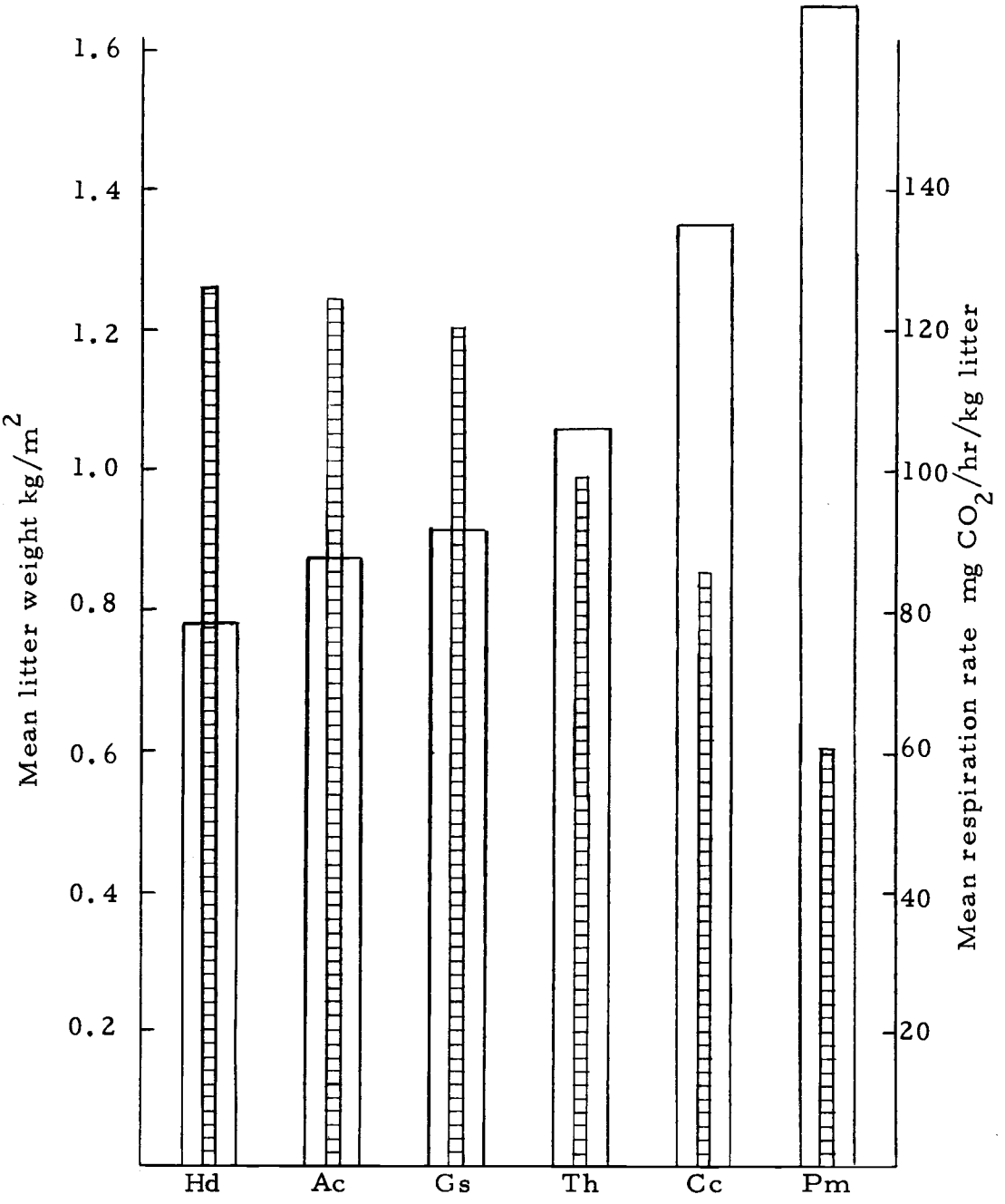



Figure 2. Comparison of mean litter weights with rate of mean normalized rate of respiration of litter subsystem.

Litter Weight (grams)

Respiration Rate (mg $CO_2$)

Hd Holodiscus discolor
Ac Acer circinatum
Gs Gaultheria shallon
Th Tsuga heterophylla
Cc Castanopsis chrysophylla
Pm Polystichum munitum

Figure 3. Normalized rates of respiration of litter subsystem by vegetation type for September, 1971.

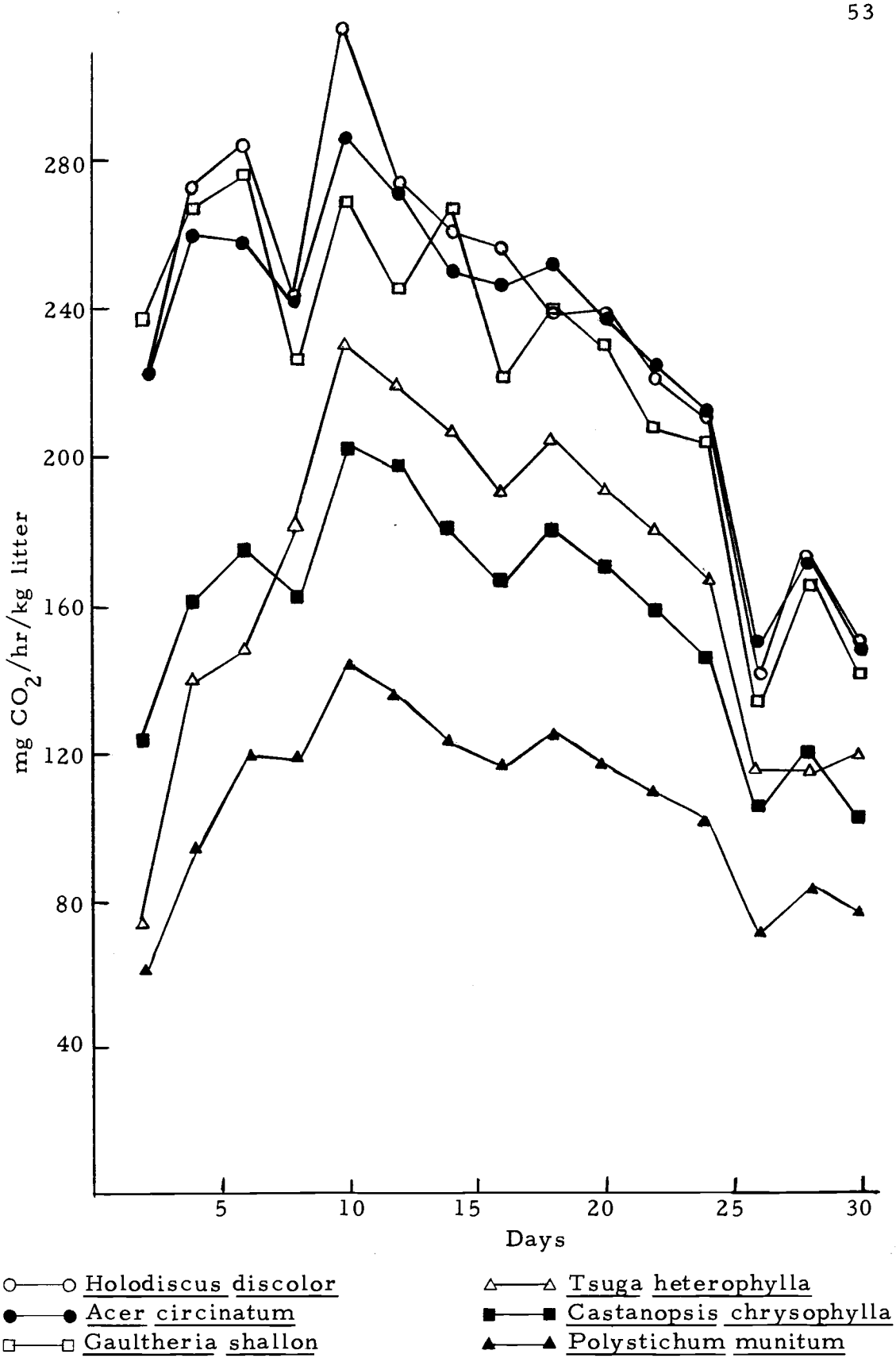

280
240
200
160
120
80
40
mg $CO_2$/hr/kg litter
5
10
15
20
25
30
Days
Holodiscus discolor
Acer circinatum
Gaultheria shallon
Tsuga heterophylla
Castanopsis chrysophylla
Polystichum munitum

Figure 4. Normalized rates of respiration of litter subsystem by vegetation type for October, 1971.

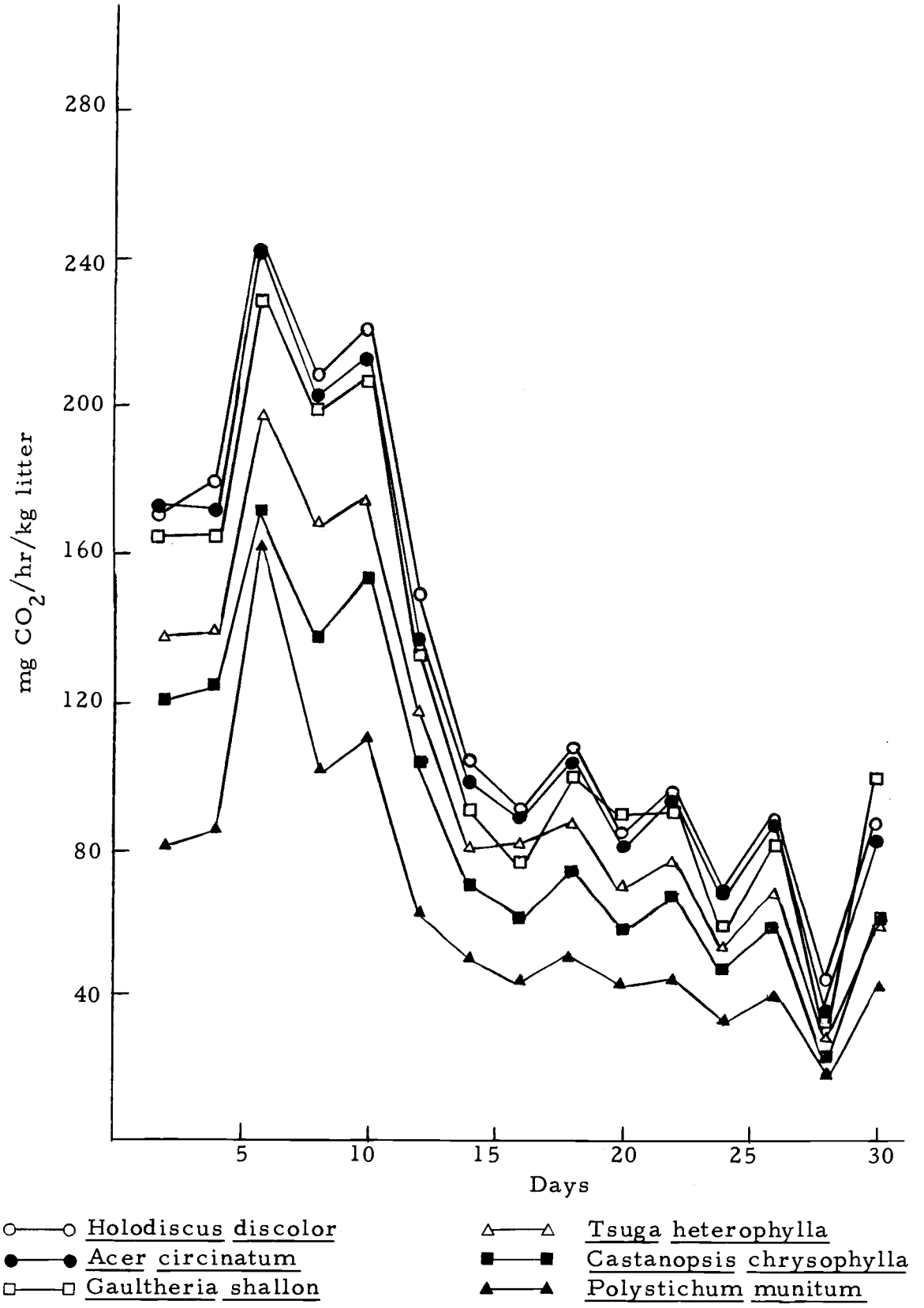

280
240
200
160
120
80
40
mg $CO_2$/hr/kg litter
5
10
15
20
25
30
Days
Holodiscus discolor
Acer circinatum
Gaultheria shallon
Tsuga heterophylla
Castanopsis chrysophylla
Polystichum munitum

Figure 5. Normalized rates of respiration of litter subsystem by vegetation type for November, 1971.

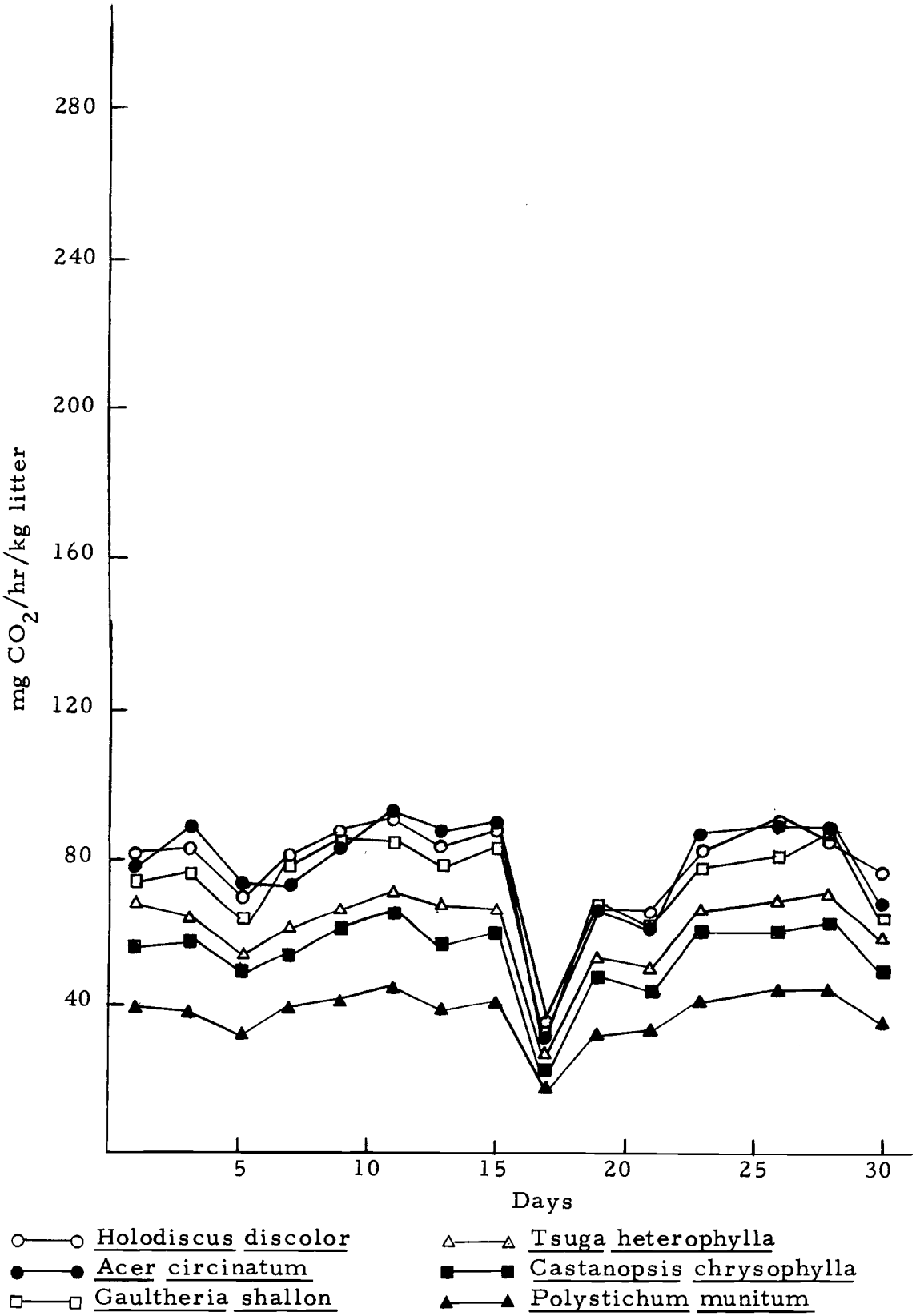

280
240
200
160
120
80
40
mg $CO_2$/hr/kg litter
5
10
15
20
25
30
Days
Holodiscus discolor
Acer circinatum
Gaultheria shallon
Tsuga heterophylla
Castanopsis chrysophylla
Polystichum munitum

Figure 6. Normalized rates of respiration of litter subsystem by vegetation type for December, 1971.

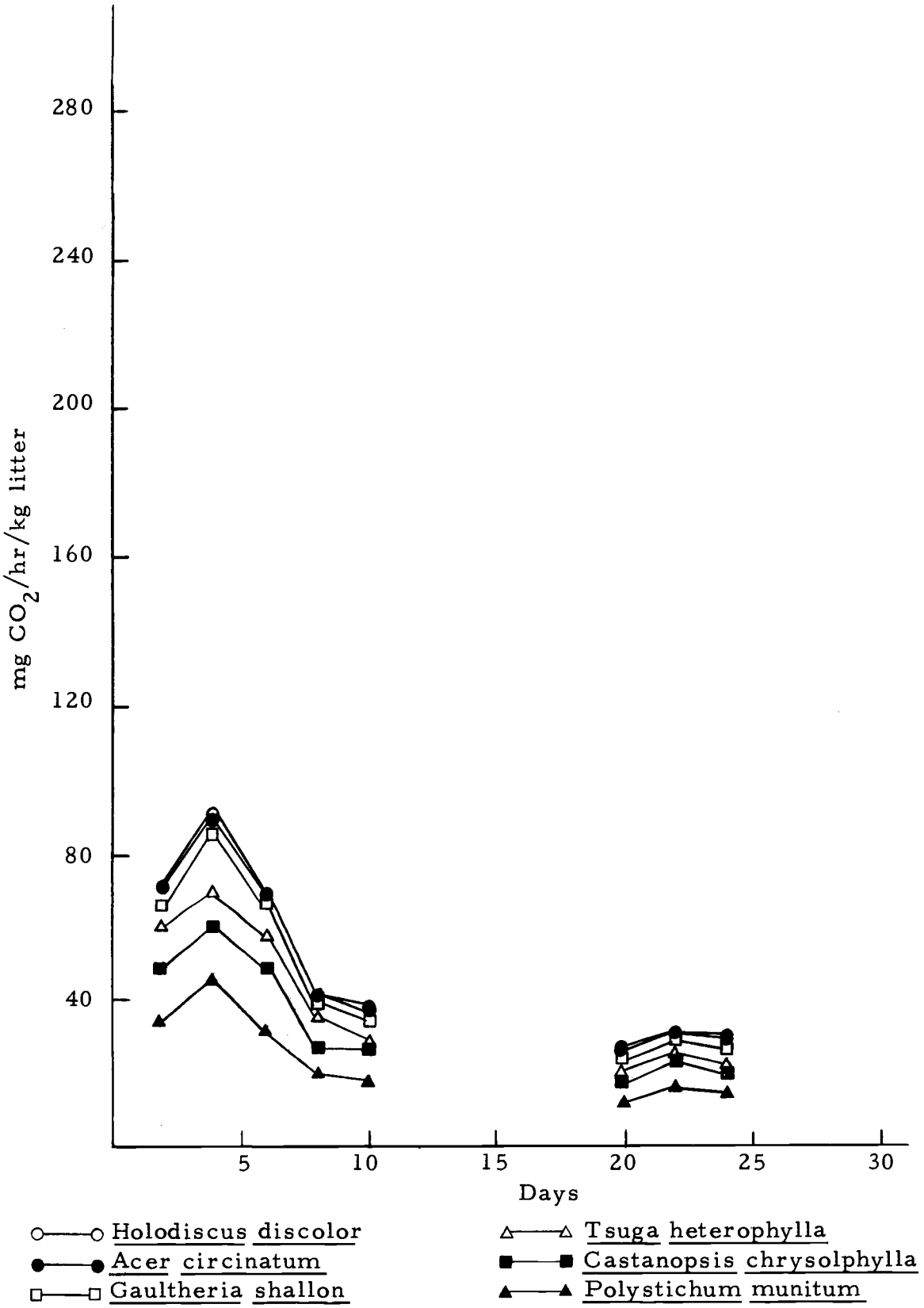

280
240
200
160
120
80
40
mg $CO_2$/hr/kg litter
5
10
15
20
25
30
Days
Holodiscus discolor
Acer circinatum
Gaultheria shallon
Tsuga heterophylla
Castanopsis chrysolphylla
Polystichum munitum

Figure 7. Normalized rates of respiration of litter subsystem by vegetation type for January, 1972.

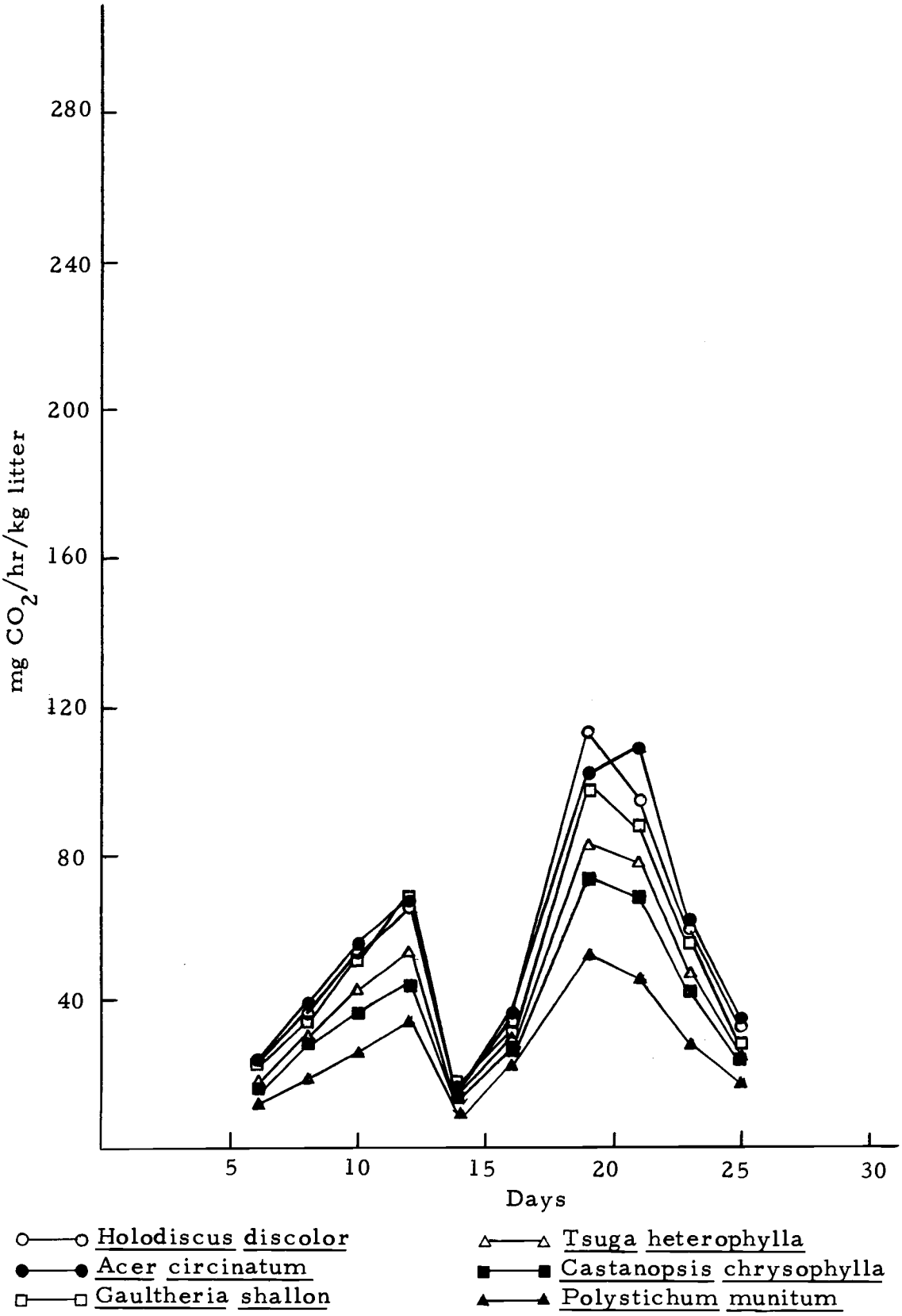

280
240
200
160
120
80
40
mg $CO_2$/hr/kg litter
5
10
15
20
25
30
Days
Holodiscus discolor
Acer circinatum
Gaultheria shallon
Tsuga heterophylla
Castanopsis chrysophylla
Polystichum munitum

Figure 8. Normalized rates of respiration of litter subsystem by vegetation type for February, 1972.

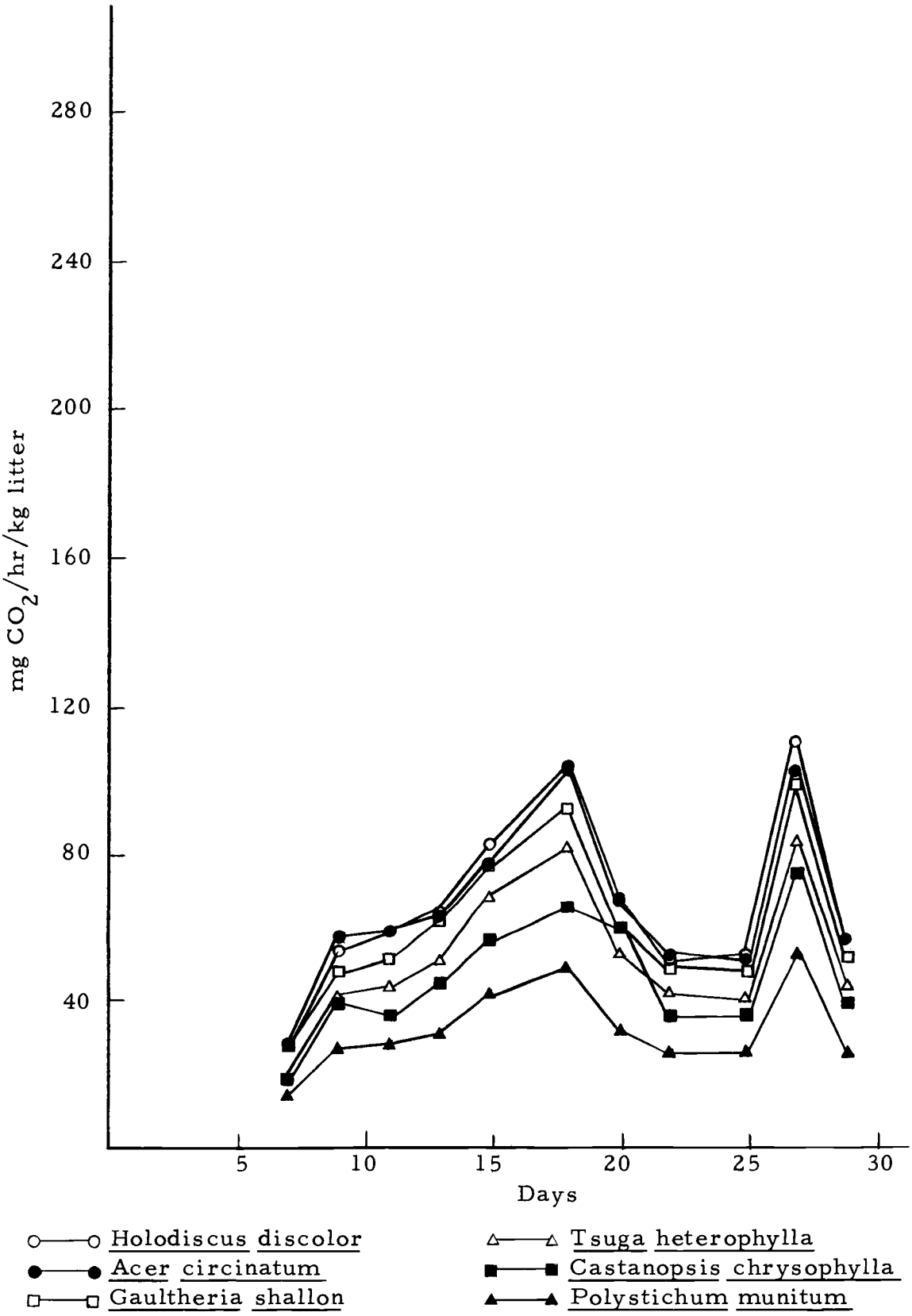

280
240
200
160
120
80
40
mg $CO_2$/hr/kg litter
5
10
15
20
25
30
Days
Holodiscus discolor
Acer circinatum
Gaultheria shallon
Tsuga heterophylla
Castanopsis chrysophylla
Polystichum munitum

Figure 9. Normalized rates of respiration of litter subsystem by vegetation type for March, 1972.

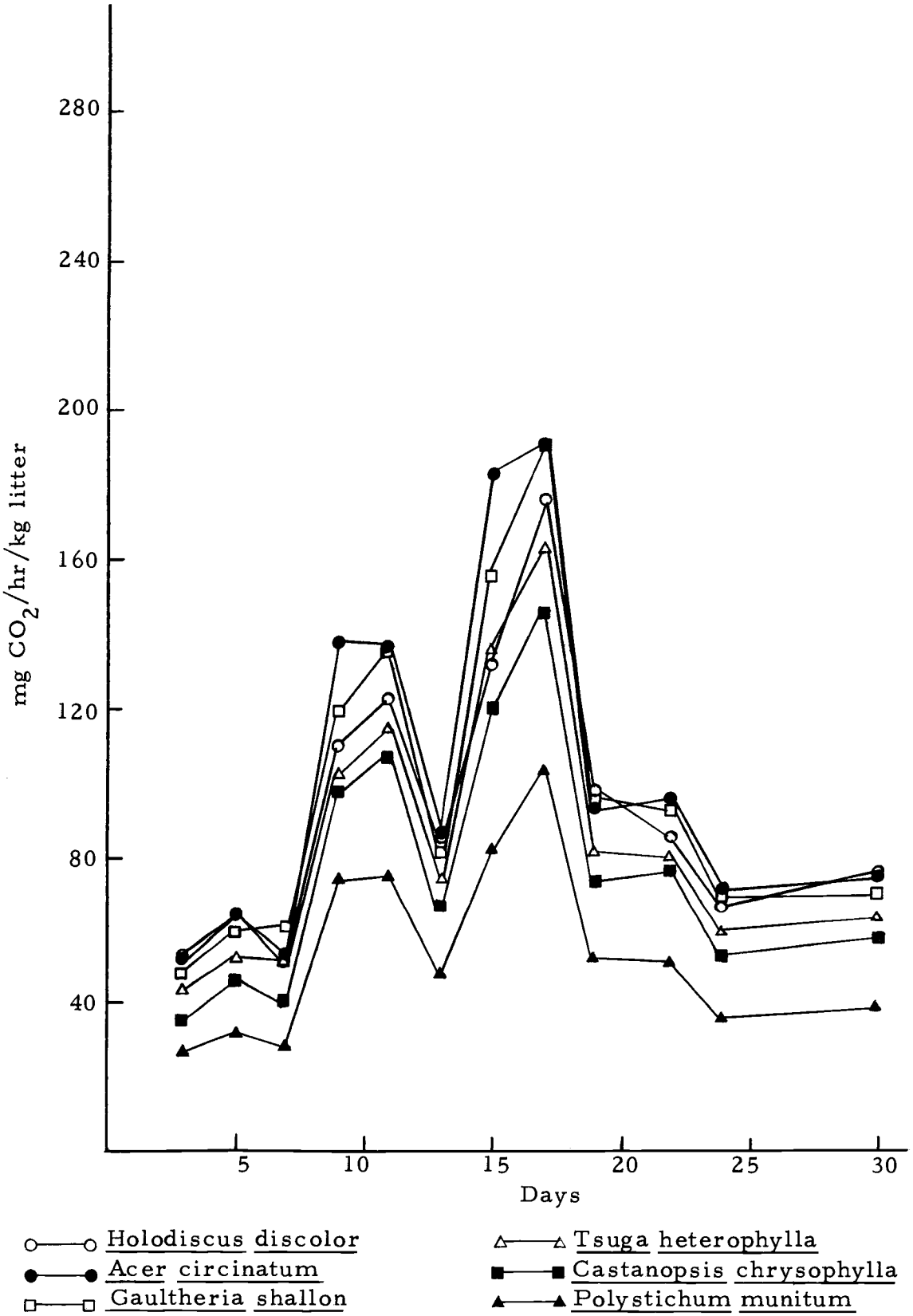

280
240
200
160
120
80
40
mg $CO_2$/hr/kg litter
5
10
15
20
25
30
Days
Holodiscus discolor
Acer circinatum
Gaultheria shallon
Tsuga heterophylla
Castanopsis chrysophylla
Polystichum munitum

Figure 10. Normalized rates of respiration of litter subsystem by vegetation type for April, 1972.

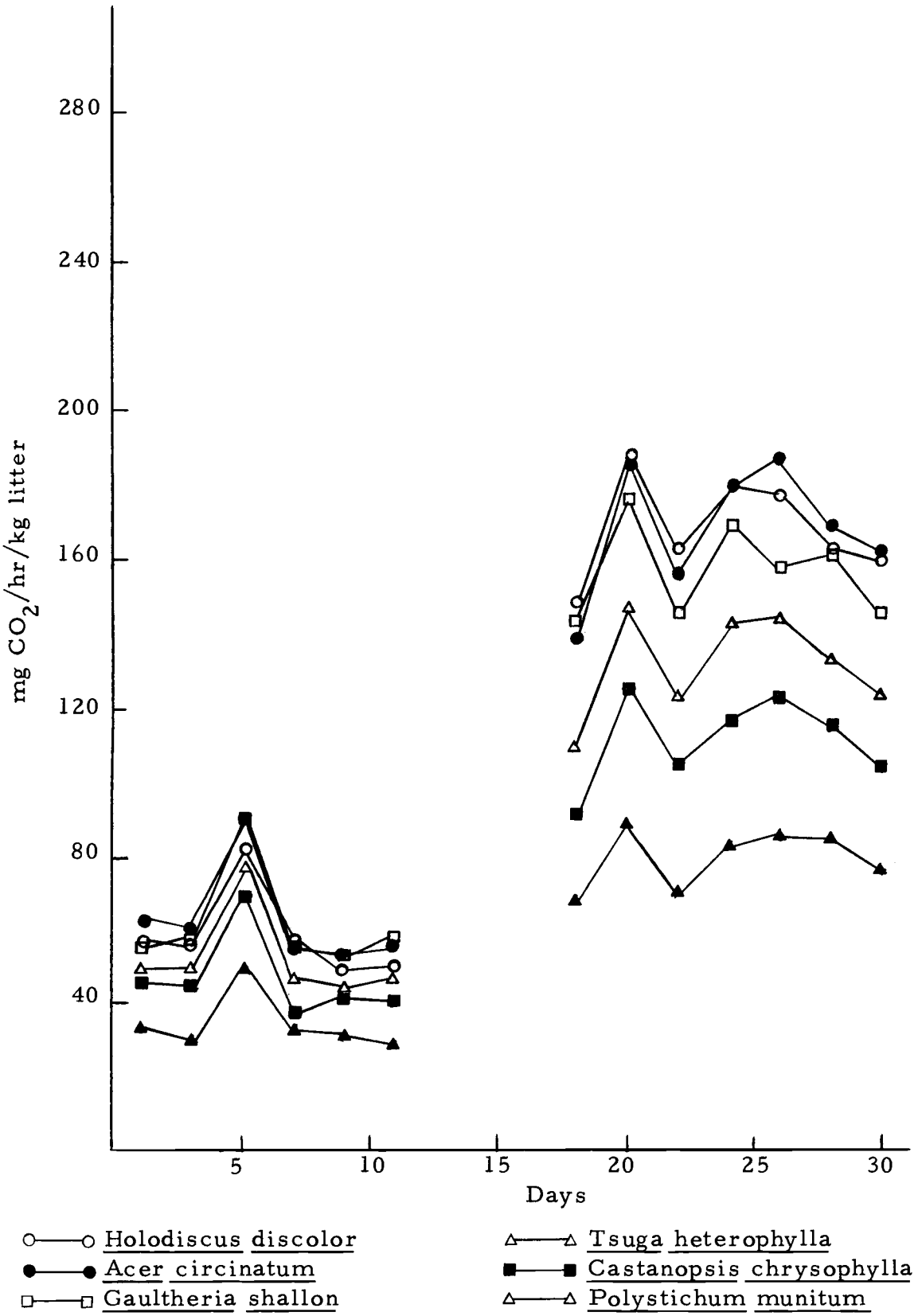

280
240
200
160
120
80
40
mg $CO_2$/hr/kg litter
5
10
15
20
25
30
Days
Holodiscus discolor
Acer circinatum
Gaultheria shallon
Tsuga heterophylla
Castanopsis chrysophylla
Polystichum munitum

Figure 11. Normalized rates of respiration of litter subsystem by vegetation type for May, 1972.

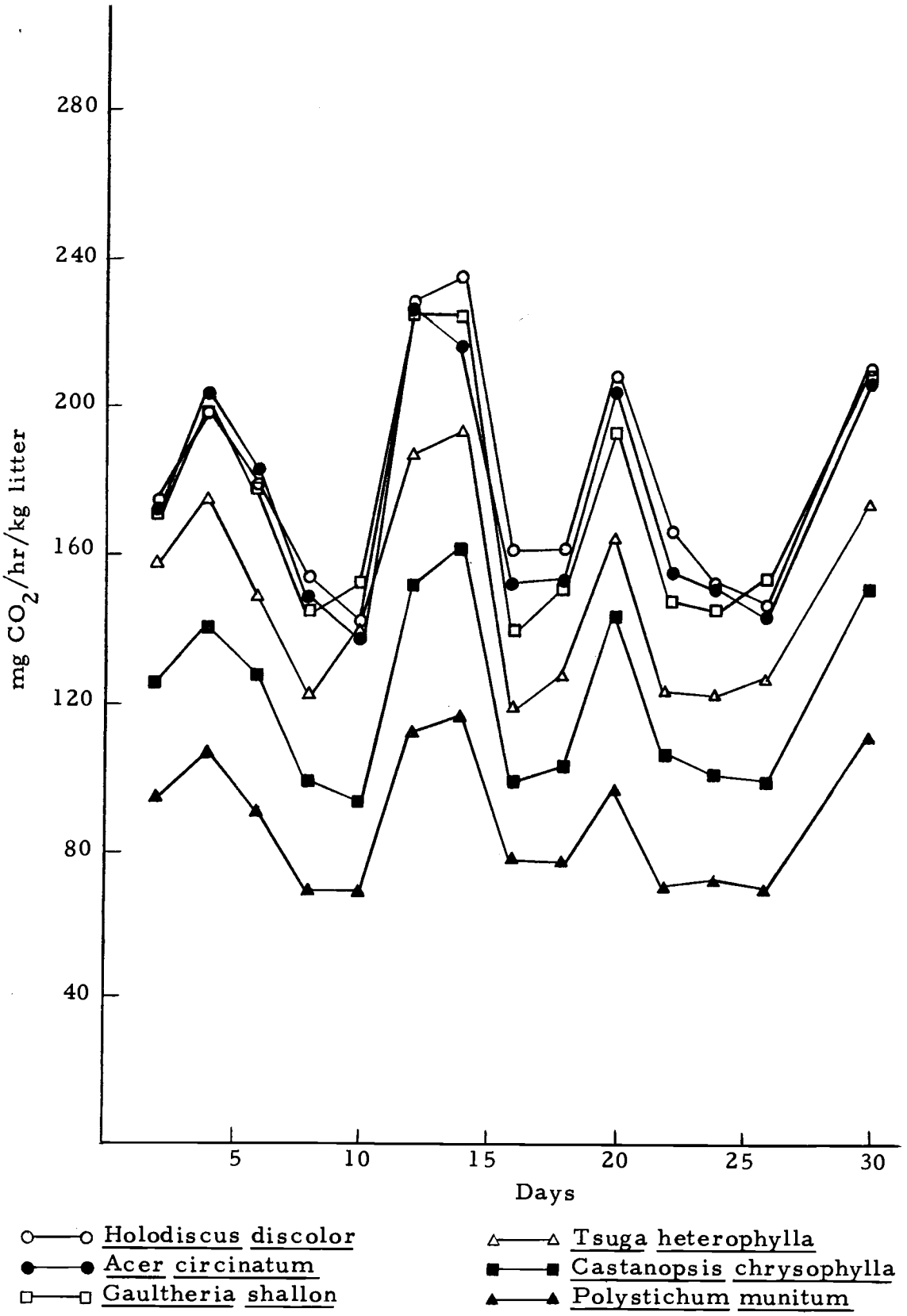
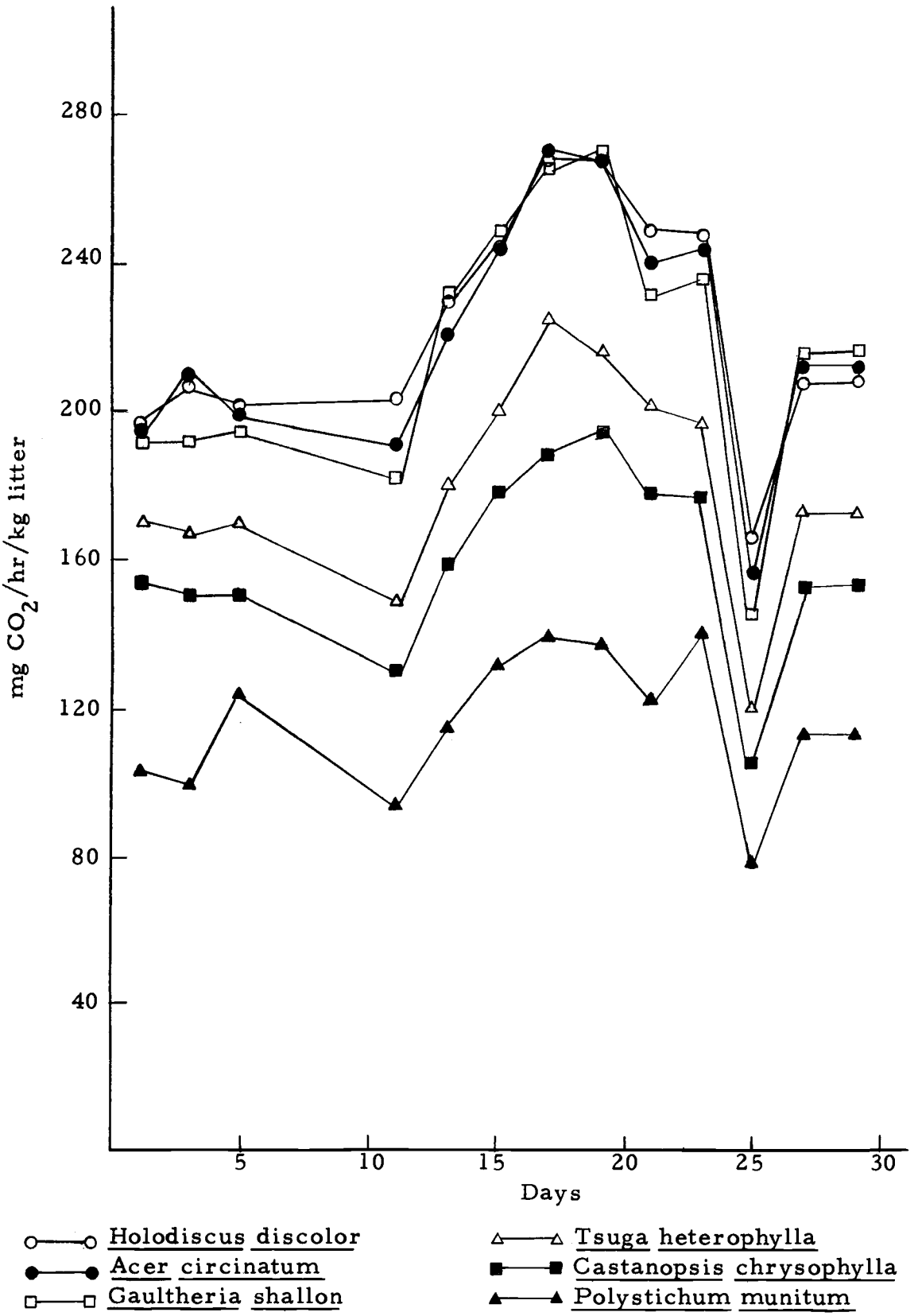

280
240
200
160
120
80
40
mg $CO_2$/hr/kg litter
5
10
15
20
25
30
Days
Holodiscus discolor
Acer circinatum
Gaultheria shallon
Tsuga heterophylla
Castanopsis chrysophylla
Polystichum munitum

Figure 12. Normalized rates of respiration of litter subsystem by vegetation type for June, 1972.


280
240
200
160
120
80
40
mg $CO_2$/hr/kg litter
5
10
15
20
25
30
Days
Holodiscus discolor
Acer circinatum
Gaultheria shallon
Tsuga heterophylla
Castanopsis chrysophylla
Polystichum munitum

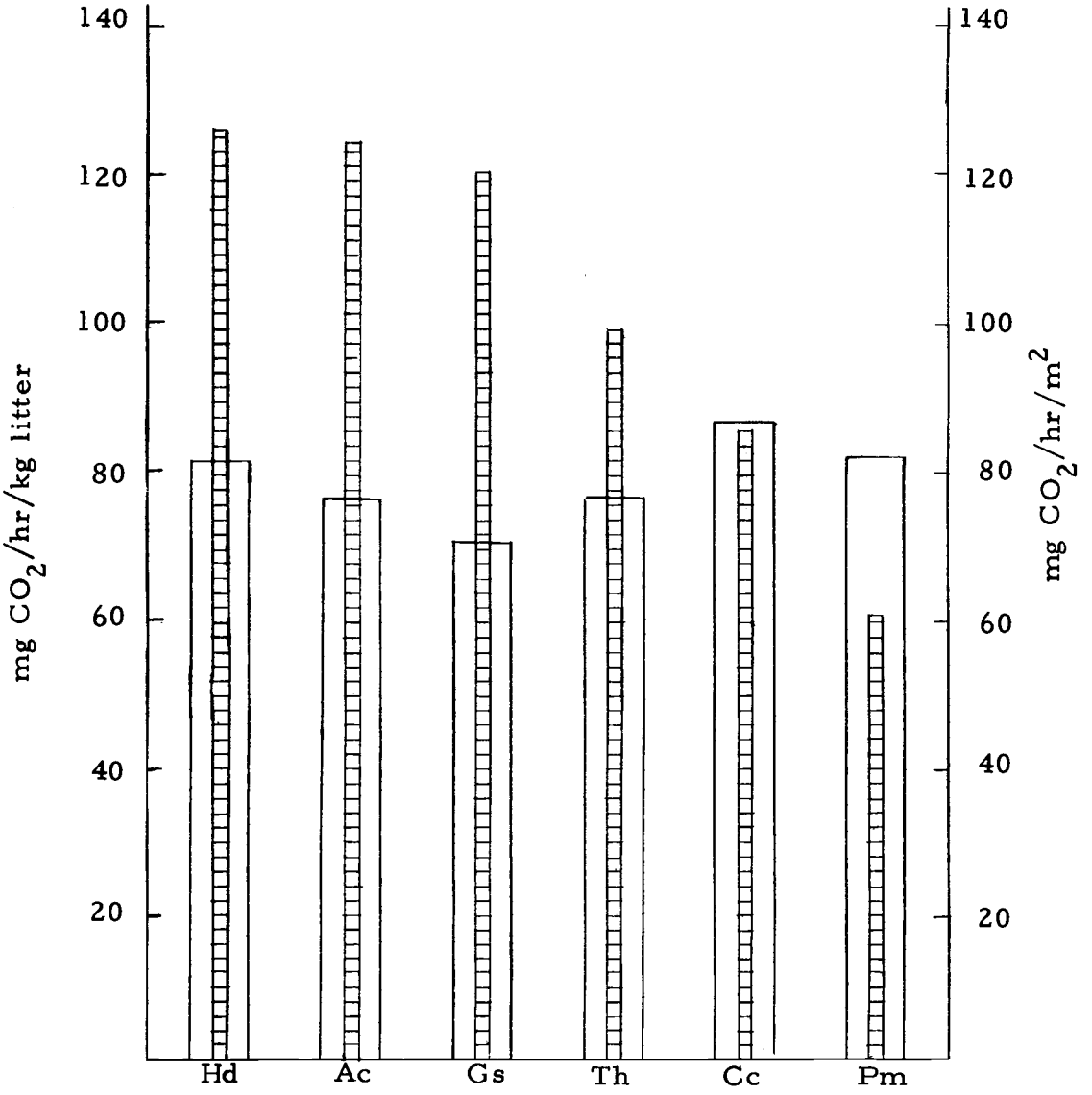



Figure 13. Comparison of mean rates of respiration for normalized litter and litter subsystems.

Litter (mg $CO_2$/hr/$m^2$

Normalized Litter (mg $CO_2$/hr/kg litter)

Hd Holodiscus discolor
Ac Acer circinatum
Gs Gautheria shallon
Th Tsuga heterophylla
Cc Castanopsis chrysophylla
Pm Polystichum munitum

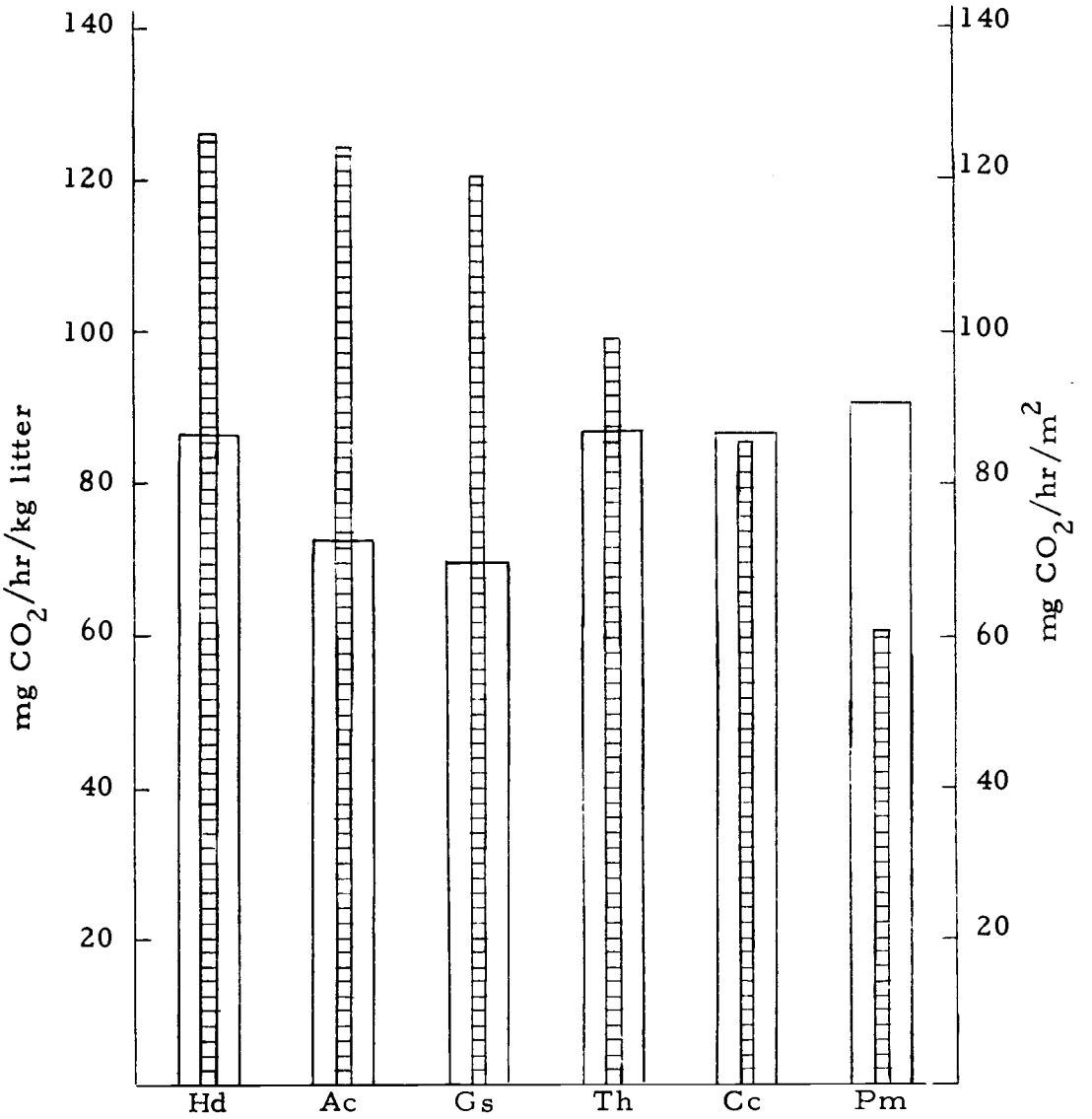



Figure 14. Comparison of mean rates of respiration for normalized litter and soil subsystems.

soil (mg $CO_2$/hr/$m^2$

normalized litter (mg $CO_2$/hr/kg litter)

Hd Holodiscus discolor
Ac Acer circinetum
Gs Gaultheria shallon
Th Tsuga heterophylla
Cc Castanopsis chrysophylla
Pm Polystichum munitum

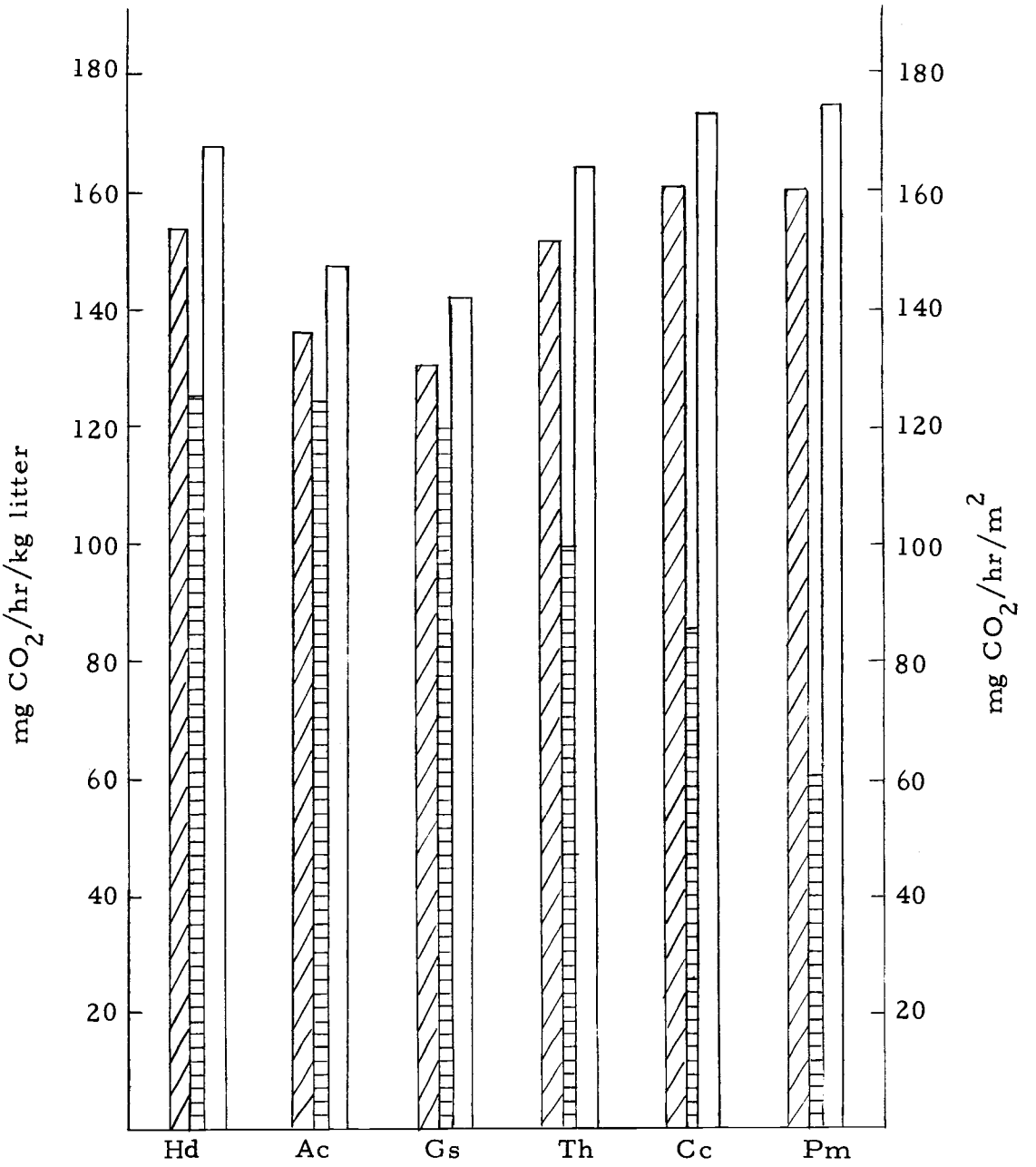



Figure 15. Comparison of mean rates of respiration for normalized litter, litter-soil, and litter plus soil subsystems.

Litter-soil (mg $CO_2$/hr/$m^2$

Normalized Litter (mg $CO_2$/hr/kg litter)

Litter plus Soil (mg $CO_2$/hr/$m^2$

Hd Holodiscus discolor
Ac Acer circinatum
Gs Gaultheria shallon
Th Tsuga heterophylla
Cc Castanopsis chrysophylla
Pm Polystichum munitum

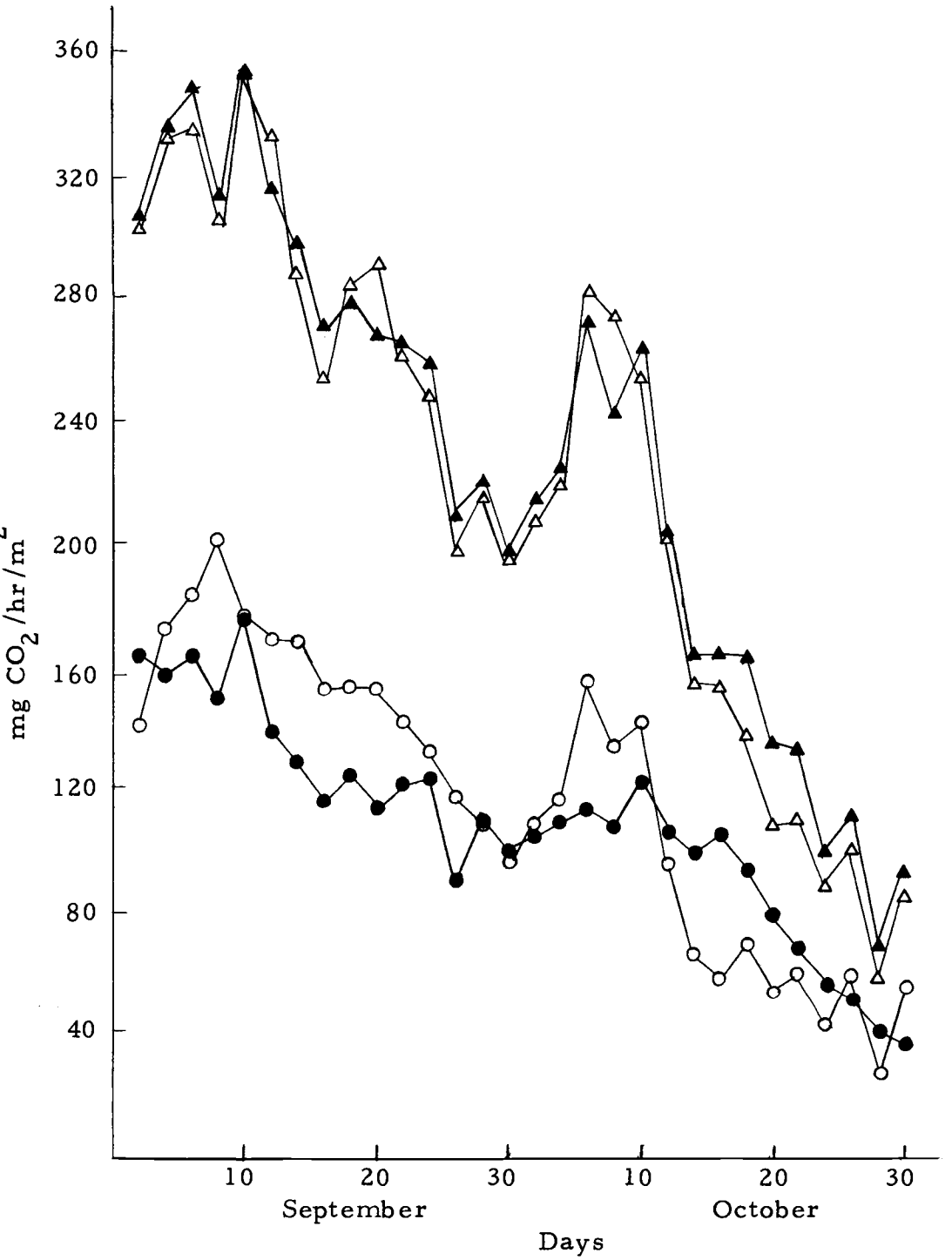



Figure 16. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Holodiscus discolor type (Sept-Oct., 1971).

▲—▲ litter plus soil △—△ litter-soil ○—○ litter ●—● soil

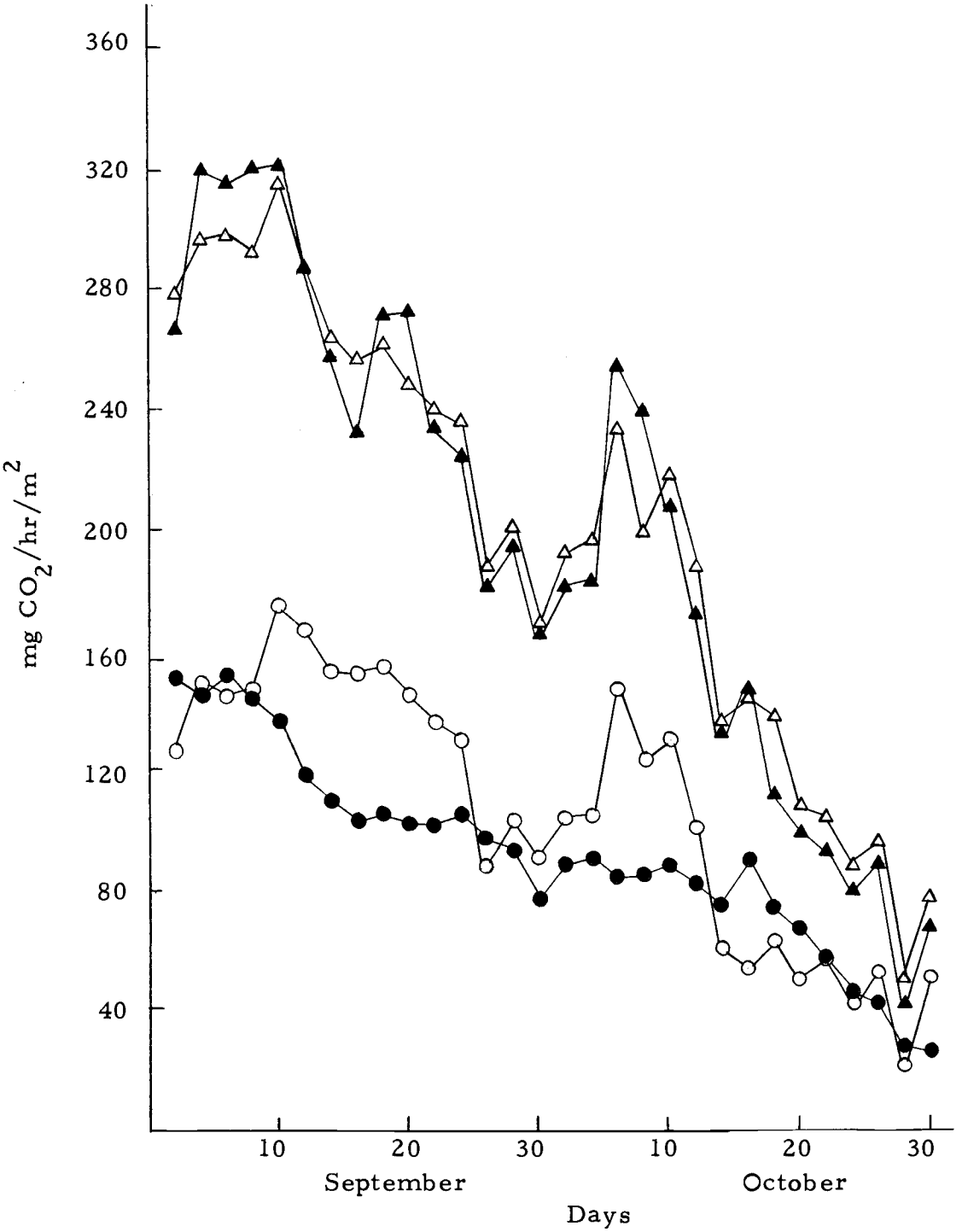



Figure 17. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Acer circinatum type (Sept. - Oct., 1971).

▲—▲ litter plus soil  △—△ litter-soil  ○—○ litter  ●—● soil

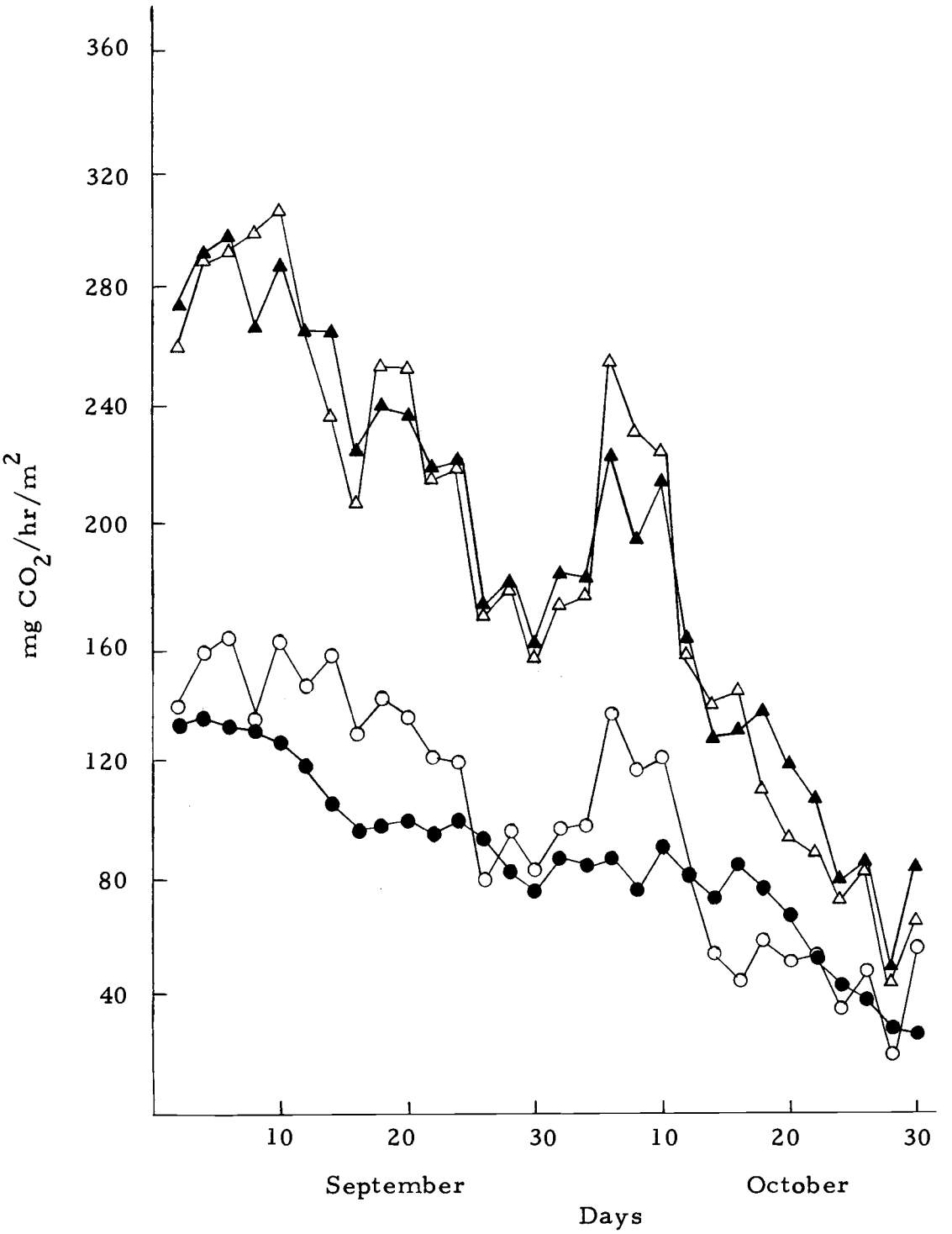



Figure 18. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Gaultheria shallon type (Sept. - Oct., 1971).

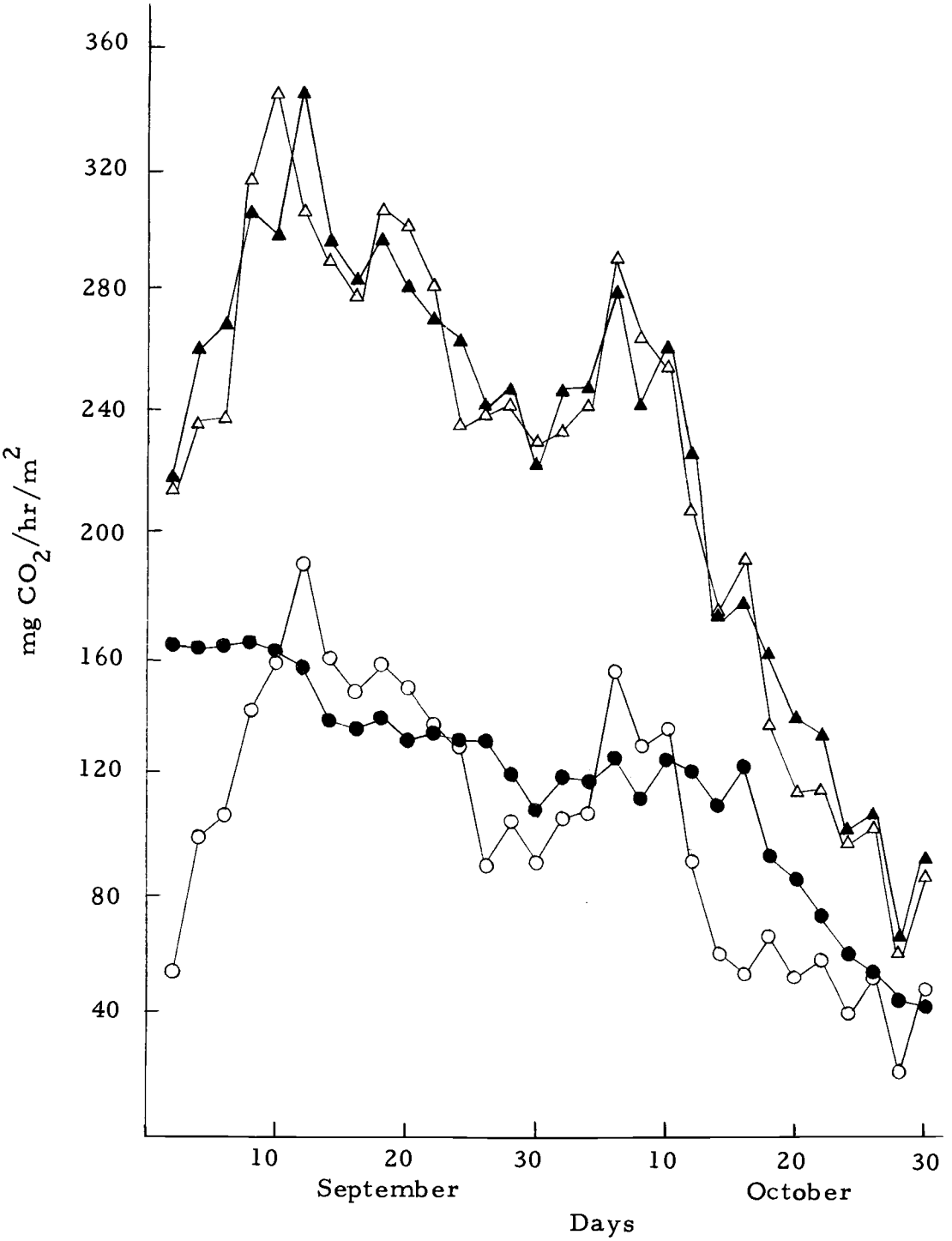



Figure 19. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Tsuga heterophylla type (Sept. - Oct., 1971).

▲—▲ litter plus soil △—△ litter-soil ○—○ litter ●—● soil

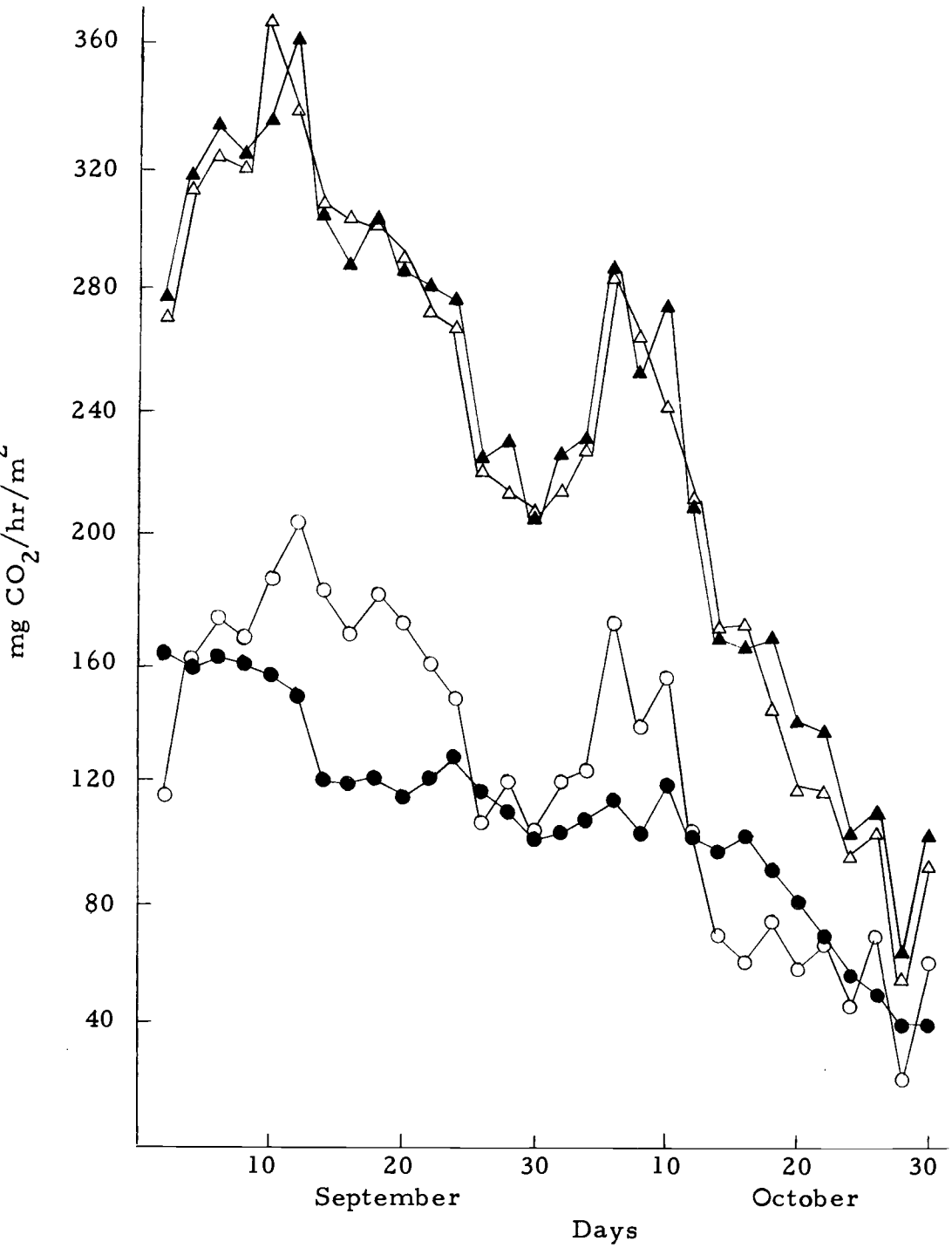



Figure 20. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Castanopsis chrysophylla type (Sept.-Oct., 1971).

▲—▲ litter plus soil △—△ litter-soil ○—○ litter ●—● soil

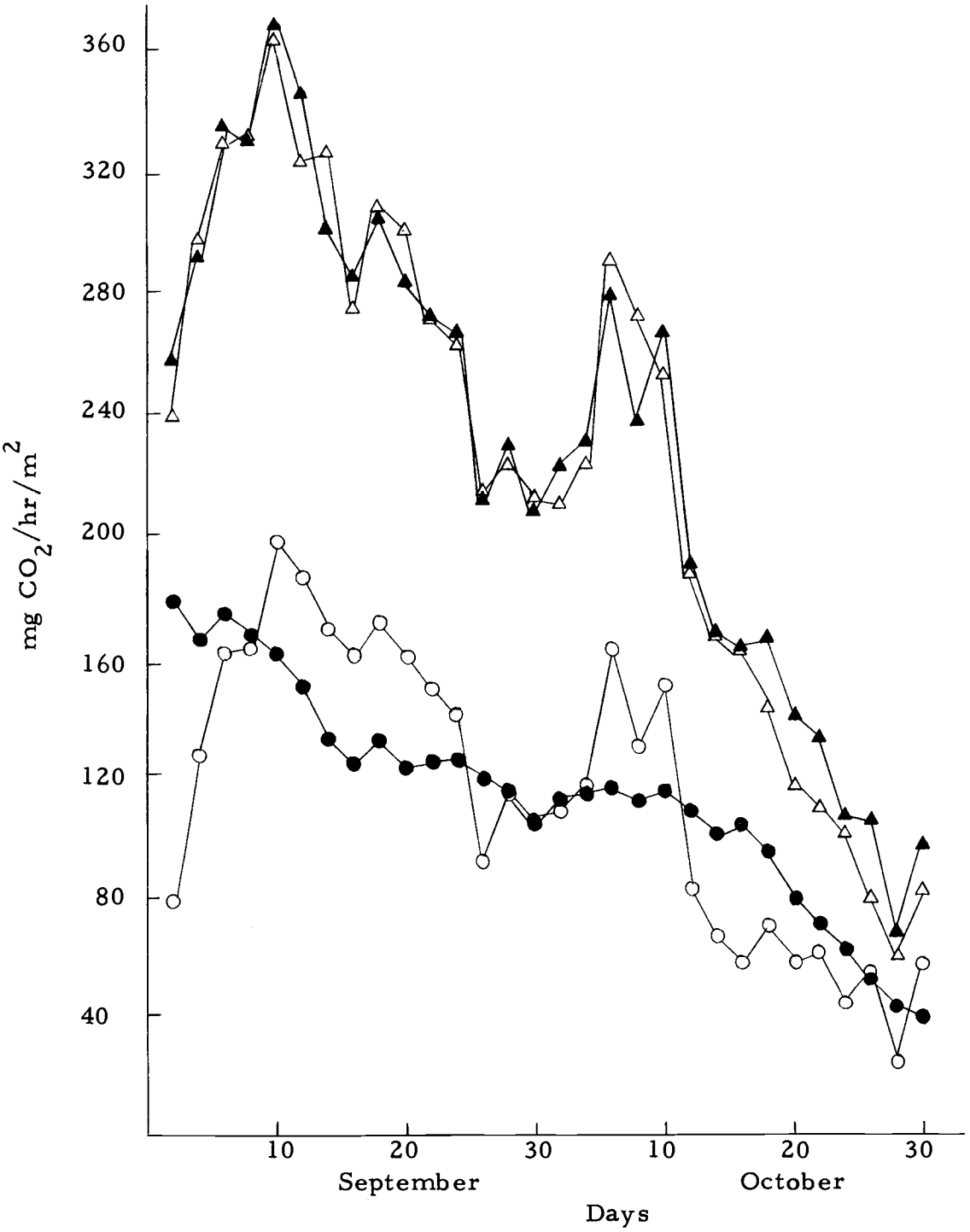



Figure 21. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Polystichum munitum type (Sept. - Oct., 1971).

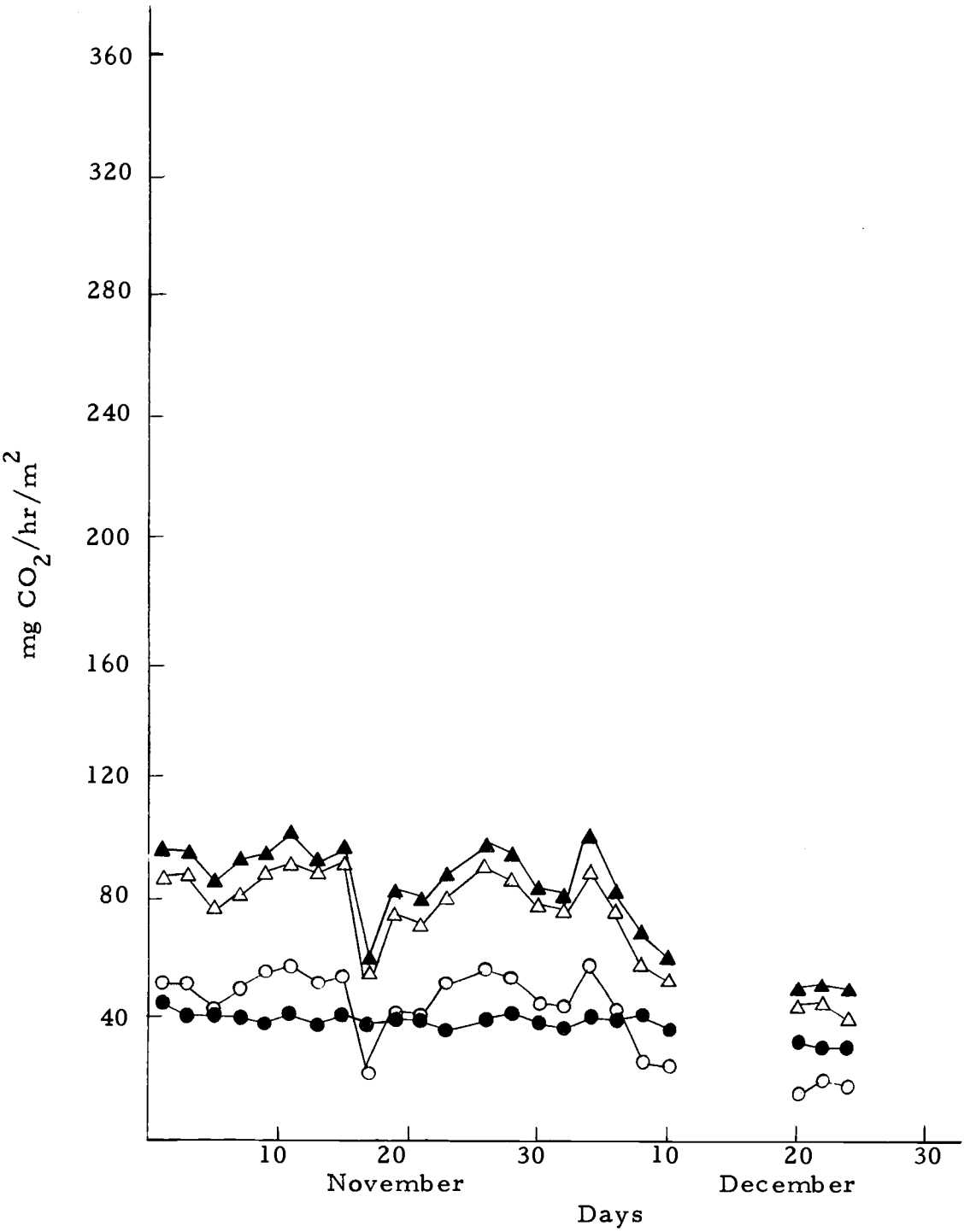



Figure 22. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Holodiscus discolor type (Nov. - Dec., 1971).

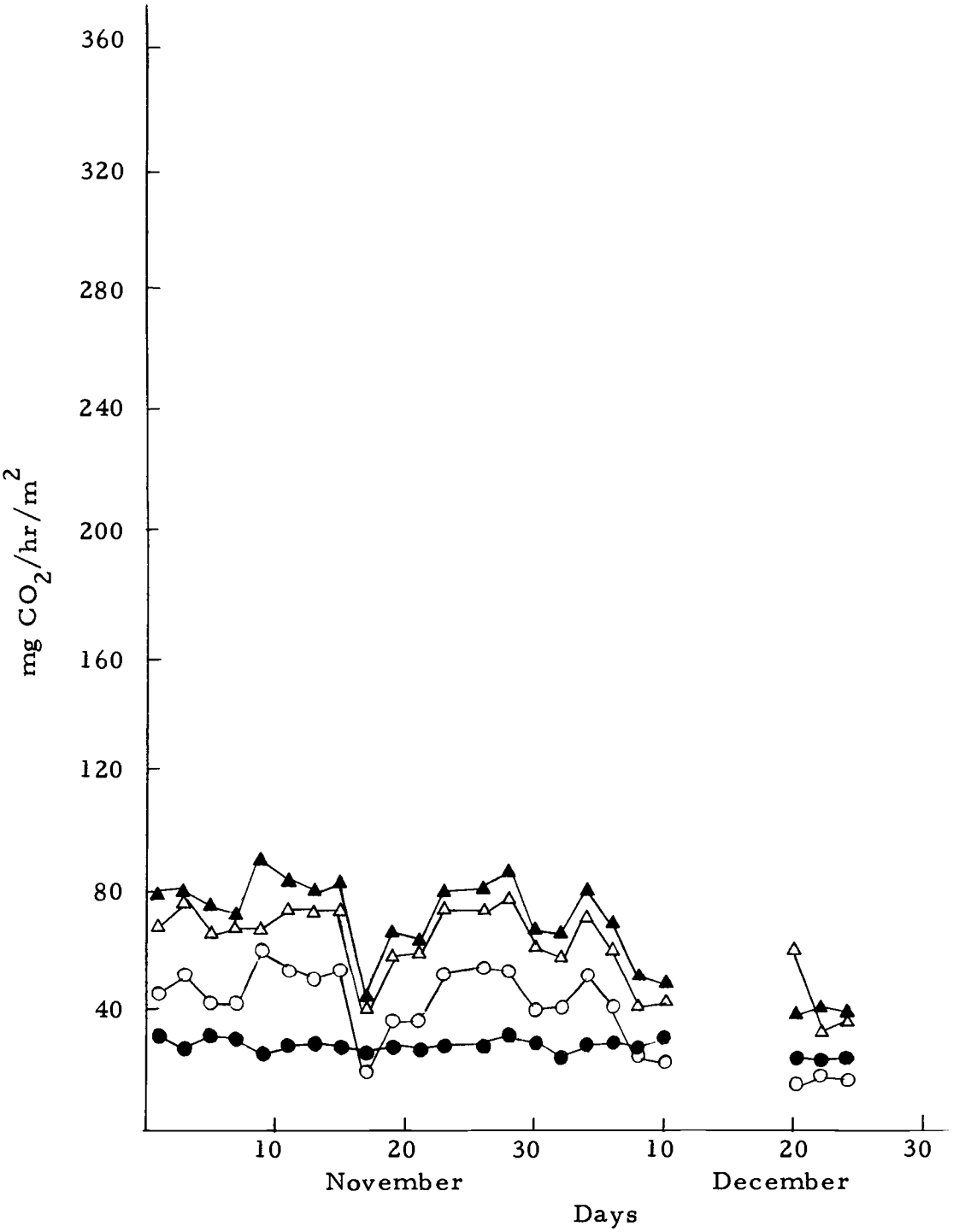



Figure 23. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Acer circinatum type (Nov. - Dec., 1971).

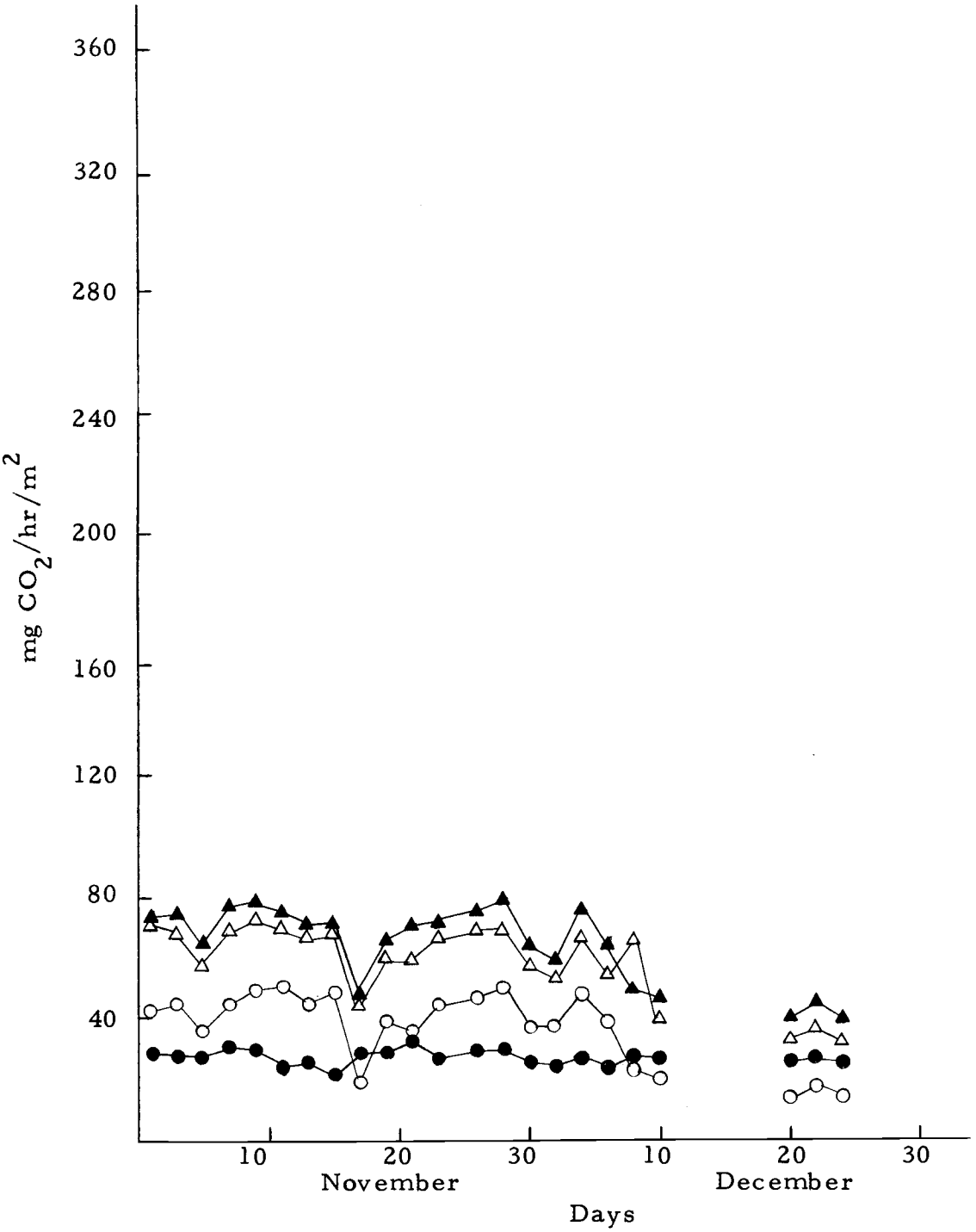



Figure 24. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Gaultheria shallon type (Nov.-Dec., 1971).

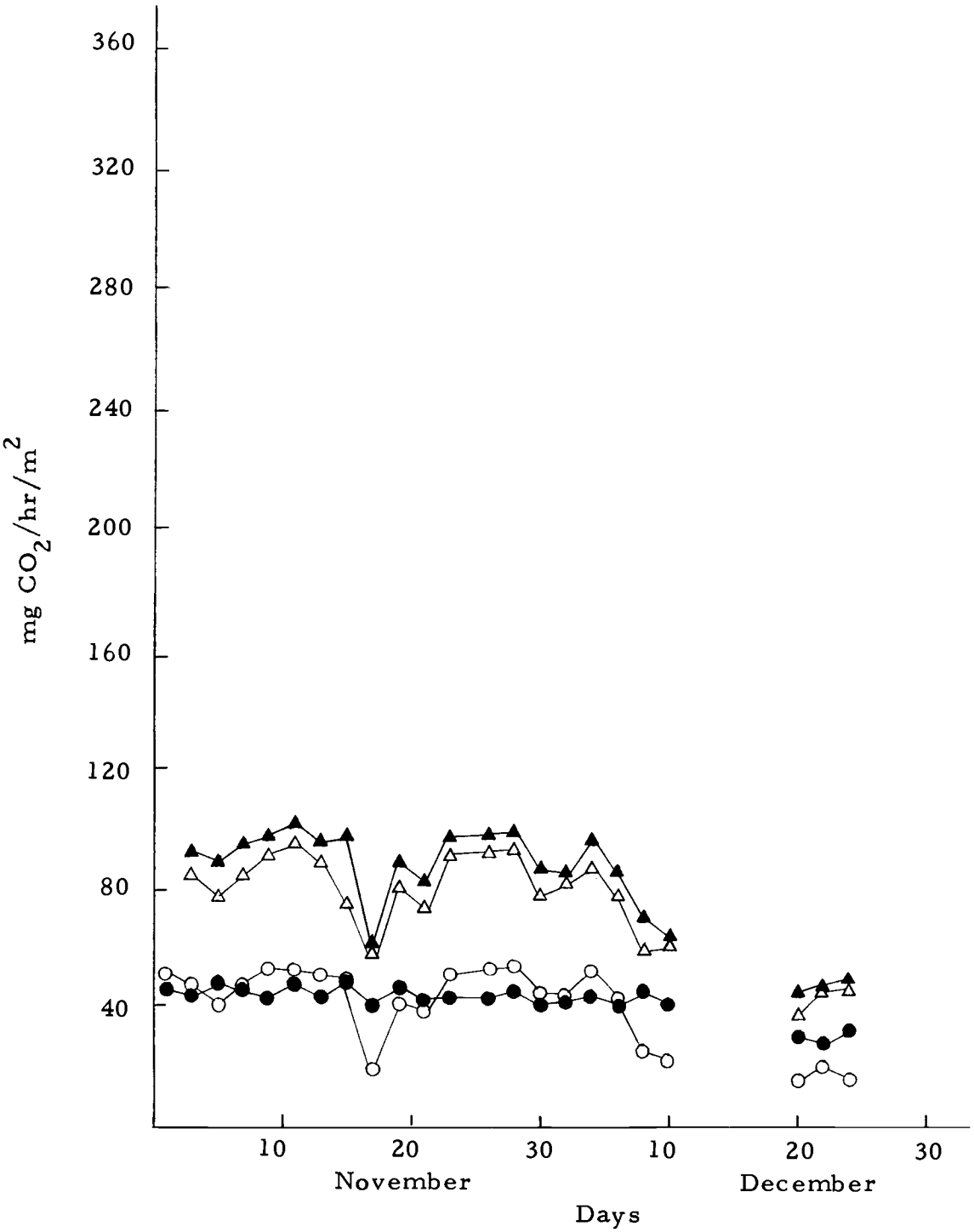



Figure 25. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Tsuga heterophylla type (Nov. - Dec., 1971).

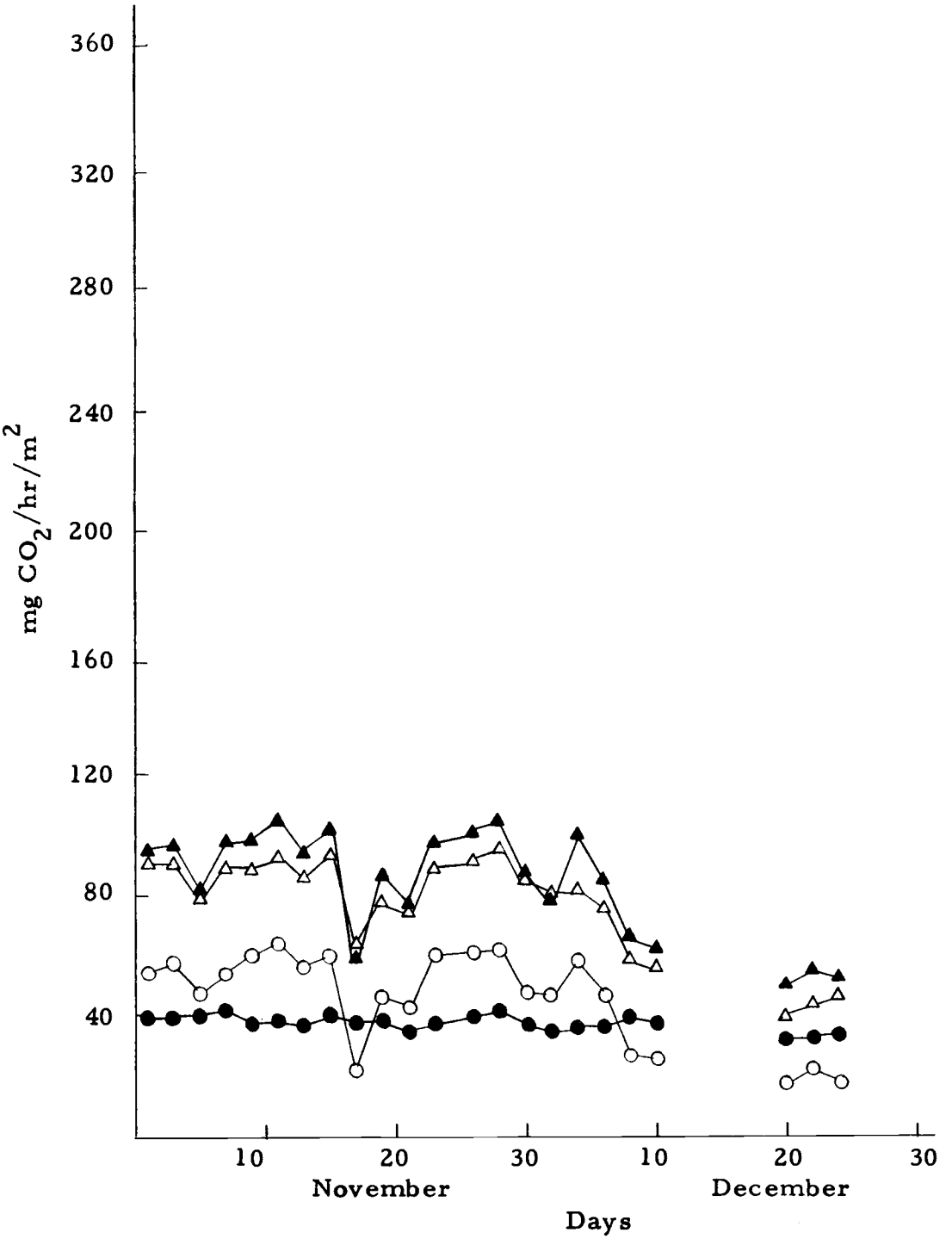



Figure 26. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Castanopsis chrysophylla type (Nov.-Dec., 1971).

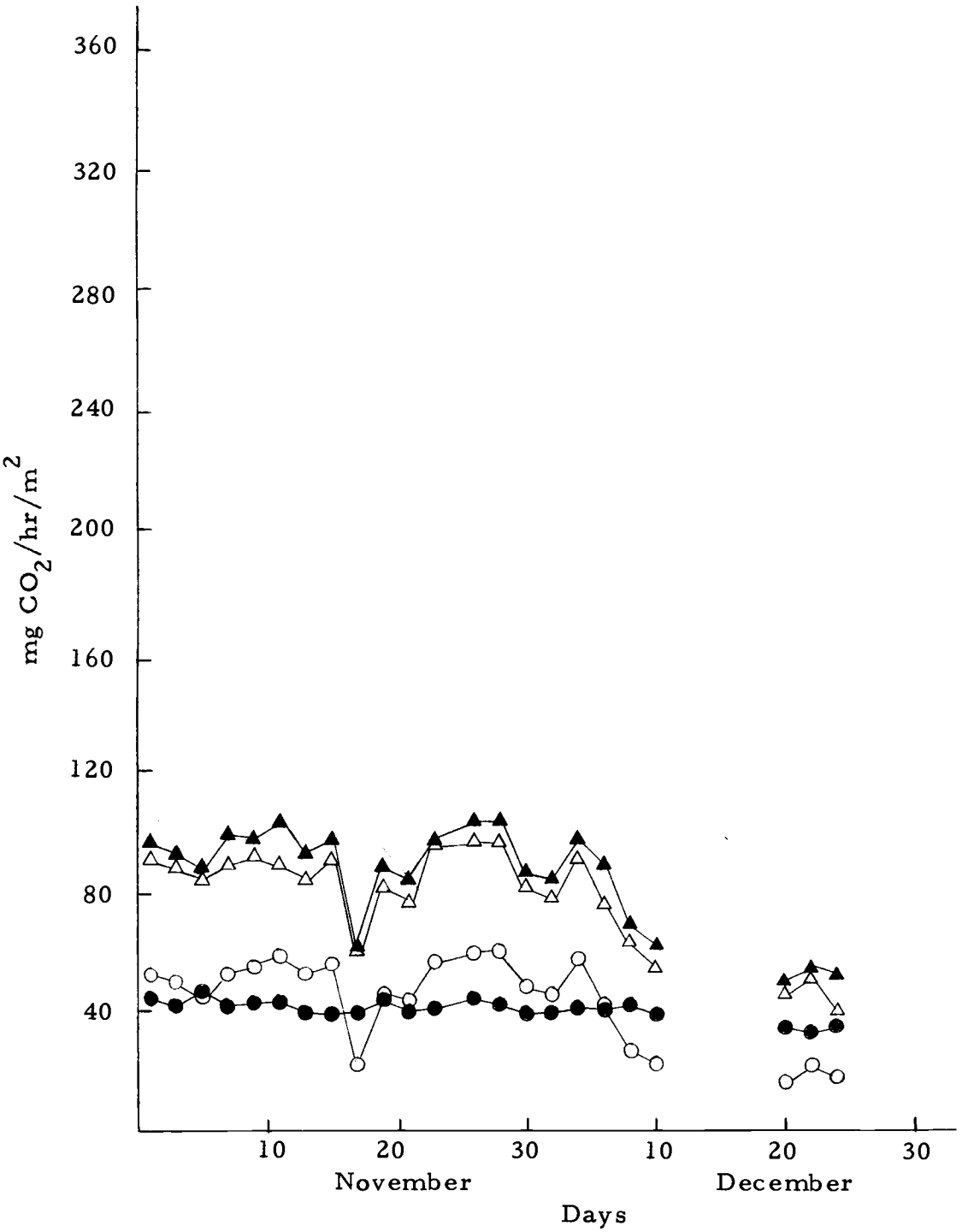



Figure 27. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Polystichum munitum type (Nov. - Dec., 1971).

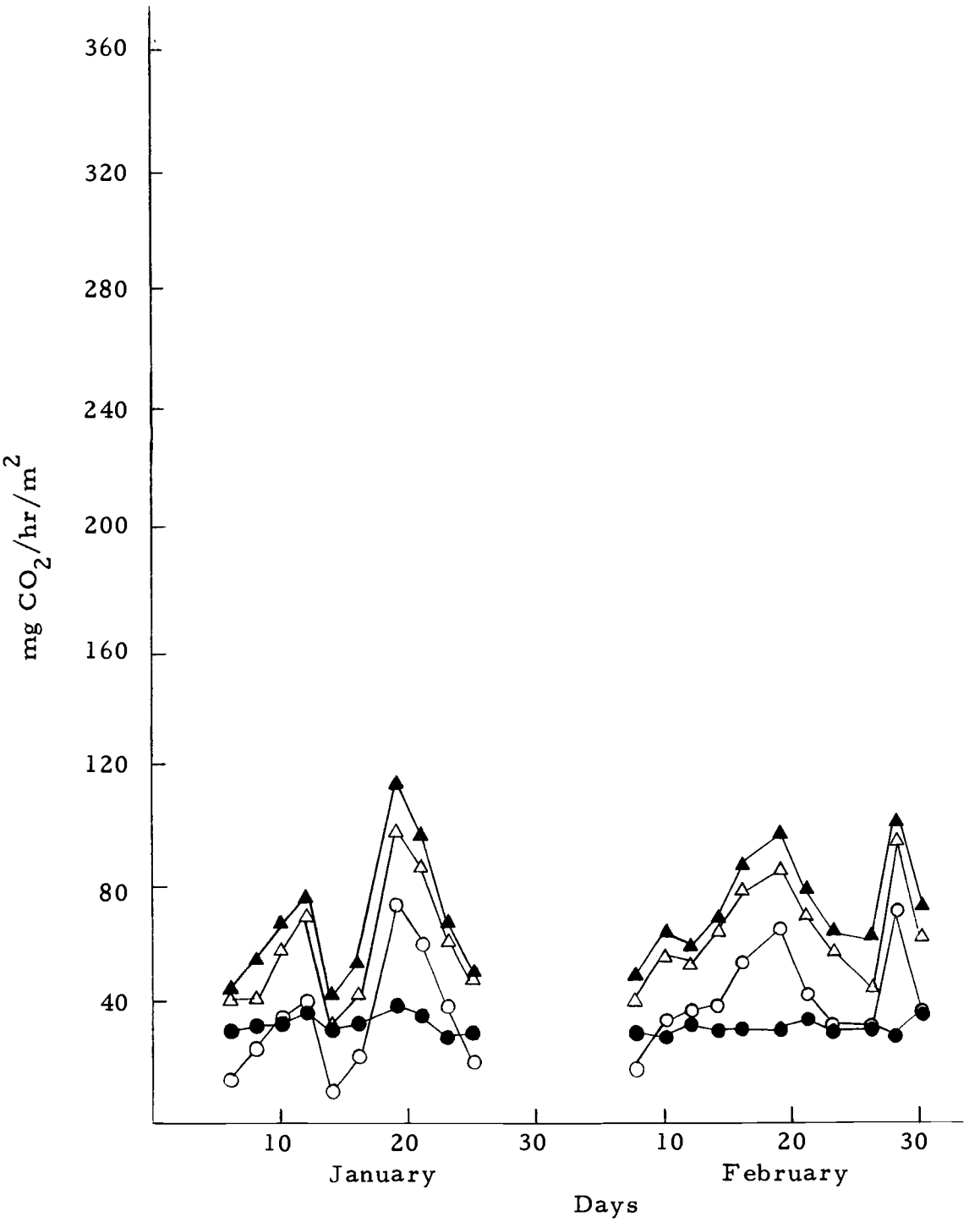



Figure 28. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Holodiscus discolor type (Jan. - Feb., 1972).

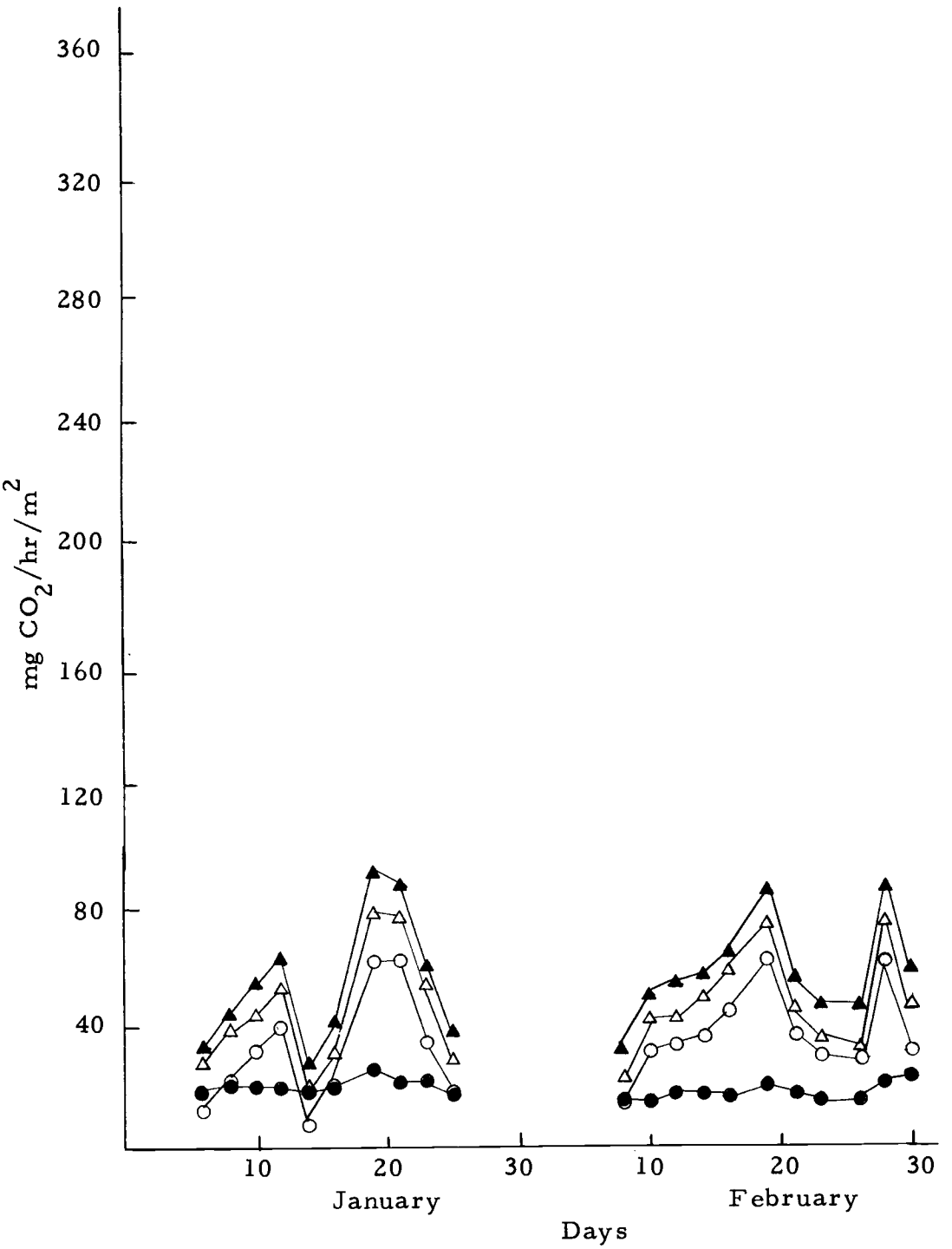



Figure 29. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Acer circinatum type (Jan. - Feb., 1972).

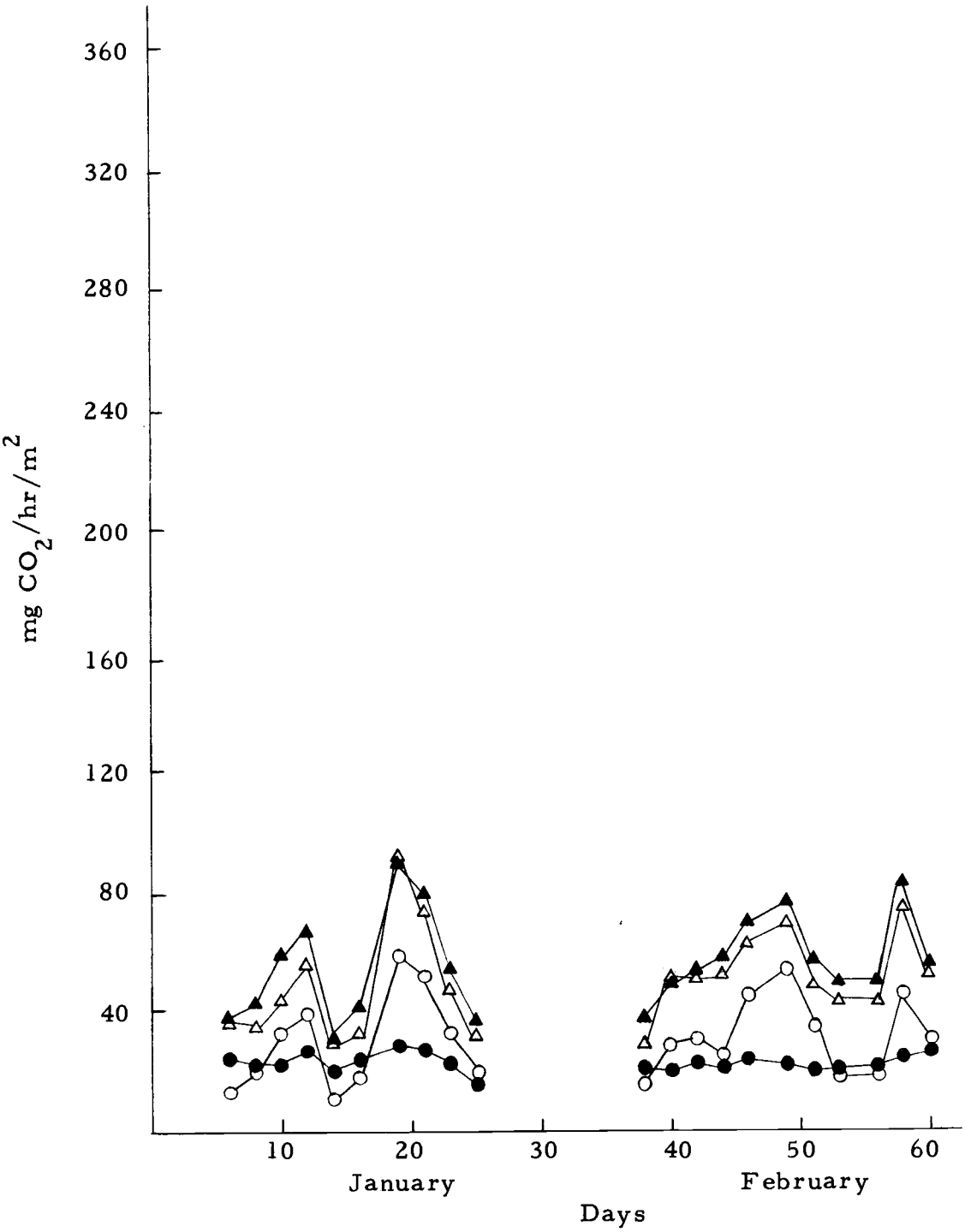



Figure 30. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Gaultheria shallon type (Jan. - Feb., 1972).

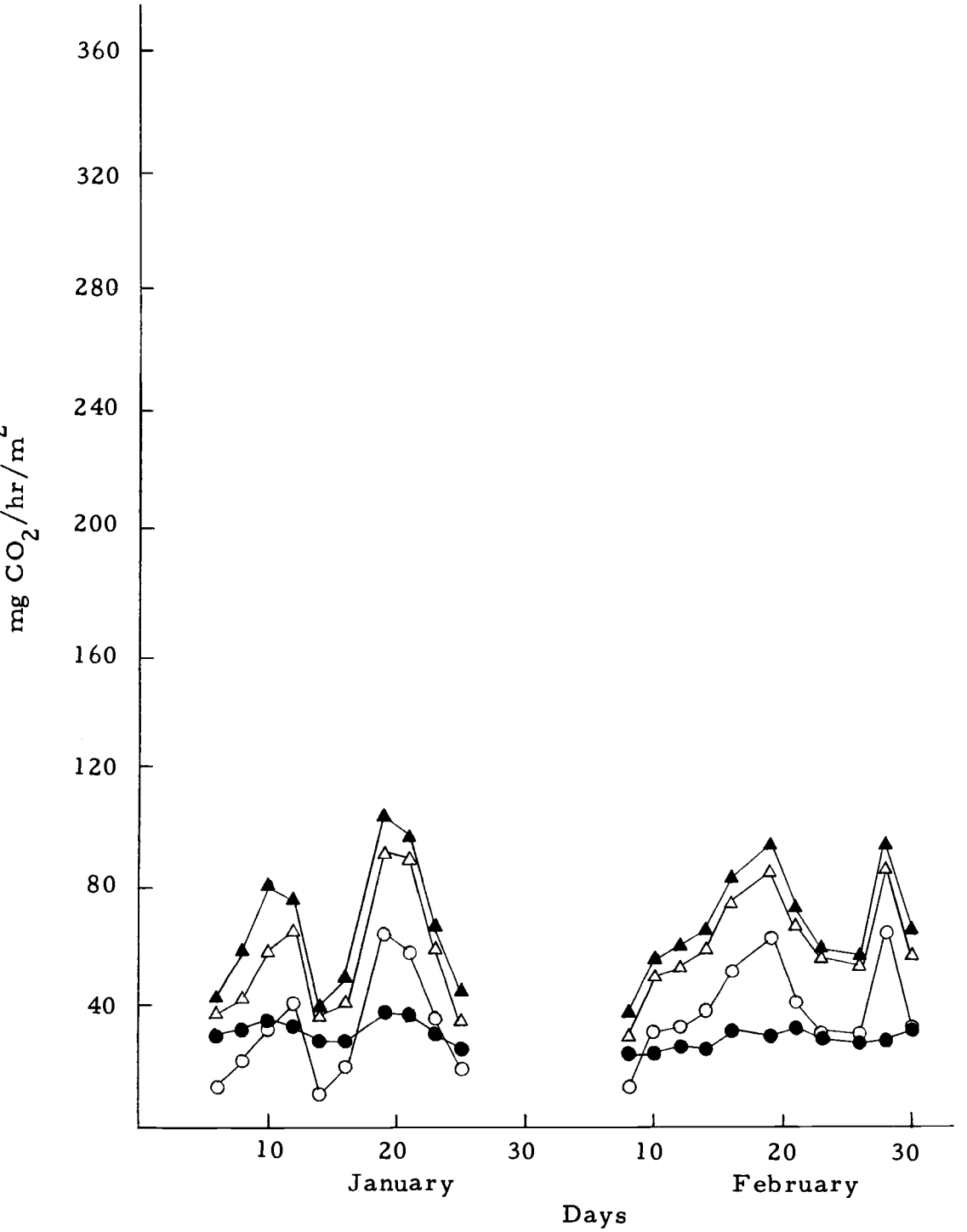



Figure 31. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Tsuga heterophylla type (Jan. - Feb., 1972).

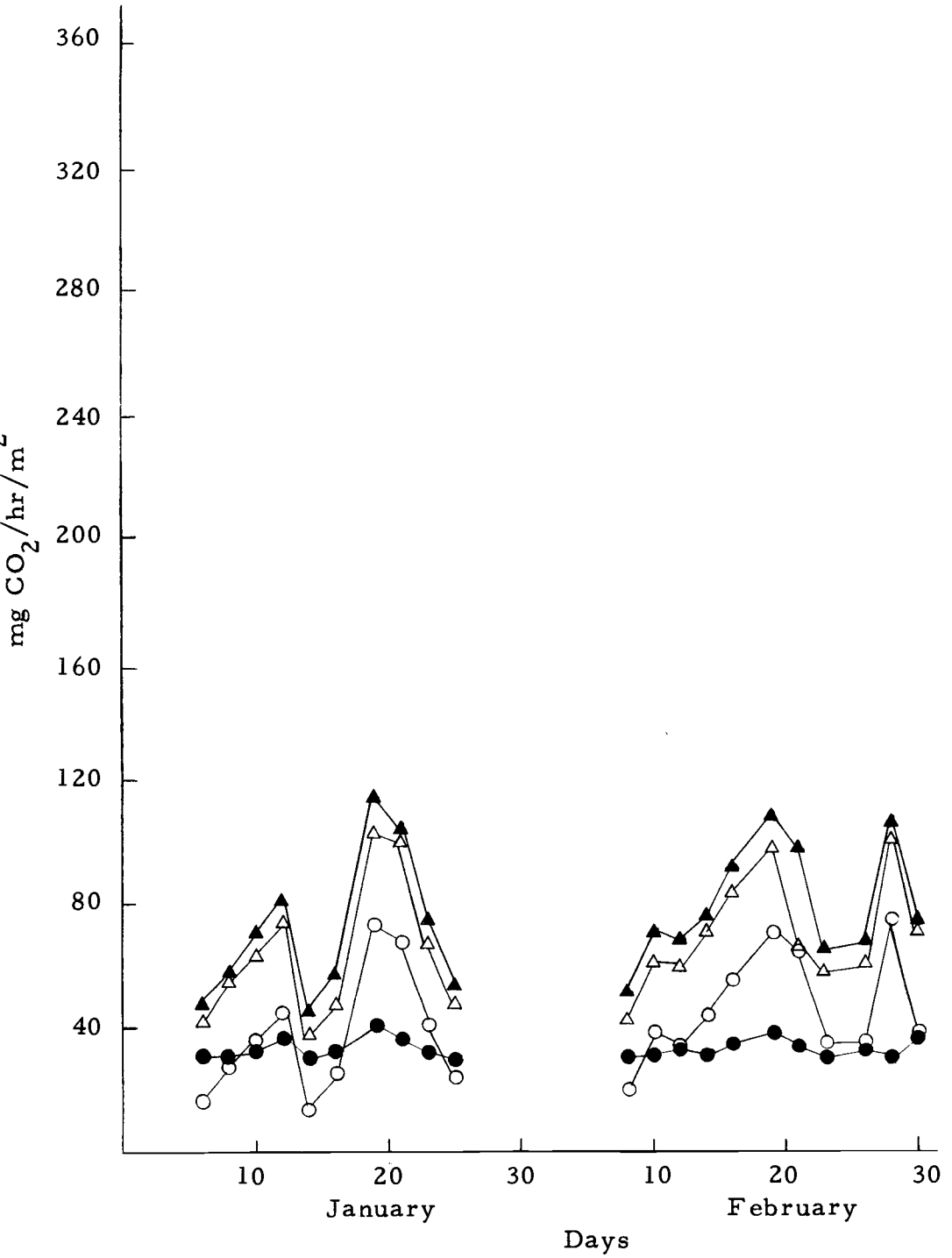



Figure 32. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Castanopsis chrysophylla type (Jan.-Feb., 1972).

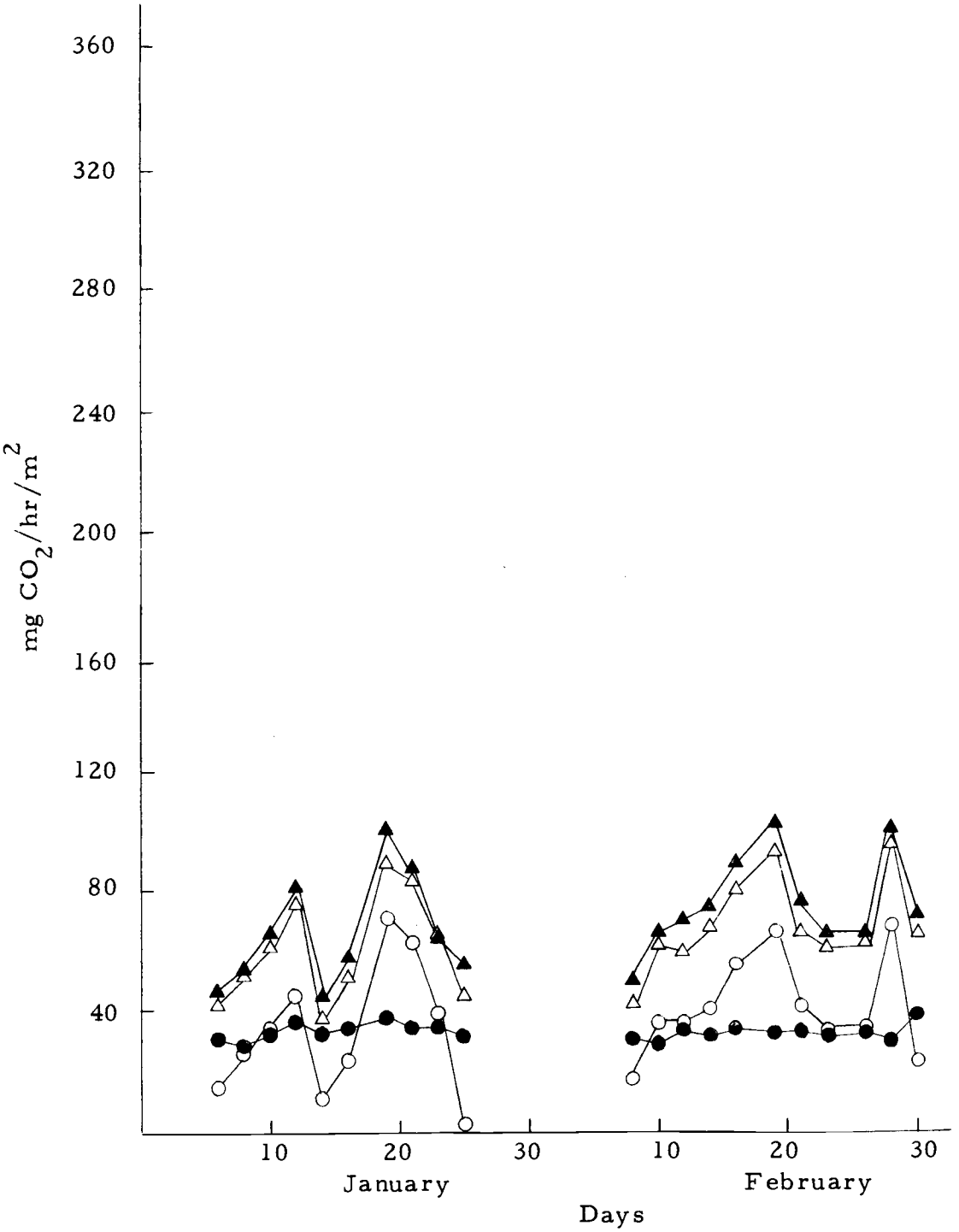



Figure 33. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Polystichum munitum type (Jan. - Feb., 1972).

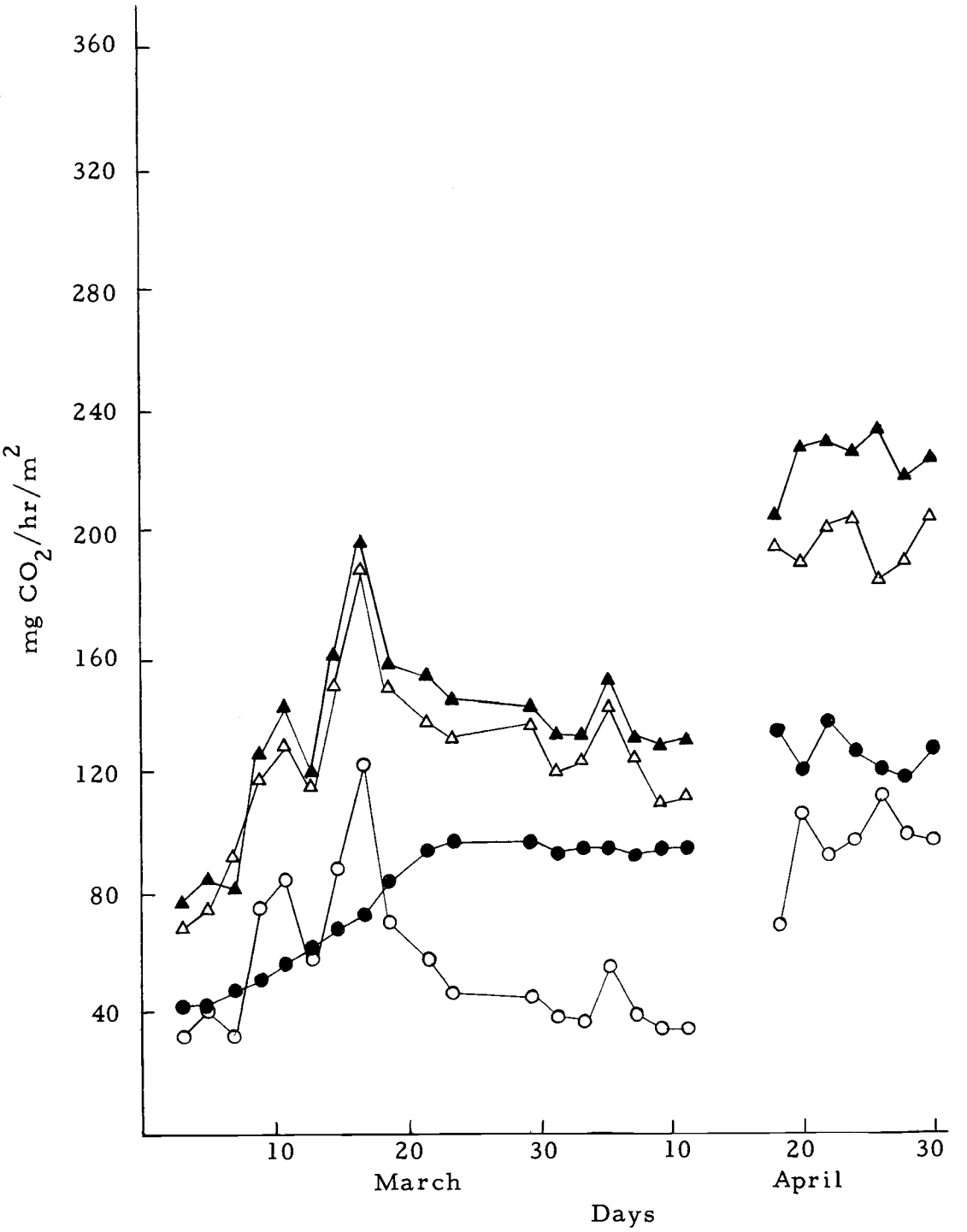



Figure 34. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Holodiscus discolor type (Mar.-Apr., 1972).

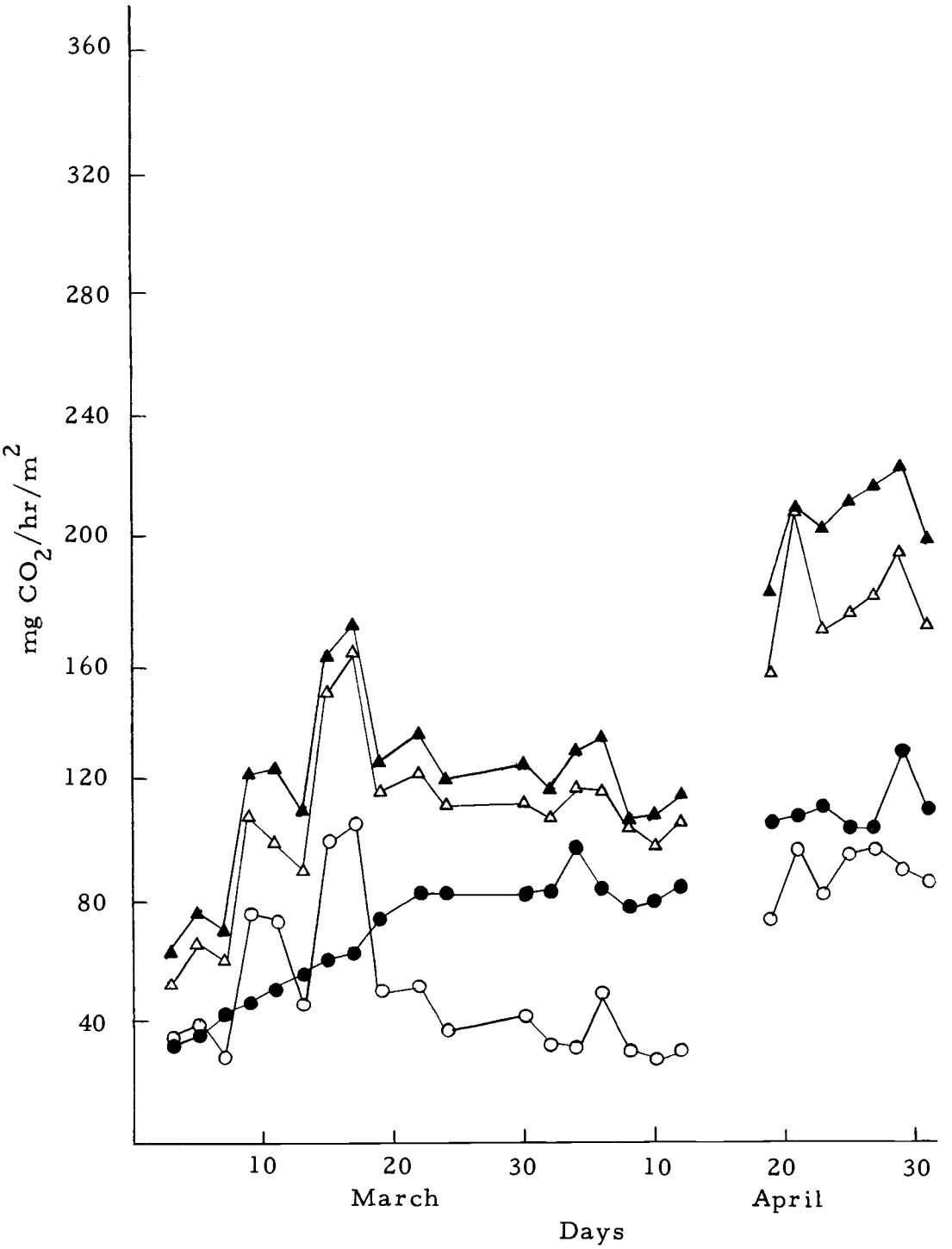



Figure 35. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Acer circinatum type (Mar. - Apr., 1972).

▲—▲ litter plus soil △—△ litter-soil ○—○ litter ●—● soil

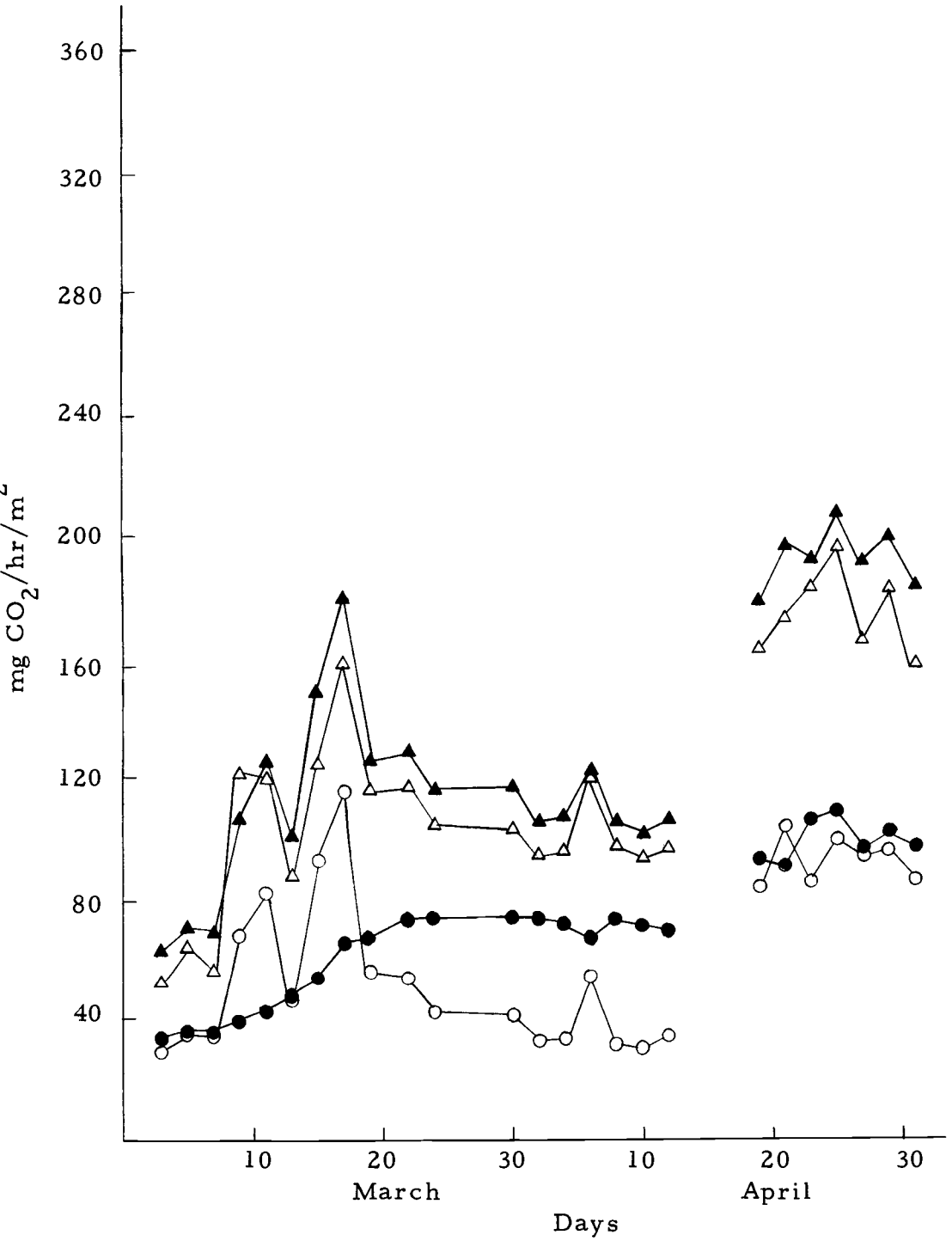



Figure 36. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Gaultheria shallon type (Mar. - Apr., 1972).

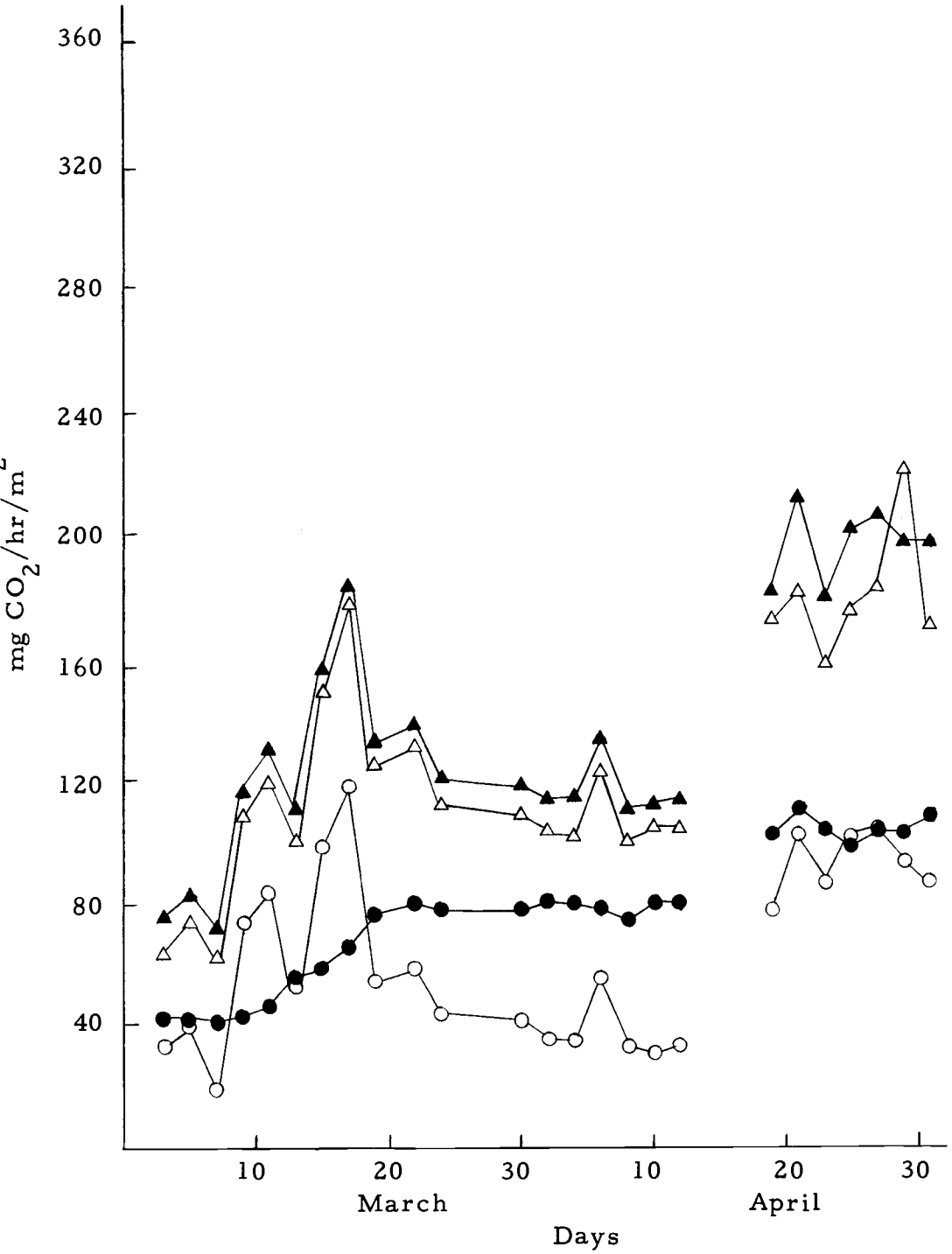



Figure 37. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Tsuga heterophylla type (Mar. - Apr., 1972).

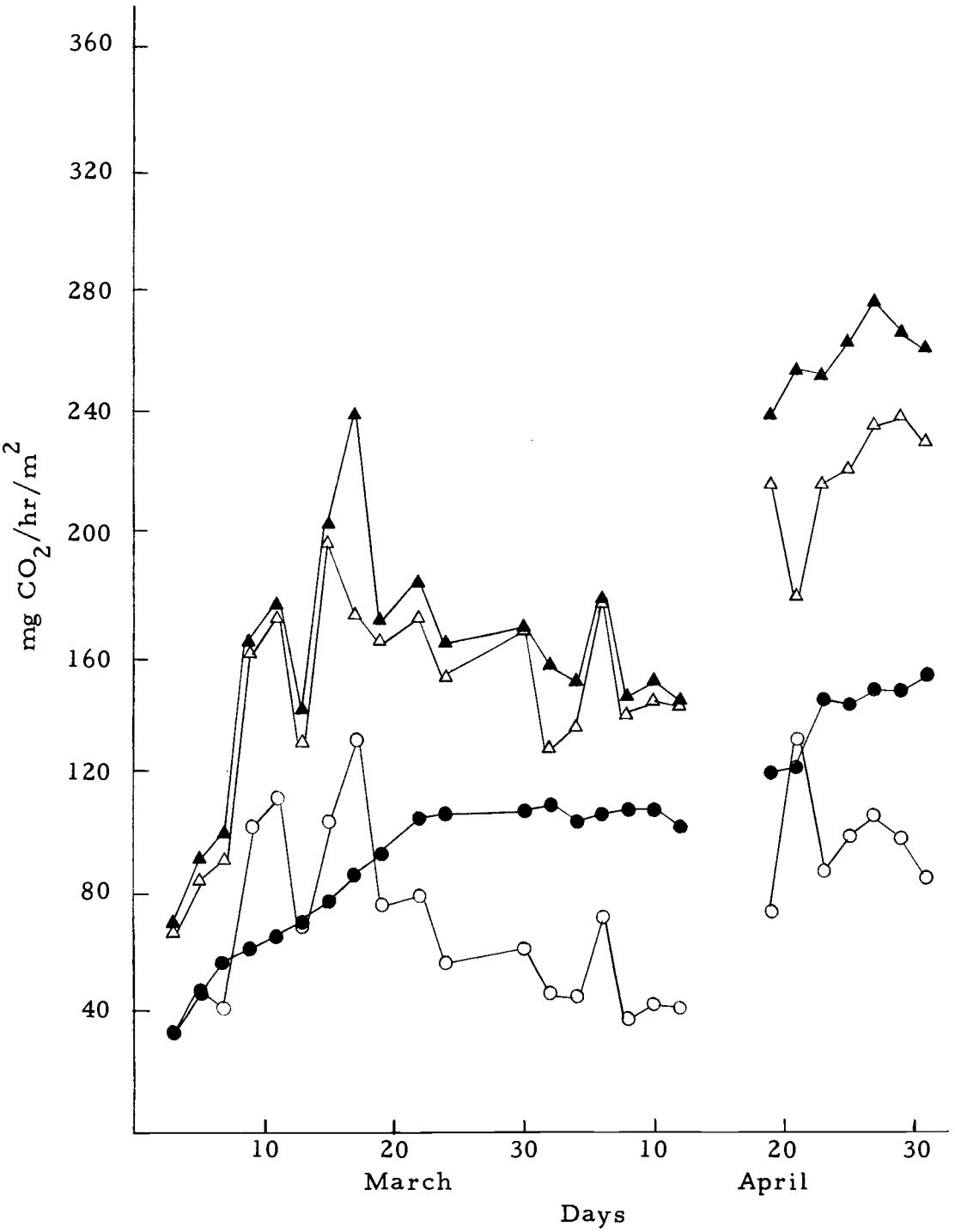



Figure 38. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Castanopsis chrysophylla type (Mar.-Apr., 1972).

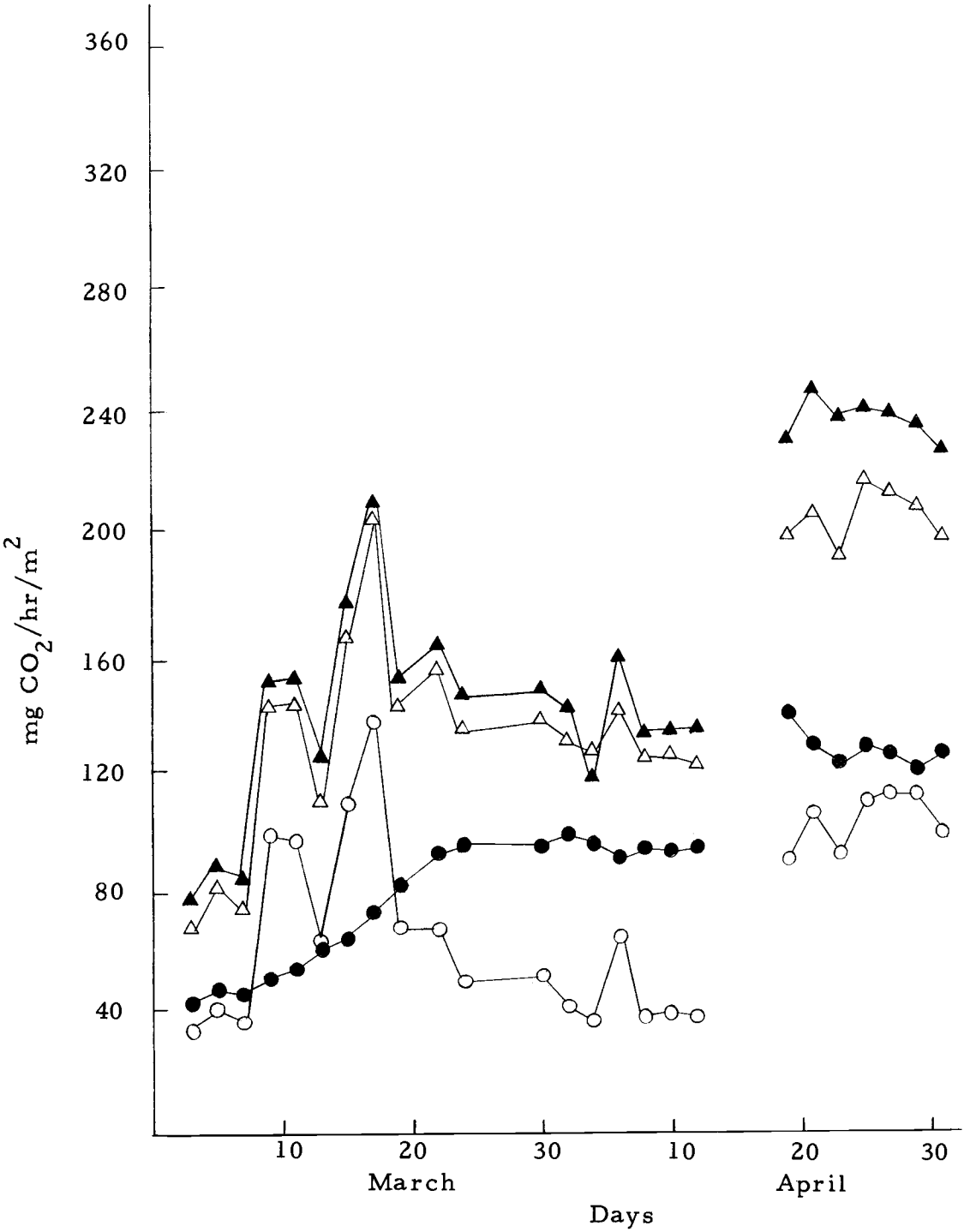



Figure 39. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Polystichum munitum type (Mar.-Apr., 1972).

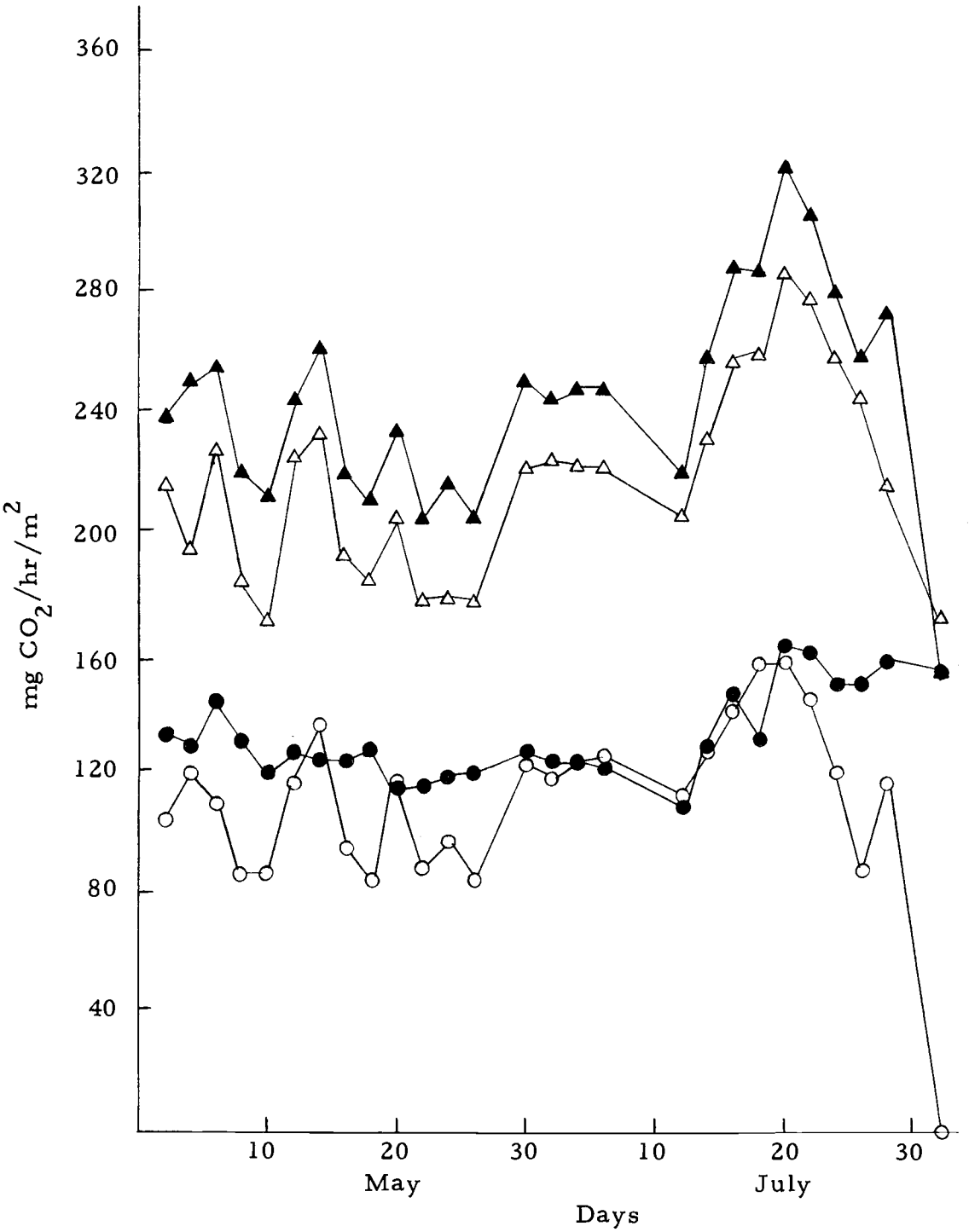



Figure 40. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Holodiscus discolor type (May-July, 1972).

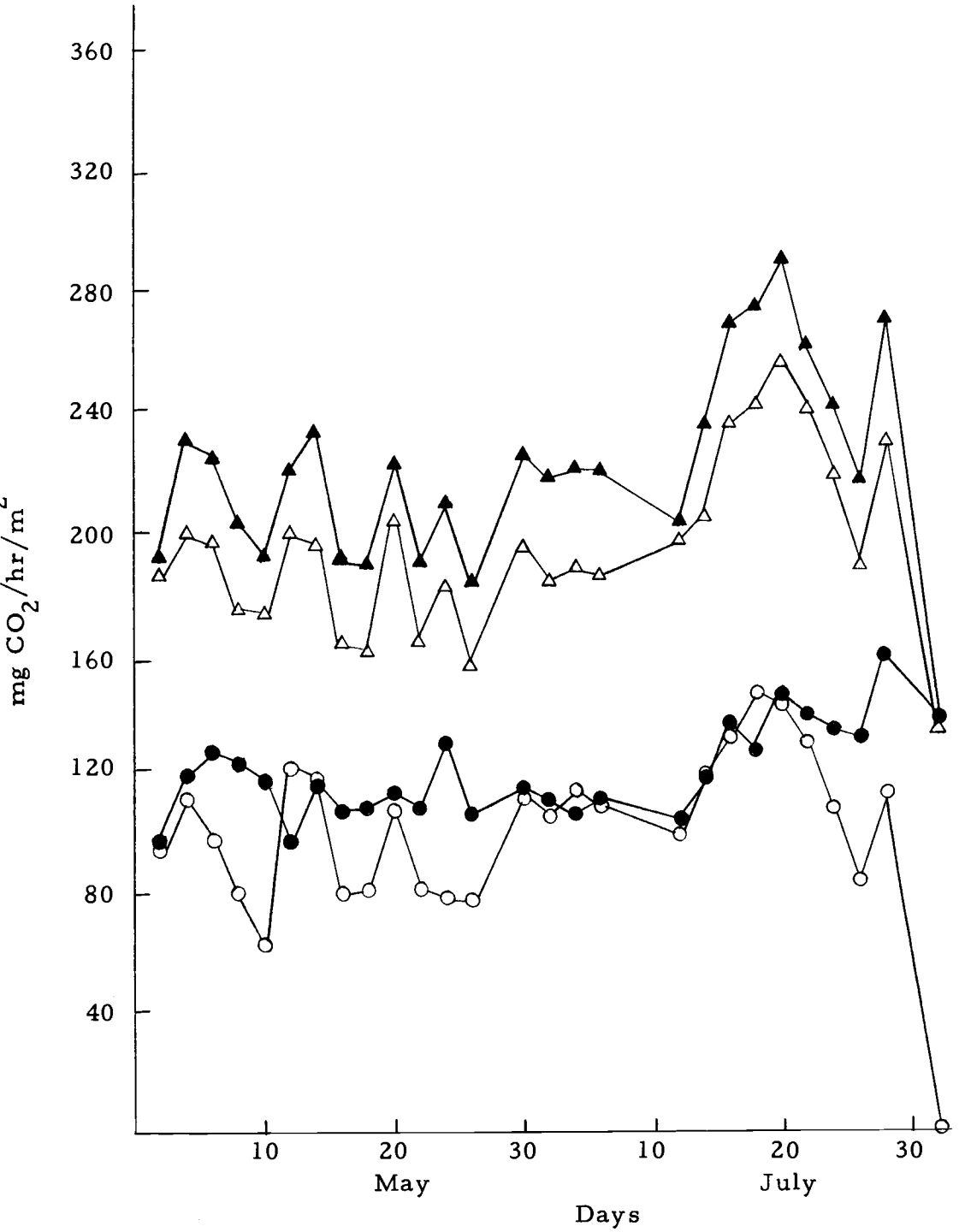



Figure 41. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Acer circinatum type (May-July, 1972).

litter plus soil  litter-soil  litter  soil

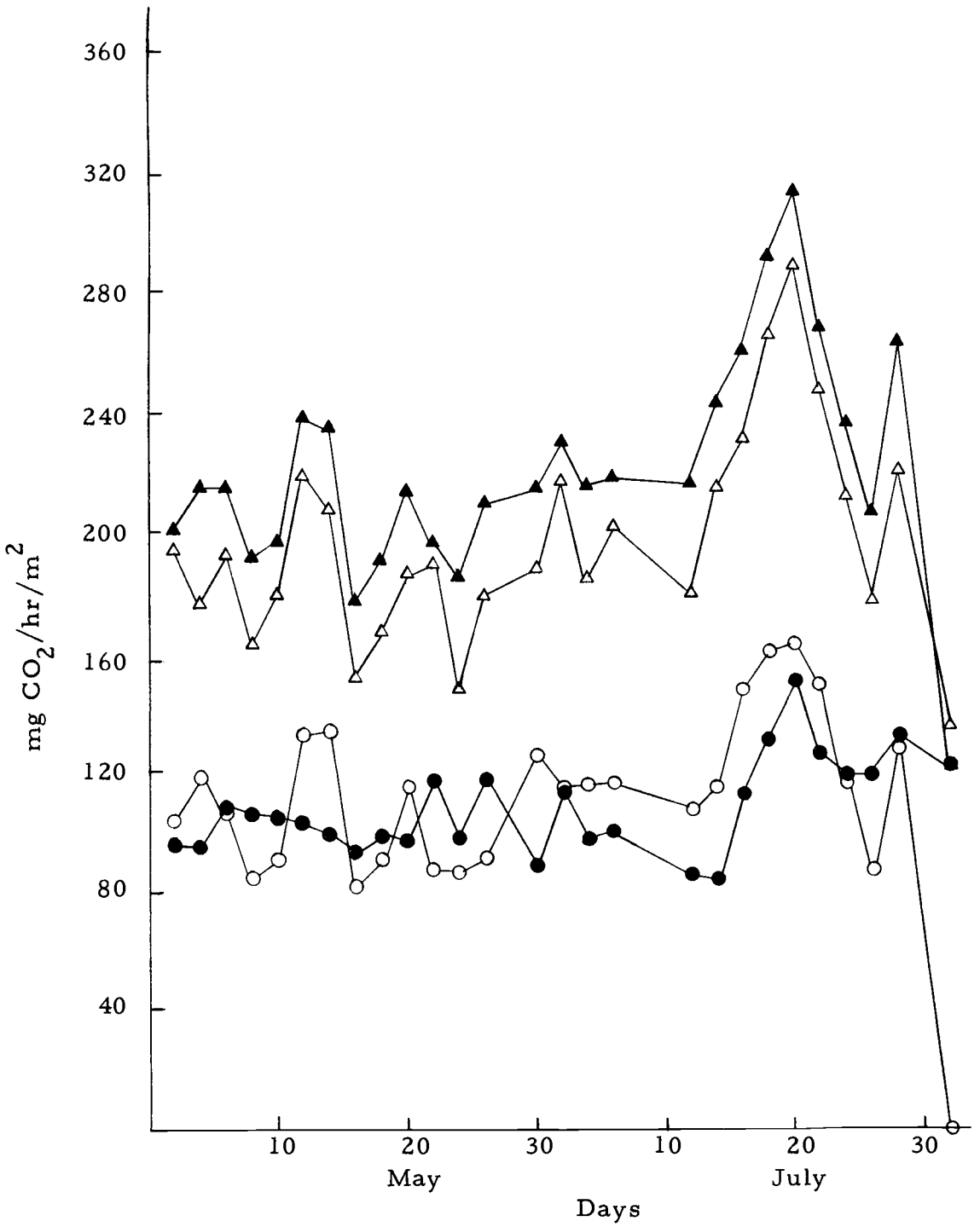



Figure 42. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Gaultheria shallon type (May-July, 1972).

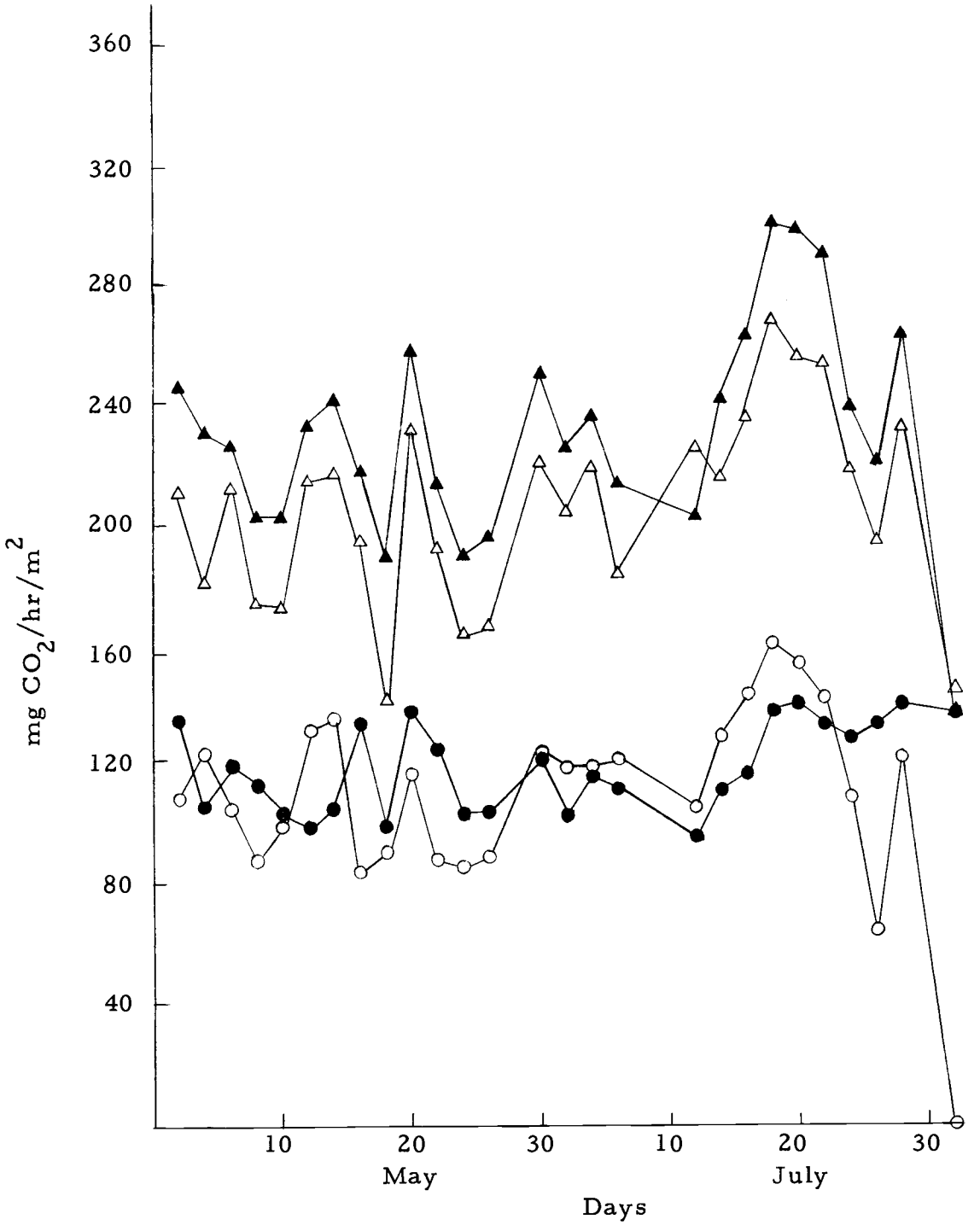



Figure 43. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Tsuga heterophylla type (May-July, 1972).

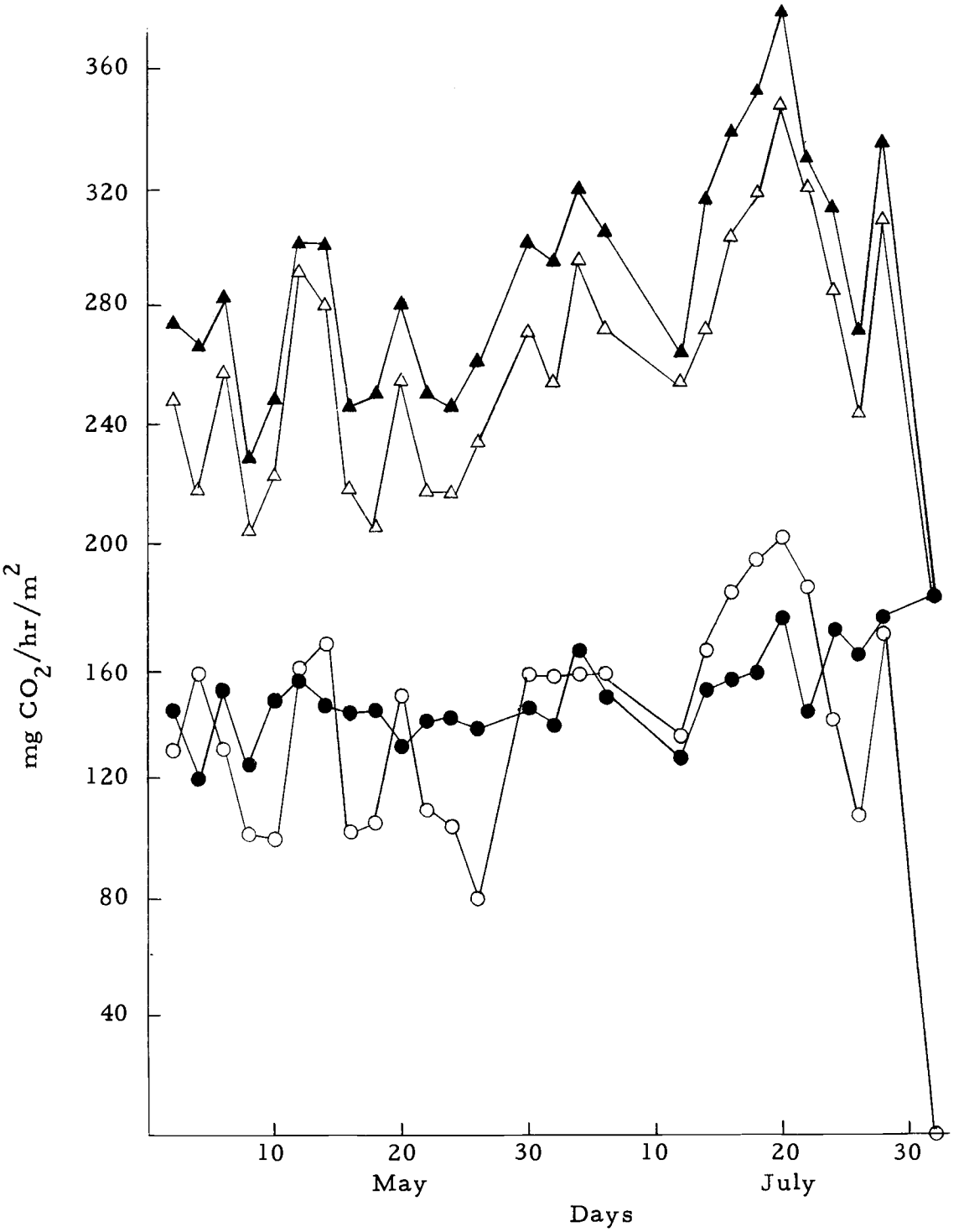



Figure 44. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Castanopsis chrysophylla type (May-July, 1972).

▲—▲ litter plus soil △—△ litter-soil ○—○ litter ●—● soil

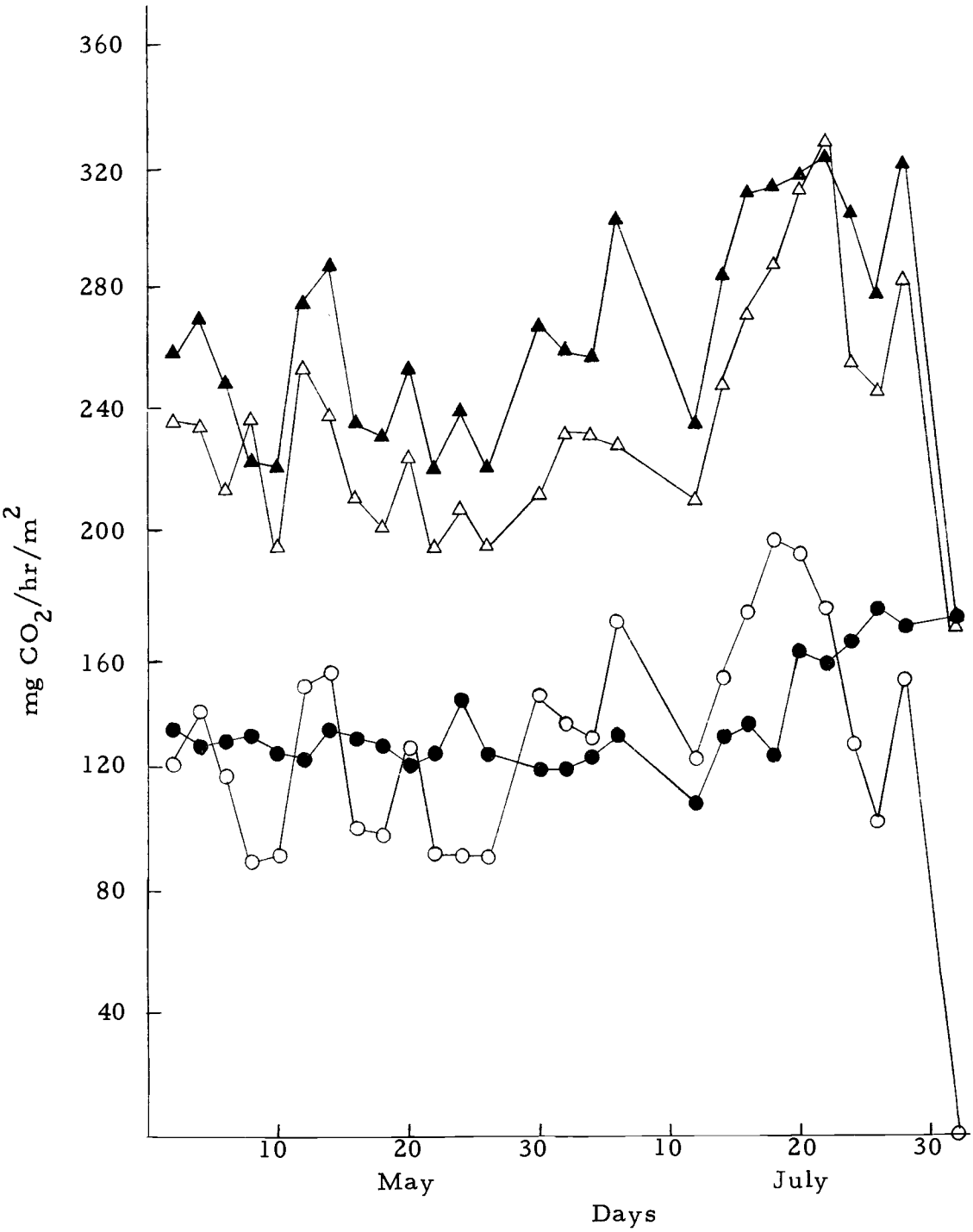



Figure 45. Rate of respiration for litter, soil, litter-soil, and litter plus soil subsystems for Polystichum munitum type (May-July, 1972).

▲—▲ litter plus soil △—△ litter-soil ○—○ litter ●—● soil

Figure 46. Percent moisture of litter subsystem by vegetation type for September - November, 1971.

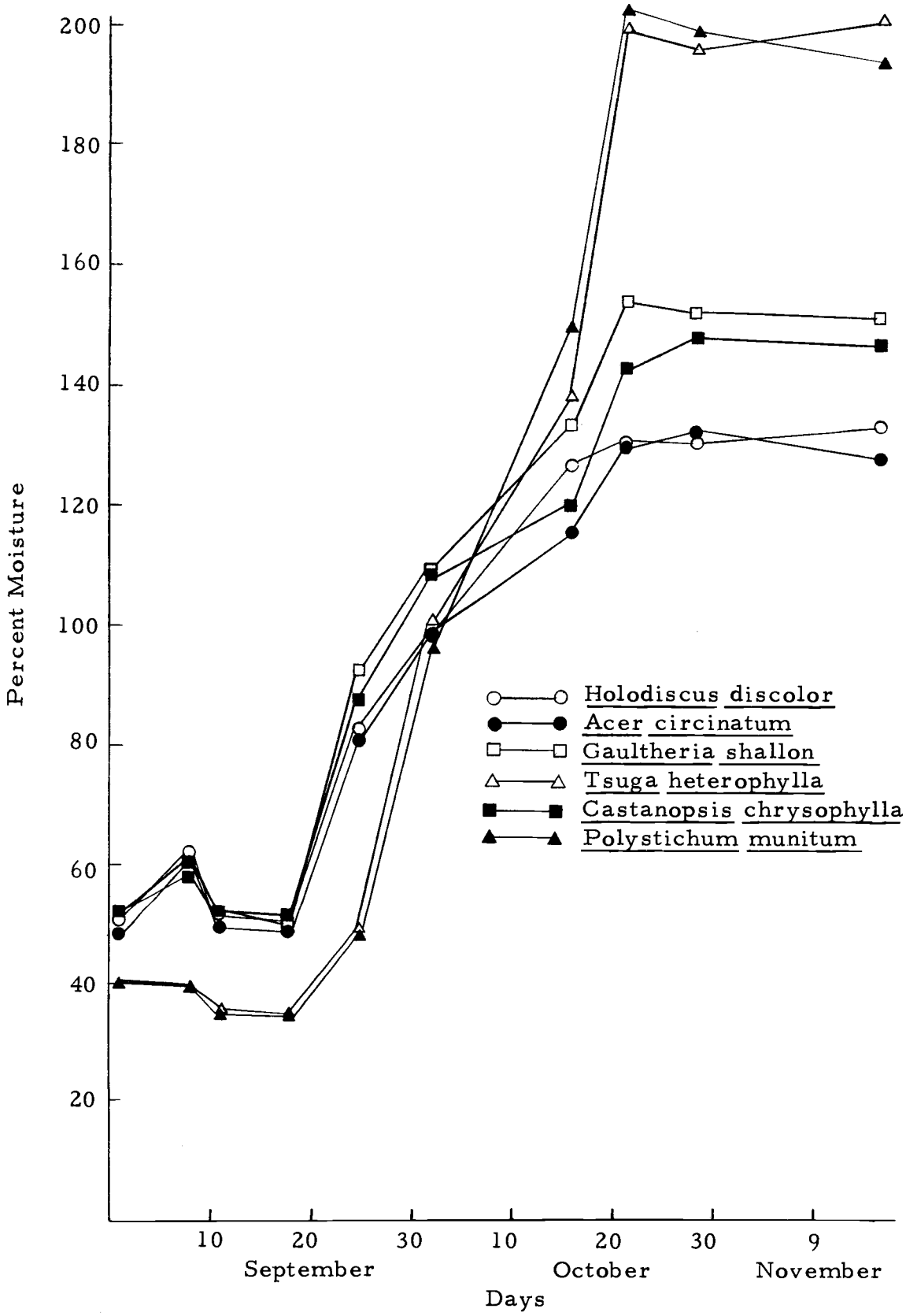
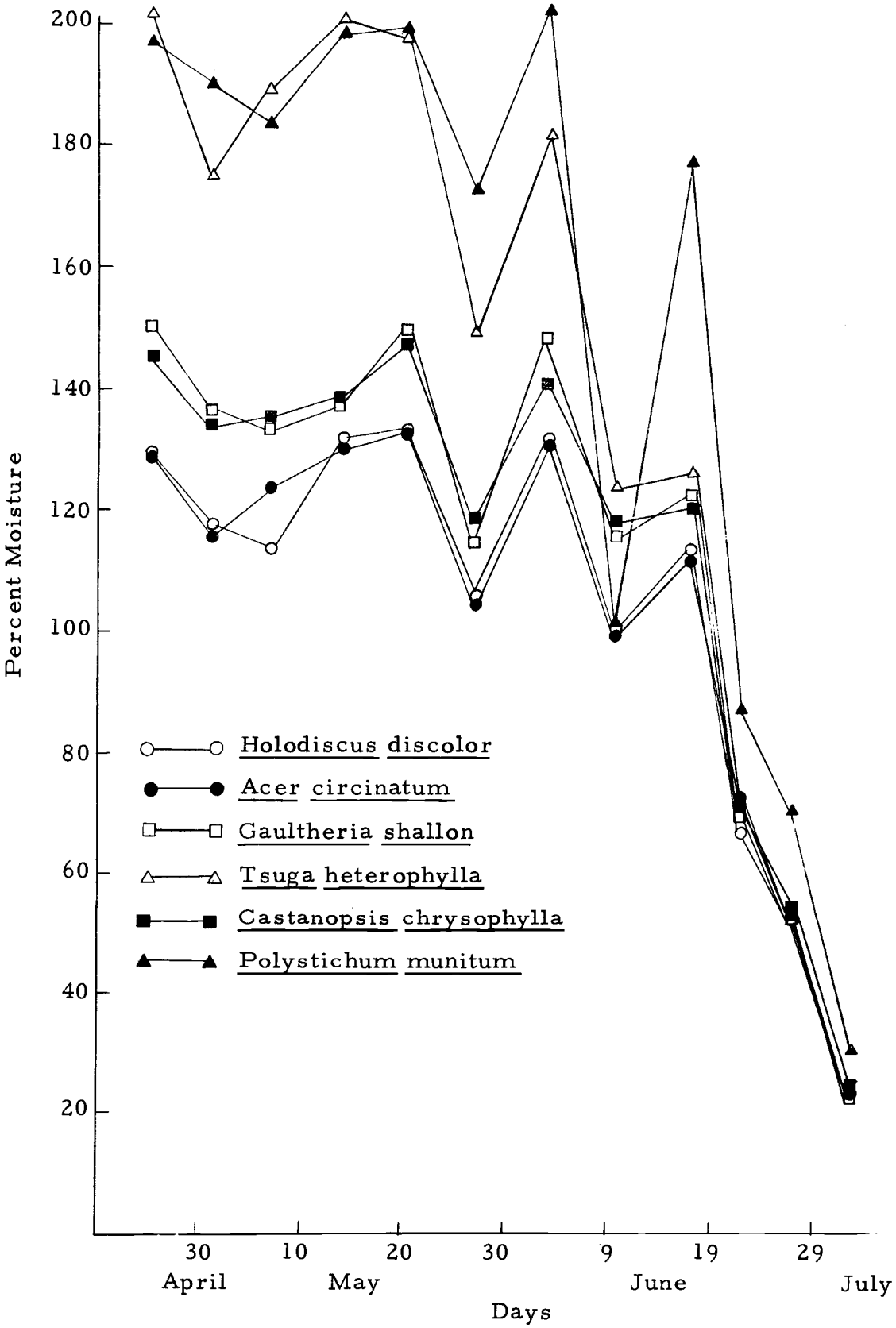

Percent Moisture
200
180
160
140
120
100
80
60
40
20
10
20
30
10
20
30
9
September
October
November
Days
Holodiscus discolor
Acer circinatum
Gaultheria shallon
Tsuga heterophylla
Castanopsis chrysophylla
Polystichum munitum

Figure 47. Percent moisture of litter subsystem by vegetation type for April - July, 1972.


Percent Moisture
200
180
160
140
120
100
80
60
40
20
Holodiscus discolor
Acer circinatum
Gaultheria shallon
Tsuga heterophylla
Castanopsis chrysophylla
Polystichum munitum
30
April
10
20
May
30
9
June
19
29
July
Days

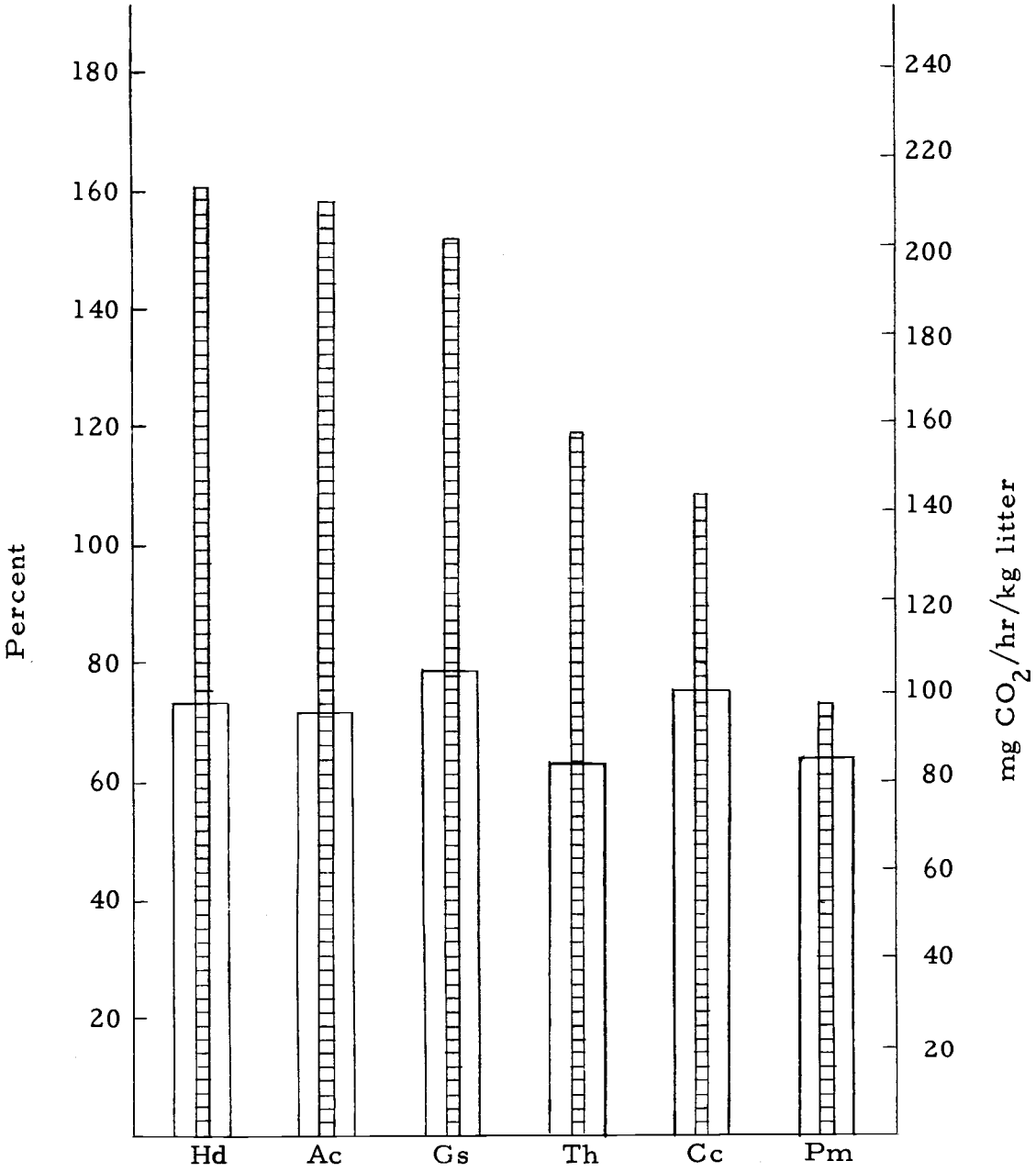



Figure 48. Comparison of mean percent moisture of litter with rate of normalized respiration of the litter subsystem for the fall season (Sep. 1 - Oct. 14, 1971).

Moisture (percent)

Respiration Rate (mg $CO_2$/hr/kg litter)

Hd Holodiscus discolor
Ac Acer circinatum
Gs Gaultheria shallon
Th Tsuga heterophylla
Cc Castanopsis chrysophylla
Pm Polystichum munitum

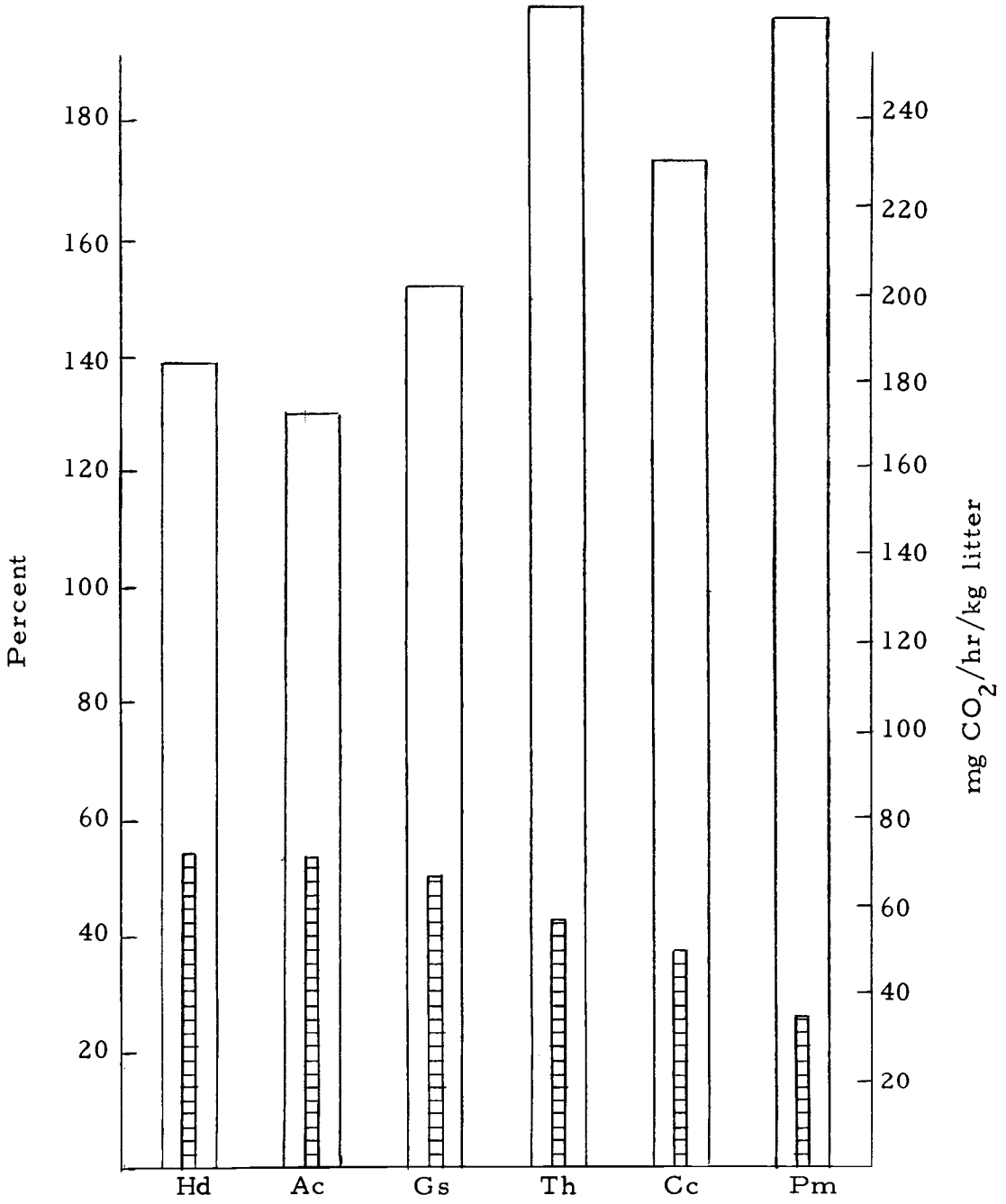



Figure 49. Comparison of mean percent moisture of litter with rate of normalized respiration of the litter subsystem for the wet season (Oct. 15, 1971 - April 30, 1972).

Moisture (percent)

Respiration Rate (mg $CO_2$/hr/kg litter)

| | |
|---|---|
| Hd | Holodiscus discolor |
| Ac | Acer circinatum |
| Gs | Gaultheria shallon |
| Th | Tsuga heterophylla |
| Cc | Castanopsis chrysophylla |
| Pm | Polystichum munitum |

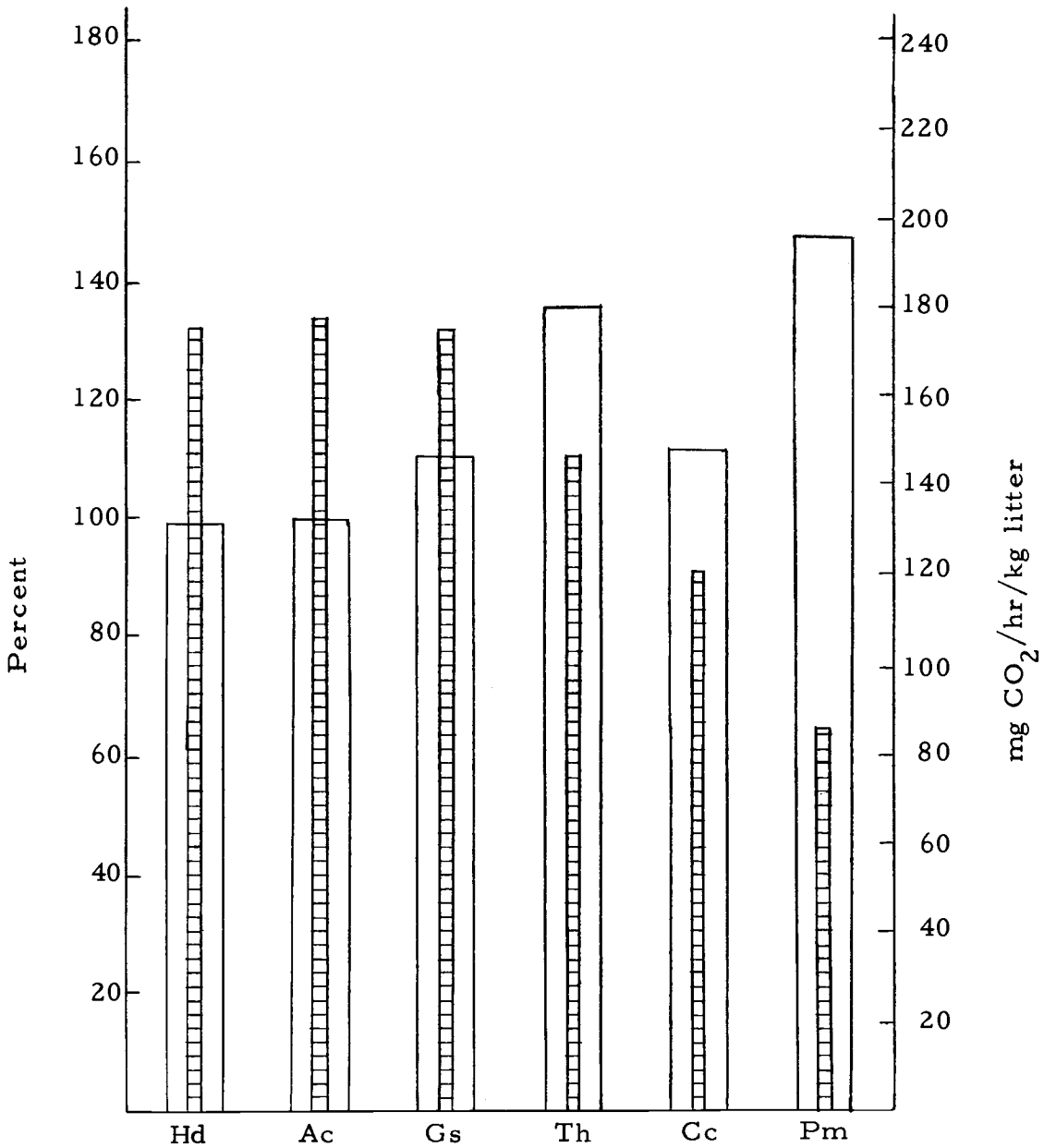



Figure 50. Comparison of mean percent moisture of litter with rate of normalized respiration of the litter subsystem for the spring season (May 1 - July 1, 1972).

Moisture (percent)

Respiration Rate (mg $CO_2$/hr/kg litter)

Hd Holodiscus discolor
Ac Acer circinatum
Gs Gaultheria shallon
Th Tsuga heterophylla
Cc Castanopsis chrysophylla
Pm Polystichum munitum

# DISCUSSION

## Reliability and Utility of Rates of Respiration of the Litter Subsystem

There are two main difficulties in determining the presence of and quantifying the magnitude of the differences in the rates of energy utilization relative to the major understory vegetation types in this forest. These difficulties are accounting for and/or controlling the influence of the other possible variables which help determine these rates, and determining the reality of the data.

The typing procedure permitted smaller sample sizes by reducing the variability of the subsystem and its immediate environment. By removing or limiting some of the confounding factors a clearer view of the relationship of the presence of the various understory types to the rates of respiration of the subsystems is possible. However, this does result in a certain loss of reliability in using these rates to estimate overall stand subsystem rates. This study did not yield information that could be used to quantify the exact departure of the "typed" average from the true average; however, the comparisons in Table 11 are suggestive.

This should not affect the comparison of the rates by understory type as there appears to be no reason to suspect that the typing differentially affected the choice of the samples by type in a manner that

would produce the rates of respiration differences observed between types. In other words there is no reason to suspect that the observed relative differences are substantially different than would be found by a purely random sampling that contained a means of separating out confounding factors.

A possible source of error is in the regular sampling sequence used in the field. The sequence, which was dictated by economy of movement in the field, is given in Table 12. As can be seen there is no apparent pattern to the relationship between a type and sampling sequence nor as Table 7 shows, is there any apparent respiration pattern related to sequence of areas. Thus it can be assumed that the regular sampling schedule did not substantially bias the rates of respiration by type or area.

Table 12. Temporal sequence of schedule followed in respiration sampling initiation and termination for type and area.[1]

| Vegetation type | Areas 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| Holodiscus discolor | 3 | 3 | 1 | 3 |
| Acer circinatum | 2 | 5 | 2 | 6 |
| Gaultheria shallon | 4 | 2 | 3 | 2 |
| Tsuga heterophylla | 1 | 6 | 5 | 1 |
| Castanopsis chrysophylla | 6 | 1 | 4 | 4 |
| Polystichum munitum | 5 | 4 | 6 | 5 |

[1] Numbers in table refer to order by type; areas were visited in order of 1-4-thus, area 1, #1 was first point sampled; area 4, #6 last.

The normalization process presents a more complicated problem. One assumption implicit in the normalization for purposes of comparison of differences uninfluenced by litter depth is that no major departures from the mean litter weight relationships between types occur throughout the season and more importantly between the mean and the end of the litter respiration season when the normalization weights were determined.

That this is potentially unrealistic is obvious in terms of deciduous species like Acer circinatum and Holodiscus discolor which discard their foliage in a period of weeks (in late October in this stand). This is in contrast to Polystichum munitum which is "beaten down" in the wet season and based on observation appears to make its major annual contribution to the organic matter of the litter subsystem in the wet season. The litter fall of the other species which are considered persistent-leaved is less clear-cut as to when they make their annual contribution. Gaultheria shallon and Castanopsis chrysophylla were observed to increase their leaf-drop in early spring; however, it was also observed that some winter storms caused similar increases. The most striking effect was observed during storms accompanied by heavy winds when litter (including branches) could be seen in the air coming from all types, except Polystichum munitum. After such a storm the roads in the area would be carpeted with

freshly fallen litter. The first of these storms occurred in late November.

Compared to the deciduous species, the amount of litter involved and the distinctness of the seasonal drop for Gaultheria shallon and Castanopsis chrysophylla appeared to be much less. These leaf-drop observations are not unique. Bray and Gorham (1964) discuss seasonal variations in leaf-drop (and also for the other parts of the plants) by persistent-leaved trees and note that seasonal highs and lows for various species are extremely variable from year to year. Richards (1957) points out that the pattern and timing of leaf replacement in persistent-leaved trees are dependent upon both external and internal factors and notes that storms are particularly important. Except for an increase after windy storms no pattern of leaf drop was observed for Tsuga heterophylla.

An additional source of potential bias related to litter type is that for certain of these species, some of the leaves dropped do not appear to become immediately available for decomposition. It was observed that many of the Gaultheria shallon leaves, most of the Polystichum munitum fronds, "beaten down" in the wet season, and some of the Castanopsis chrysophylla leaves were green when they entered the litter subsystem and remained so throughout the wet season. It was only after the advent of drying periods in the spring that the leaves "browned." Whether this means little or no

decomposition occurs for those leaves dropped in the wet season until they partially desiccate at least once, is not clear, but it is a possibility and would be a factor in assigning any error to the normalization procedure.

The physical and possibly chemical structure of the leaf appears to be the important determining factors in this. Kucera (1959) studied the decomposition rates of various types of leaves as a function of physical structure of the leaf and concluded that thick "leathery" leaves such as oak are slower to initiate decomposition than thinner leaves such as elm and also had longer turn-over times. Witkamp (1966b) noted a similar effect and suggests that in "tough" leaves the relatively larger quantities of cellulose and lignin which are resistant to decomposition, as well as the leaf's resistance to fragmentation (by weather and/or fauna), result in slower decomposition rates. He suggests that the greatest effect is in the first few weeks following leaf-drop with the differences becoming less as the leaves become fragmented.

Whether these weight changes are significant and can account for the differences seen between types depends upon their magnitude relative to the weight of the litter subsystem. It is possible to make some rough estimates to answer that using the following relationships based on the ideal goal of using the average weight of the litter to normalize the average respiration rate.

$$E = 1/M_y\ (F_l)\ (0.5 - F_r)$$

Where:

$E$ = approximate error in litter weights used for normalization with the sign indicating whether it is an over or underestimate.

$M_y$ = turnover time in years for litter in subsystem. Dividing this into one yields the fraction of litter expected to be turned over in one respiration season.

$F_l$ = fraction of total litter in annual litter fall produced by understory.

0.5 = is the ideal point in the litter respiration season (in terms of total respiration not time) to measure the litter weight to yield average weight.

$F_r$ = the fraction of total litter respiration season that has occurred between the seasonal leaf drop and July 3, 1972 when weights were determined (fractional time weighted to respiration by use of Table 6).

$M_y$ can be estimated from the following relationship.

$$M_y = M_w/M_f$$

where:

$M_w$ = mean weight of litter in subsystem which can be estimated from the mean weights in Table 10.

$M_f$ = mean rate of utilization of the litter which can be estimated in two ways, both based on the assumption that the annual input of organic matter from all sources into the litter subsystem is in equilibrium with the annual removal of organic matter from the subsystem.

The first approach is to estimate the input of organic matter to the litter subsystem. The best available estimate appears to be from Abee and Lavender's (1972) study in a mature Pseudotsuga menziesii

forest. Converting their mean data to a per $g/m^2$ basis we get an estimate of 570 grams of litter for annual input to the litter subsystem. Based on this $M_f$ value, $M_y$'s of 1.4 and 1.5 result for Holodiscus discolor and Acer circinatum, respectively.

The second approach is to estimate the output. The annual respiration rate per type in mg $CO_2$ (Table 13) can be converted to grams of carbon. For Holodiscus discolor and Acer circinatum this is 170 and 187 grams of carbon, respectively. Forty-five percent average carbon content for litter is a commonly accepted estimate for various litter types (Reiners, 1968; Olson, 1970). Using this average the mean litter weights in Table 10 can also be converted to grams of carbon. The mean litter weights for Holodiscus discolor and Acer circinatum are 352 and 393 grams of carbon, respectively. Based on these values, $M_y$'s of 2.07 and 2.10 result for Holodiscus discolor and Acer circinatum, respectively. These estimates would be expected to be too large by some percent because $M_f$ calculated this way does not take into account the transport of material to the soil from the litter subsystem.

Witkamp (1966b) in a study involving temperate deciduous forest litter, estimates that perhaps as much as 40 percent of the litter loss, in the initial year it enters the subsystem, results from factors other than decay, presumably transport to the soil. This is probably much too large an estimate for the subsystems in this study as

Table 13. Mean annual rates of respiration for litter subsystem during the litter respiration season 1971-1972.

| Vegetation type | Grams $CO_2/yr/m^2$ |
|---|---|
| Holodiscus discolor | 621.47 |
| Acer circinatum | 685.93 |
| Gaultheria shallon | 695.70 |
| Tsuga heterophylla | 667.65 |
| Castanopsis chrysophylla | 731.98 |
| Polystichum munitum | 629.90 |

Witkamp's subsystems consisted only of an L layer whereas the subsystem in this study consists of all the organic matter above the mineral soil (L and F layer, there was essentially no H layer in this stand).

I can only guess at the magnitude of this effect in the stand in this study but a conservative guess might be that less than 20 percent by weight of the litter is accounted for by transport out of the subsystem. This figure would suggest that $M_y$ would be approximately 1.4 - 1.8. That $M_y$ has to be at least more than 1 is dictated by the observation in the field that Holodiscus discolor and Acer circinatum litter was always visible as a component of the litter subsystem even just prior to the fall leaf drop. The average $M_y$ for the forest stand in this study was approximately 2.0.

These $M_y$'s are, of course, assuming that all components of the litter decompose at a similar average rate over this time span. This is probably unrealistic as differential decomposition rates for various parts of the same species as well as between species have been noted by many researchers (Kucera, 1959; Witkamp, 1963; Minderman, 1968). However as indicated by field observation they are not likely to decompose much faster (as a close inspection of Figures 3-12 also supports). A longer time span, as Minderman (1968) discusses as a possible significant role for minor (by weight) components of the litter subsystem, would decrease the error.

These $M_y$ values are of interest in themselves and can be compared to existing estimates for other forests which range from one or less for some deciduous forests particularly tropical, to one plus years for temperate deciduous forests, to 3 to 5 years for coniferous forests in Great Britain (Ovington, 1962). The most reliable data are probably those based on disappearance of litter from litter bags (see for example Bobcock and Gilbert, 1957). These methods, however, represent only part of the litter subsystem (the L) so direct comparisons are hazardous. However, they do suggest that Pseudotsuga menziesii forests as compared to many temperature coniferous forests have a very short turnover time.

One could speculate that this high rate is a function of the angiosperms in the understory. They have long been suspected as playing such a role in mixed forests although at least one study (Thomas, 1968) does not support this contention. The high turnover rate could be a function of Pseudotsuga menziesii litter and/or a function of the western Oregon climate, and/or the soil either through affecting nutrient content of litter or transport out of the system (leaching) or even aeration (for example degree of waterlogging). The chemical effect would not even have to be either a nutritional or inhibitory effect, as McColl (1969) suggests that pH plays a large role in degree of transport of some substances in the litter-soil subsystem

through cation transport. These speculations await more definitive studies for their answers.

$F_1$ can be estimated by using Abee and Lavender's (1972) data for the mean annual litter fall from the understory expressed as a fraction of the total. $F_1$ then would be approximately 6 percent. Contingent upon these assumptions and estimated quantities, and keeping in mind the possibilities of the nonlinearity of some of the relationships, an E for the Holodiscus discolor type would be calculated as follows:

$$E = (1/1.5)(0.06)(0.5 - 0.8)$$

$$E = 0.012$$

A similar error would be estimated for Acer circinatum and indicates that the July measurements may underestimate the average annual weight of the subsystem by as much as 1.2 percent. Increasing the normalizing litter weights by this factor would decrease the normalized litter respirations (Table 5) for Holodiscus discolor and Acer circinatum to 124.3 and 122.9, respectively.

This decreases the difference between Gaultheria shallon and Acer circinatum although the difference would still be significant at 0.05 as tested by Scheffé's Test. This difference could be small enough to be nonsignificant if the spring bias in Gaultheria shallon leaf-drop is large enough (it would have to be about 50 percent of the total assuming that there is no decomposition before next fall of

these leaves). However lacking any way to estimate it with reasonable confidence this is very conjectural. It is also possible that the understory litter contribution for this stand is larger than 6 percent, say 12 or even 15 percent. If so, this would change the relationship, and the difference between the Acer circinatum type and Gaultheria shallon type might not be real.

Three things can be strongly inferred about the hierarchy shown in Table 5 in terms of this possible seasonal bias in the normalization. This first is the probable E's would not significantly alter the hierarchal position for Polystichum munitum, Castanopsis chrysophylla and Tsuga heterophylla types relative to each other or the other types, nor the relative hierarchal position of the Holodiscus discolor and Acer circinatum types to each other. Second, unless the understory contribution to the litter subsystem is substantially larger than is suspected, the hierarchal position of Gaultheria shallon and Holodiscus discolor would not be changed although the difference may be less than is shown in Table 5. Third, the difference between Gaultheria shallon and Acer circinatum may be more apparent than real and could be an artifact of differential seasonal leaf-drops by type.

## Reliability and Utility of Mean Weight of Litter Determinations

The litter weight determinations (Table 10) also could be biased as an estimate of mean annual weight of the litter subsystem. These

measurements were made in early December and the weights shown for Holodiscus discolor and Acer circinatum could be slightly higher than the means by type, while the means shown for the other types, particularly Polystichum munitum may be slightly too low. Since the errors due to this are likely much smaller than those due to the sampling size (estimated at ± 10 percent, see methodology section), these are probably unimportant to the study.

There are three published studies that give litter weight data for more or less comparable Pseudotsuga menziesii forests. Youngberg (1966), in a study of 9 forest floor types in Pseudotsuga menziesii forests in the Coast Range of Oregon, measured the weight of the litter subsystem and found the following relationships:

| Type | | $g/m^2$ |
|---|---|---|
| Holodiscus discolor - Gaultheria shallon | - | 2230 |
| Acer circinatum | - | 2290 |
| Gaultheria shallon | - | 2710 |
| Polystichum munitum (wide range depending upon associates) | - | 2780 - 8000 |

Since Youngberg's sampling technique was different, his topographic range undefined, and his sampling not restricted to as narrow a classification scheme for his types as I exercised in this study (for example avoidance of downed logs, non-inclusion of live procumbent vegetation, avoidance of immediate vicinity of tree boles)

these numbers are not directly comparable to Table 10. However, it is interesting to note that the order of the hierarchy exhibited in Table 10 is in agreement with Youngberg's results and the relative differences are suggestive of what my study found. If one assumes that overstory litter contribution is not strongly correlated with the distribution of these understory species in these forests, which field observations and the data in Table 3 infer, then given the differential rates of litter respiration per type such a hierarchy of weights would be expected.

Cole, Gessel, and Dice (1968) give the mean dry weight of the litter of a Pseudotsuga menziesii forest in Washington at 2,277 $g/m^2$. These figures include 777 $g/m^2$ of large branches and logs (which were avoided in my study) so 1500 $g/m^2$ is a better figure for comparison with Table 10. Grier and McColl (1971) estimate the litter subsystem for the same forest studied by Cole et al. to be 1, 430 $g/m^2$.

The difference between these published values and the 956 $g/m^2$ for the stand in this study could just reflect the differences in forest. These forest differences could be due to site, topography, age of stand and/or the difference in the time of measurement (season or year). The mean weight differences could also be primarily a function of the differences in sampling methods utilized. Whether these method differences and/or a favorable year for litter subsystem respiration (it was wetter than average) and/or lower litter fall account

for the difference between my data and these others I do not have enough information to determine. It does suggest that the $M_y$ values may not be a good estimate of the typical values for Pseudotsuga menziesii forests and may be too low. Dimock (1958) indicates that weather can be a big factor in litter fall, indicating that the 10 month needle fall for a Pseudotsuga menziesii forest in Washington following a severe cold spell was nearly three times as large as that of previous years. Thus, considerable variability can occur. If one were to assume that the figures in Table 10 are low, then by a similar percent the estimates for annual yields in Tables 9, 11, and 13 are also low.

Inference that this would not be the result of an error in the mean litter weights comes from a consideration of Table 11. Comparison of measured litter respiration with the estimated litter respiration in Table 11 reveals that all the estimates are substantially higher (an average of 34 percent). This would indicate that the normalizing weights used are greatly underestimating the mean annual average and/or the Table 10 weights taken in December are overestimates. If we assume that the overstory contribution is relatively constant throughout the year, this difference should not exist except as a function of the 2-3 months accumulation during the dry period, which would make fall season weights heavier than spring season weights. The difference in sample sizes between the

normalizing weight measurements and the December mean weight measurements would not be expected to yield such a consistent and large difference.

Evidence that litter falls are not consistent comes from the observations of increased litter fall during windy storms, expecially in the wet season. Abee and Lavender (1972) report that the vast majority of litter fell during the winter and spring due to snow breaking branches, however they also note that needle-cast appeared greatest in the fall. No snow occurred before my weight measurements, so this bias would not seem in the right direction to explain Table 11, but it might be a factor in the relatively lower subsystem weights I found, compared to the published data discussed previously.

Both of Abee and Lavender's conclusions are not necessarily a factor in Table 11's results, since their samples included all debris and, as noted elsewhere, mine did not. Thus, my data would be expected to be biased towards needle cast. Bray and Gorham (1964) state that Pseudotsuga menziesii forests show no definite seasonal variations in litter drop, apparently based mainly on Dimock's (1958) study of a variety of young Pseudotsuga menziesii stands.

The first storm of the litter respiration season to bring down large quantities of litter did occur just prior to the December sampling, but there were more storms after the sampling and based on observation the first storm did not appear to yield exceptionally large

quantities of litter relative to the later storms. Thus, it could be a factor of some significance, but it is probably not a 34 percent one, nor would it seem that the slight fall needle-cast bias would account for an appreciable part of the 34 percent either.

If we assume that the aforementioned factors are not the major source, there remains what could be called a summer induced bias. For 2-3 months or 17-20 percent maximum of the year (the dry summer), litter falls without decomposing and thus, the end of a litter respiration season would be expected to be the lowest point of the year for the subsystem's weight. Reducing the 17-20 percent by $1/M_y$ to account for what would be expected to be left at the end of the litter respiration season, yields a 10-13 percent maximum difference.

Since only approximately 30 percent of the litter respiration season (as a function of total respiration, not time) had passed by the time of the December litter weight measurements and 50 percent is the ideal mean point for sampling, 20 percent of the 10-13 percent maximum difference could be expected to act as a bias on the December measurements. Thus the December measurements could be 2-3 percent too large due to the summer bias. In the summer by a similar reasoning there would be a minus 50 percent difference resulting in 5-6 percent underestimate for the normalizing weights. Both the summer bias and the winter bias would increase the respiration estimates, so we can account for perhaps as much as 20-30 percent of the

error (i. e. of the 34 percent). Thus, a maximum of less than one-third of the difference could be attributed to the summer effect. If the summer dry period for 1971 was short (based on rainfall records I expect it was less than 2 months) this would account for even less of the differences.

Whether the other 24-plus percent difference is mostly due to the normalization weights or the mean weights is of major importance in assessing the confidence in the annual estimates and in the $M_y$ values. An increase in the normalizing weights would decrease the annual yield and increase $M_y$ (for respiration method) and a decrease in mean weights would decrease the annual yield and for the estimated litter input method also lower the $M_y$ values. Since the litter subsystem never came close to disappearing in the field, it would appear that the $M_y$ values cannot go down much and the error would seem most likely to be in the normalization weights. The annual yield may be as much as 34 percent too high with the normalizing weights low by 31 plus percent. This, of course, assumes the reality of applying Abee and Lavender's annual litter fall data as input in this stand for calculation of $M_y$. It might not be.

One final observation can be considered. The normalization weights came from the litter subsystem enclosed by a cylinder of 15.65 cm in diameter. A bias entered into the placement of these cylinders in that they were positioned to avoid cutting large live roots

and enclosing stems of live members of the vegetation types (herbs and live procumbent vegetation were just gently removed). In reflecting upon this, it appeared that in doing this the sample weights would not include much representation of the litter subsystem immediately near the stems of the understory vegetation nor in areas of densest concentration of these stems. However, the cylinders used to sample the litter subsystem to determine mean weights were 3.5 cm in diameter and because of this small size and lack of need to avoid cutting roots, these samples included measurements near stems, fallen branches and small logs, all of which are areas under-represented in the normalizing weight samples due to the use of the larger cylinders. This difference could be considerable as it can readily be observed that the stems and the larger litter materials act both as channels and as traps to catch and hold litter causing deeper depths of litter in their vicinity. This would suggest that the December mean weights are likely a more realistic measure of the mean weight of the subsystem and that the sample areas used for respiration measurements, which also yield the normalization weights, are biased in the direction of underestimating the total mean weight of litter in the entire subsystem.

If this is true and this is the source of most of the error (24 plus percent) this error would be more apparent than real. Assuming that litter depth is not a significant factor in determining a realistic per

gram rate of respiration which the high F values (Appendix) for rates of respiration would infer is true, especially in view of the varied weights of the samples used to represent the subsystem (Table 2), then the per gram respiration rates and the annual rates are not in significant errors and the estimated values in Table 11 are a good measure of the annual rate per type.

As I discussed in the introduction to this thesis, Macfadyen (1970) and others (see Froment, 1972) maintain that the static sampling of $CO_2$ by the inverted box method probably underestimates the actual rates of $CO_2$ evolution. In addition, Macfadyen (1970) also suggests that enclosure of the litter-soil subsystem causes build up of $CO_2$ in the subsystem which may affect the activity of the heterotrophs, possibly inhibiting their respiration. Thus, it could be the December weights are in error and are inflating the annual yield estimates, and if it is, the error in estimation of weight could be mostly compensated by existing methodology-related errors. Froment (1972) cites Haber (1959) as recommending increasing the measured yields by 25 percent to compensate for suspected underestimates caused by methodology. However, due to the varied methodologies employed it is difficult to ascertain the reality of the 25 percent as an error estimate and its applicability to this study. Thus, whether or not underestimation of true rates of respiration is a factor remains quite speculative. If,

however, the errors are compensating it would suggest that the annual yields given in Table 9 are good estimates of annual rates of respiration for this forest.

It is interesting to note that a similar argument could be employed to explain why the litter subsystem might give better estimates of the fate of all the organic matter entering the litter subsystem than does the litter-soil subsystem. The litter subsystem could give better estimates even though export of some of the organic matter to the soil subsystem from the litter subsystem does occur. The assumption previously made was that most of the organic matter entering the litter subsystem is decomposed there and only a minor fraction is exported to the soil subsystem. Thus this subsystem is a better measure than the litter-soil subsystem with its confounding factors of respiration related to the activity and turnover rates of the roots and possible lateral gas exchanges. However, neither the magnitude of the export of organic matter from the litter subsystem nor the inhibition effect of the static method is well established and it could be the methodology causes stimulation of respiration in the litter subsystem and is masking a larger export of organic matter. In other words the apparent agreement (see pages 125-126) between inflow of litter and outflow of $CO_2$ for the litter subsystem could just be a matter of compensating errors.

Support of a very tentative fashion for the conclusion that the differences in Table 11 are more apparent than real and that the estimated values are realistic, comes from examining the litter moisture data. These are biased toward the immediate vicinity of the samples of the subsystem used for respiration measurements and constitute a much smaller sample than was made for the mean weight determinations. However, taken as a rough estimate of the mean litter weights based on 8 separate days in the fall, 4 in the wet period, and 11 in the spring (see Figures 46-47), they indicate that substantial differences within a type for the litter weight by season do not occur. In addition, a mean value calculated from these numbers is in closer agreement with the December values than the summer weights (Appendix).

These are very simplistic linear assumptions for what are probably mainly complex relationships in time and in space and a number of unquantified observations are included. Thus, these estimates as an absolute error can hold little credibility. However, they do serve to point to the probable errors and to a rough idea of the magnitudes involved.

Based upon the data available and the most likely sources of error it appears most probable that the differences seen in Table 11 do not mean that the annual rates and normalized rates are in a 30-34 percent error, but that the summer bias may have caused as much as

5-9 percent overestimate in the annual respiration rate yields and a 5-7 percent overestimate of the respiration rates per unit weight of litter. However the possibility that the overestimate could be as great as 30-34 percent cannot be completely discounted with the data available.

Pseudotsuga menziesii forests appear to be low in weight for their litter subsystem when compared to many other forests. Mader and Lull (1968) for example, report 4,000 $g/m^2$ under Pinus strobus in Massachusetts; Brown (1966) reports 3,300 $g/m^2$ under Pinus resinosa and 2,300 $g/m^2$ under Pinus banksiana in Minnesota; and Van Cleve and Noonan (1971) report 4,052 $g/m^2$ and 4,200 $g/m^2$ for Betula papyrifera and Populus tremuloides respectively in Alaska. Even taking into account the different definitions of the subsystems, these figures, with the exception of Pinus banksiana, are much higher than those found for the Pseudotsuga menziesii forests studied This lends further credibility to the reality of the high turnover rates for Pseudotsuga menziesii forests and to the credibility of the data in this study. It is especially interesting if one views Abee and Lavender's (1972) annual litter fall data in the perspective of the data in Bray and Gorham's 1964 paper as it indicates that Pseudotsuga menziesii forests are above average in litter fall compared to other cool temperate coniferous forests.

These two facts, low relative weights of the litter subsystem and above average litter fall, would predict relatively high annual rates of respiration and quick turnover for organic matter. This is not necessarily entirely due to the forest type. It may be due more to a favorable climate for decomposers and/or edaphic conditions for transport by leaching.

## Reliability and Utility of Accumulative Annual Respiration Estimate

One of the objectives of this study was to generate an annual estimate of accumulative rate of respiration of the litter subsystem of a Pseudotsuga menziesii forest for comparison to other forest types. Only two studies exist which give extensive enough data for meaningful comparisons. These are Witkamp's (1966a) study which was based on biweekly measurements in oak, pine and maple forests in Tennessee and Reiners' (1968) study of the forest floors of three Minnesota forests.

Witkamp (1966a) used the inverted box method with static absorption of KOH and found 1,520 g $CO_2/m^2$/year. However, his measurements were for the litter-soil subsystem and based on his estimates of input data (litter fall) his rates are about twice as much as would be expected if the forests were in equilibrium. He attributes this apparent overestimation to carbon dioxide drawn from the soil reservoir, perhaps enhanced by diffusion of $CO_2$ along temperature

gradients, by changes in barometric pressure, and/or by replacement of soil air by moisture. Presumably, as he notes in his later study (Witkamp, 1969), root respiration also was a factor.

Reiners (1968) found even higher accumulative rates of 2, 592 to 3, 912 g $CO_2/m^2$/year. He utilized a continuous gas flow system inside a metal enclosure and based on his input estimates he believes his respiration figures to be three times too large. He used the litter-soil subsystem and attributes the apparent overestimation to root respiration. In addition, unlike the 2.5 cm depths used by Witkamp and myself he used metal sleeves which penetrated 20 cm into the soil. This was to curb lateral movement of carbon dioxide into the enclosure from outside the sample area and to control root respiration by severing major roots. As he notes this may have just substituted green manuring by the recently-killed roots for the root respiration. He also mentions possible error due to methodology relative to rates of air flow used.

My study yielded an annual accumulative rate estimate of 671 g $CO_2/m^2$/year. If we use Abee and Lavender's (1972) 570 grams litter input/$m^2$/year as a rough estimate of input for litter to this litter subsystem and convert it to grams of carbon basis using the 45 percent figure that Reiners and Witkamp utilized for carbon content of litter, this becomes 256 grams carbon/$m^2$/year. The 671 g $CO_2/m^2$/year converted to carbon is 185 g/$m^2$/year which is fairly

good agreement. The difference between input and output supports Macfadyen's (see page 120) contention that the static method underestimates respiration rate.

I believe the reason my figures are closer to what appears to be the equilibrium between input to and removal from the litter subsystem of the detritus than the previous studies were, was due to a combination of three main factors. First, the 24-hour sampling schedule controlled the 24-hour diurnal fluctuations that Witkamp (1969) showed could be quite large. Both Reiners and Witkamp's annual studies were based on shorter sampling periods, Reiners for various short periods between 0900 and 1700 hours, and Witkamp for 1-hour runs. In addition, I sampled in 126 separate 24-hour periods, Witkamp in 25 separate 24-hour periods, and Reiners in 41 separate 24-hour periods. Second, the use of the litter subsystem as a distinct and separate unit avoids the problem of root respiration and soil flushes and diffusion into the sample area of carbon dioxide generated outside the sample area. Third, the normalization procedure allowed me to expand the representativeness of my small sample (24) to a larger area, using the easier to get mean weight measurements. Reiners had only 6 samples in each of his 3 communities, although his sample covered larger areas (1000 $cm^2$ for Reiners compared to 192 $cm^2$ for mine). Witkamp used 5 samples located 30 cm apart and with an area of 177 $cm^2$ each.

The relative closeness of the data is, of course, contingent upon the appropriateness of Abee and Lavender's (1972) data for estimating the litter input in my stand. Their data are for a different stand and year (1970-1971) and as discussed earlier in this paper considerable variation may occur from year to year. Confounding this is the fact that if the turnover time is longer than a year the litter weight measurements are a function of that longer period of time rather than of one year. Thus the previously noted reasonably close agreement of the turnover times calculated based on respiration rate with that based on litter input may be just due to chance and the turnover times be in considerable error. As Froment (1972) and others have noted, the static method is believed to underestimate by as much as 25 percent although methodologies vary so much, as do the underestimate estimates, that this appears to be still an undefined point. In any case it can be said that relative to previously existing estimates the approach used in this study appears to result in a good estimate of cumulative annual respiration.

These results also suggest that the transport of materials to the soil from the litter subsystem is much less than that converted to carbon dioxide in the litter subsystem. Further support for the usefulness of recognition of two distinct subsystems in the litter-soil subsystem can be seen in Figure 15. Using the litter-soil subsystem as an estimate would apparently overestimate the annual rate of

respiration that is due to decomposition of organic matter in the litter-soil, by a factor of about two. It is interesting to note that this is in general agreement with Witkamp's (1966a) observation concerning his own data.

In addition, without the separation into separate subsystems the ability of the normalization procedure to quantify the differences between types would be diluted. Figures 13-45 illustrate this as the differences between subsystems can be seen. Thus, to demonstrate differences in rates relative to some factor(s) affecting decomposition rates with a comparable degree of confidence you would need a larger sample if the litter-soil subsystem is used in place of the litter subsystem.

## Reliability and Utility of the Rates of Respiration of the Soil and the Litter-Soil Subsystems

It should not be assumed that all of the similarity between the litter subsystems and the soil or litter-soil subsystems necessarily reflects the decomposition of organic matter under similar conditions. Some of the similarity is probably due to a common response to temperature changes which would be expected to be the most common universal factor determining rates of respiration, particularly during the wet season when the frequent rains probably act as the major agent for temperature change in the subsystems. Witkamp (1969), for

example, reports a 0.92 correlation for litter temperature and subsystem respiration (static method). However, this does not mean only decomposition, as respiration of the trees and presumably their roots (directly or through the effect of the canopy on the roots) is also strongly correlated with temperature (Woodwell and Whittaker, 1968).

The apparent differences between the soil and the litter subsystems, particularly in March, as seen in Figures 13-45, are of even greater interest than the similarities. The soil and litter subsystems appear at times to be responding to different factors or to the same factors differently (Figures 16-45). The most probable answer for this would seem to be root respiration, perhaps in March relating to a spring increase in activity of the understory, and/or the overstory. Such seasonal changes in plant respiration have been noted by others (Lieth, 1970). Additional inference that root related respiration is a significant factor comes from the magnitude of the rate of respiration of the soil subsystem. It is comparable to the litter subsystem (Figure 13). Unless we assume that approximately one half the organic matter of the litter subsystems is transported to the soil subsystem, something else has to be producing the carbon dioxide observed. As was discussed earlier it seems unlikely that the transport is this high.

Attempts to estimate the biomass of forest roots are much less common than those for the above-ground parts of the plants (Bray, 1963; Monk, 1966; Duvigneaud and Denaeyer-De Smet, 1970; Heller,

1971; Meyer and Göttsche, 1971). Even less common are studies which estimate the contribution of the roots to the organic matter available for decomposition in the soil subsystem. While some success has come from attempts to determine turnover rates in grassland roots (Dahlman and Kucera, 1965; Sator and Bommer, 1971), attempts to gain useful annual estimates of productivity and turnover of roots in forest soils have not been very successful (Head, 1970). Thus, a considerable portion of the soil respiration could be due to decomposition of organic matter if the rate of turnover and the biomass of the roots is high, but at the present these are largely unknown quantities for forests.

However, because of some serious doubts as to the reality of the absolute magnitude of the rates of respiration of the soil as measured, it is hazardous to immediately assume the methodology for sampling soil respiration used in this study represents a good way to study root respiration, even if one could account for the likely input of decomposable detritus to the soil subsystem. These doubts are based mainly on field observations indicating methodology weaknesses.

To avoid cutting live roots and causing a problem with green manuring, the cylinders were seated only 2.5 cm into the soil. This was successful in avoiding cutting any large roots. However, the soil in this forest is quite stony and porous and the cylinders never seemed to "seat" tightly into the soil. This could be felt when the container

tops were sealed and unsealed. This was predominately a vertical movement. In addition, at the termination of the experiment, the cylinders were removed and it was observed that most had what appeared to be small tunnels (less than 1 mm diameter) around and under the bottom rim of the cylinder. These may have been caused by small invertebrates possibly attracted to the surface of the cylinder. These conditions could contribute to importing of $CO_2$ by diffusion from surrounding areas and, thus, the soil respiration would be an overestimate. How large a bias this would cause I do not know, but I suspect it might be quite large. As mentioned previously, Witkamp (1966a) suspected soil moisture changes causing soil flushes of $CO_2$. If it rained heavily (and it often did in this study) when the container tops were sealed for respiration measurements, this could force $CO_2$ "flushing" into the cylinders from the areas outside. The litter-soil subsystem measurements would probably be affected by the same conditions as similar observations in looseness of the containers were noticed. The litter subsystem, being completely sealed off from the surrounding litter and soil surfaces during measurements, would not have such problems, which is another advantage of measuring the isolated subsystem.

The major reason for inclusion of the soil and the litter-soil subsystem measurements in this study was to test if the isolation of the litter subsystems was the cause somehow of the observed

differential rates (rather than some direct effect of the understory types). Figures 14-45 show that while magnitude differences existed, comparison of the litter-soil with the litter plus soil rates per type indicate a general agreement with no bias toward type as a result of the handling and removal method used for sampling the litter subsystem. The differences in magnitude, based on the arguments given previously for soil respiration, I would expect was due mainly to enhanced diffusion into the isolated soil subsystem as opposed to less diffusion in the soil of the litter-soil subsystem. But the reality of this assumption is not testable here and the possibility remains that the litter subsystem rates are overestimates causing all or some of the 7-8 percent observed differences between the litter-soil subsystem and the litter plus soil subsystem. Presumably, this would be due to some effect of handling and/or different conditions (higher mean temperature and/or lower mean $CO_2$) in the containers used to measure respiration of the litter subsystem which the other subsystems were not exposed to. Also, being in a container with a bottom for approximately 42 percent of the litter respiration season might result in significantly less transport to the soil subsystem as compared to the other subsystems. If this latter is true then the normalization procedure might be expected to compensate for that effect. In any case the conditions of this study do not permit resolution of this possibility.

## Reliability and Utility of the Percent *Pseudotsuga menziesii* Needles

The data in Table 3 represent the results of an attempt to provide information to directly test the assumption that the production of overstory litter is not biased as to type of understory in a way that would suggest that the observed respiration differences are due to the presence of certain understory vegetation types being correlated with the amount of litter the overstory produces per type. Indirect support was given by the inverse relationship between litter weight by type and respiration rate by type as seen in Figure 2.

The percent *Pseudotsuga menziesii* needles by understory types supports the contention that the overstory litter contribution, while showing significant differences between types, was not biased in a direction that would explain all the normalized respiration differences between types. The difference between the highest and the lowest was about 20 percent and it is tempting to speculate on a possible role for this; however, caution should be exercised in viewing these numbers as absolute values for two reasons.

According to Abee and Lavender's (1972) data we would expect the needles to make up only about 50 percent of the total litter fall. The rest is wood, reproductive structures, and understory litter. This is, of course, assuming linearity of decomposition for different types of

litter materials, which is an unreal assumption. On surface area alone needles would be expected to decompose the fastest. Thus the percent needles could be lower for the entire subsystem than input would predict. Second of that approximately 50 percent, only those needles that were recognizable and separate from the rest of the materials composed the measured percentages. In practice, most of the needles separated came from the L layer, the F layer being mostly "fused" together. In terms of the 50 percent figure, Table 3 thus represents only 50 to 60 percent of the needles that were probably present.

These could be important factors, as the confidence I felt in separation of needles as a measure of overstory input varied depending upon the understory type they were associated with. For example, in the four broad-leaved understory types (Holodiscus discolor, Acer circinatum, Gaultheria shallon, and Castanopsis chrysophylla) it was harder to separate needles from the other materials and it appeared that many were lost due to tight adherence to the angiosperm leaves, particularly when "sandwiched" between them. This appeared to be most severe for the more "tender" Acer circinatum and Holodiscus discolor leaves than the tougher Gaultheria shallon and Castanopsis chrysophylla leaves.

Thus, the differences in percentage could be more apparent than real and/or in significantly different order. One can speculate on the most probable direction of change based upon the observations

of degree of difficulty in separation. These observations would indicate that relative to the Tsuga heterophylla and Polystichum munitum, Holodiscus discolor and Acer circinatum should be increased the most with Gaultheria shallon and Castanopsis chrysophylla also increased, but to a lesser degree. Analyzed this way, the data yield support for the idea that the differences by type may not be significant or at least are of smaller magnitude than Table 3 indicates. In connection with this it is interesting to note that Tsuga heterophylla which appeared the easiest to separate and which, if overstory input is not biased to type of understory, should have the highest percent needles, did not. This would suggest that perhaps Gaultheria shallon did receive a little more input from the overstory than did the other types (Table 3).

This is, of course, complicated by area as the information given in Table 8 indicates, because for some of the species the sample areas are much smaller and thus influenced by fewer trees. Presumably, their variation would be expected to be less, but their potential for error larger. As analyzed, the statistical approaches used do not account for this.

In summary it appears that there is some real doubt as to the reality of the differences between some types in percent Pseudotsuga menziesii needles being as large as measured. In any case, the existing differences were too small and in the wrong directions to

explain much of the differential rates of litter respiration by types as shown in Table 5.

## Reliability and Utility of the Moisture Results

The moisture data in Figures 46-47 reveal large differences between the Tsuga heterophylla and Polystichum munitum types and the other four types. These two are drier in the fall season and wetter in the wet and early spring seasons. Moisture has been speculated to be a possible factor in accumulation of litter in Pseudotsuga menziesii forests (Youngberg, 1966), although he attributes this to less frequent burning in wet areas than to differential rates of respiration. To explain the observed rates of respiration differences (or at least some of them) it would presumably be a lack of moisture (limiting heterotrophic activity) for these two types in the fall and excess of moisture (causing aeration problems) in the wet season. If this is true then some other factor is operating to limit Castanopsis chrysophylla respiration, and to cause the differences in rates of respiration in Tsuga heterophylla and Polystichum munitum (Table 6).

Reiners (1968) and Witkamp (1966a) both show a correlation with moisture levels and respiration rate, however these correlations were weaker than the temperature correlations and also strongly coupled to the temperature correlations, so it is difficult to assign

magnitudes. Daubenmire and Prusso (1963) in a series of microcosm studies, including some with Pseudotsuga menziesii forest materials, cite Mork's (1938) work indicating that for similar temperatures the moisture content differences, for the levels I observed, would not be significant. It is hard to assess the significance of these findings, in terms of my study, because they were for laboratory microcosms in which the litter subsystem was subjected to a great deal of modification of its physical structure.

Alexander (1961) maintains that no soil is ever sufficiently aerated to maintain maximal microbial activity, that is, oxygen is always limiting. Thus, the added effect of area occupied by water should make moisture percentage have an effect. Presumably 20 percent of the space occupied by water would otherwise be taken up by oxygen assuming no change in space in the subsystem with moisture changes. However, the litter does visibly swell with the addition of water and contract with drying. This occurs mainly to the litter with less than 100 percent moisture, so as Figures 46-47 indicate this would only be a factor in early fall and late spring. The water could actually have an effect greater than its volume indicates, if it is attracted preferentially to the surface, thus creating a barrier slowing down gas exchange in the very places the microorganisms are most likely to be active (Brock, 1966).

Thus, as can be seen, the problem gets extremely complex. It would seem that to answer this question you would need to know to what degree, at various levels and temperatures, oxygen is limiting and be able either to measure directly the oxygen levels available in the subsystem to the microorganisms, or be able to demonstrate an effect unconfounded by other factors. Unfortunately, because of the extreme heterogeneity of the subsystems these are going to be very difficult experiments.

Conceivably, due to its greater porosity and closer vicinity to the oxygen reservoir of the surface atmosphere, the litter subsystem is not significantly affected under the range of moisture conditions observed in this study, or at least not enough to explain most of the differences in rates of respiration observed. This too may have been a factor in the differences between the litter-soil and litter plus soil subsystems with the greater exposure to the surface air of the litter and the soil subsystems when measured separately than were the litter and soil in the litter-soil subsystem, causing an increased rate of respiration over that which normally occurs under forest floor conditions. If so, it is a 7-8 percent combined effect at most and would indicate that aeration is not a big enough factor to account for the differences in rates of respiration observed.

Figures 46-47 do indicate a direct moisture effect in that litter types did dry and rewet at differential rates, presumably a function

of understory, and/or overstory canopy differences. For instance it was easy to observe that certain species were drier to stand under than others due to differential interception and channeling of precipitation. A close look at Figures 3-12 as well as 16-45 indicate an apparent differential effect on rate of respiration according to type. It appears that this occurs only when moisture drops below about 100 percent (of dry weight) and in relation to the magnitude of the observed difference in rates of respiration between types this is not a very significant effect.

## Reliability and Utility of the Temperature Results

While in some forests, litter and soil temperatures may be correlated with understory vegetation type as a function of temperature or temperature and moisture, no such correlations were observed in this forest. I suspect that the prevalent cloud cover and frequent rains during most of the litter respiration season (note that during the wet season almost all the clear days occurred during cold periods when snow covered the areas and no samples were taken).inhibited the development of temperature differences in the litter subsystem by type. However, even during the sunny periods at the beginning and end of the respiration season significant temperature differences by type were not observed, although since all temperatures were taken in the morning it may be that the lack of differences were

due more to equilibrium attained overnight than to lack of differences during the day. If this is true then the sampling schedule used in this study for gathering temperature data was a poor choice. The litter is probably a good insulator (Old, 1969) though and the measurements were at or near the soil surface so for any reasonable $Q_{10}$ (2.5-3.0 from Witkamp, 1969) that would explain much of the differences found, I would expect the temperature differences to show up and that a very strong bias would be exhibited in the compartmentalized data (Table 6) and it was not. Thus I think it probable that temperature was not significant in causing the differential rates of respiration by type (Figures 3-15).

## Conclusions

In conclusion, it can be said that the major objectives of the study were realized. The existence of significant differences which were relatively large except for those between Holodiscus discolor, Acer circinatum, and Gaultheria shallon and were mostly attributable to the type of understory species associated with the litter subsystem was demonstrated and quantified. The litter subsystem was shown to be a meaningful and useful subsystem of the forest ecosystem. Relatively large moisture differences were found associated with two of the vegetation types, which may be a factor in their rates of respiration but it appears more probable that moisture was not the major

cause of the differences between observed rates of respiration. Temperature did not appear to be a significant factor in the difference of rates of respiration between types. The annual respiration yields as a probable result of the specific methodology used appear to yield more reasonable estimates for rates of decomposition of organic matter in a forest floor than the major previous studies.

# SUMMARY

1. Six understory vegetation types (Holodiscus discolor, Acer circinatum, Gaultheria shallon, Tsuga heterophylla, Castanopsis chrysophylla, and Polystichum munitum were delimited for a study of their relationship to rates of respiration on the floor of a Pseudotsuga menziesii forest and four sample spots established for each type.
2. One hundred and twenty-six, 24-hour rates of respiration measurements at each sample spot were made for the litter, soil,and litter-soil subsystems of a Pseudotsuga menziesii forest during the litter respiration season 1971-1972. An adaption of the inverted box static method for $CO_2$ determinations was used.
3. Mean weights, periodic moisture levels, and periodic soil and air temperatures for the litter subsystem of each vegetation type were measured.
4. Mean percent Pseudotsuga menziesii needles per oven-dry weight of the litter subsystems were determined by manual separation of litter subsystem components.
5. Significant differences ($F_{0.05}$) were observed for litter subsystem rates of respiration, normalized by weight, between types by season and by area. No bias to types of overstory litter production, moisture, temperature or technique was found of

of sufficient magnitude to probably account for more than a minor fraction of the observed differences in rates of respiration.

6. An inverse relationship exists between litter weight and rate of respiration of the litter subsystem by vegetation types.

7. Comparison of litter subsystem and soil subsystem rates of respiration indicate that they are distinct systems possessing characteristics which make their separation a meaningful and useful division of this forest ecosystem.

8. Comparison of litter-soil subsystem rates of respiration with the litter plus soil subsystem rates of respiration support the contention that the litter rates of respiration are not an artifact caused by methodology.

9. Both the soil and litter-soil subsystem results are suspect as absolute values for some undetermined percentage, possibly quite large, due to methodology limitations. The general trends and relationships between types are nonetheless probably real. The litter rates of respiration as absolute values are also suspect, probably to a lesser degree, due to a variety of methodology problems, none of which probably significantly affect the relationship between types.

10. The annual estimate of litter respiration has numerous possible sources of error inherent in the methodology used, however it

appears to represent an improvement over values achieved for other forests. The results indicate that Pseudotsuga menziesii forests compared to other temperate coniferous forests appear to have a rapid turnover rate for organic matter entering the litter subsystem.[2]

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[2] A complete set on punch cards of the individual measurements made in this study is on file in the General Science Department at Oregon State University.

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# APPENDIX

Normalized Litter Respiration: Two-Way
Analysis of Covariance

Factors: A = Vegetation type; B = Area
Variables: Mean temperature and normalized litter respiration

F Values: A = 239.0; B = 17.3

| Source | DF | SS | MS |
|---|---|---|---|
| Error | 2987 | 24.44 | 0.0082 |
| Factor A + Error | 2992 | 34.24 | 0.0114 |
| Factor B + Error | 2990 | 24.87 | 0.0083 |
| Interaction + Error | 3002 | 25.88 | 0.0086 |
| Regression on Error | 1 | 42.52 | 42.5275 |
| Factor A Adjusted for Average Error Regression | 5 | 9.79 | 1.9591 |
| Factor B Adjusted for Average Error Regression | 3 | 0.42 | 0.1431 |
| Interaction Adjusted for Average Error Regression | 15 | 1.43 | 0.0958 |

Litter Respiration: Two-Way Analysis of Covariance

Factors: A = Vegetation type; B = Area
Variables: Mean temperature and litter respiration

F Values: A = 19.6; B = 40.2

| Source | DF | SS | MS |
|---|---|---|---|
| Error | 2987 | 491726.04 | 164.6220 |
| Factor A + Error | 2992 | 507845.11 | 169.7343 |
| Interaction + Error | 3002 | 615241.03 | 204.9437 |
| Regression on Error | 1 | 934389.22 | 934389.2290 |
| Factor A Adjusted for Average Error Regression | 5 | 16119.07 | 3223.8143 |
| Factor B Adjusted for Average Error Regression | 3 | 19834.90 | 6611.6337 |
| Interaction Adjusted for Average Error Regression | 15 | 123514.99 | 8234.3328 |

Soil Respiration: Two-Way Analysis of Covariance

Factors: A = Vegetation type; B = Area
Variables: Mean temperature and soil respiration

F Values: A = 41.8; B = 23.1

| Source | DF | SS | MS |
|---|---|---|---|
| Error | 3014 | 603760.93 | 200.3188 |
| Factor A + Error | 3019 | 645590.54 | 213.8425 |
| Factor B + Error | 3017 | 617564.62 | 204.6949 |
| Interaction + Error | 3029 | 696881.26 | 230.0697 |
| Regression on Error | 1 | 743407.13 | 743407.1335 |
| Factor A Adjusted for Average Error Regression | 5 | 41829.61 | 8365.9225 |
| Factor B Adjusted for Average Error Regression | 3 | 13803.68 | 4601.2292 |
| Interaction Adjusted for Average Error Regression | 15 | 93120.32 | 6208.0219 |

Litter-Soil Respiration: Two-Way
Analysis of Covariance

Factors: A = Vegetation type; B = Area
Variables: Mean temperature and Litter-Soil respiration

F Values: A = 34.6; B = 41.5

| Source | DF | SS | MS |
|---|---|---|---|
| Error | 2971 | 1493412.24 | 502.6632 |
| Factor A + Error | 2976 | 1580176.26 | 530.9732 |
| Factor B + Error | 2974 | 1555950.61 | 523.1845 |
| Interaction + Error | 2986 | 1794857.84 | 601.0910 |
| Regression on Error | 1 | 3044539.54 | 3044539.5427 |
| Factor A Adjusted for Average Error Regression | 5 | 86764.01 | 17352.8033 |
| Factor B Adjusted for Average Error Regression | 3 | 62538.35 | 20846.1191 |
| Interaction Adjusted for Average Error Regression | 15 | 301445.59 | 20096.3728 |

Litter Plus Soil Respiration: Two-Way
Analysis of Covariance

Factors: A = Vegetation type; B = Area
Variables: Mean temperature and litter plus soil respiration

F Values: A = 36.2; B = 36.7

| Source | DF | SS | MS |
|---|---|---|---|
| Error | 2977 | 1643135.55 | 551.9434 |
| Factor A + Error | 2982 | 1742925.60 | 584.4821 |
| Factor B + Error | 2980 | 1704078.43 | 571.8384 |
| Interaction + Error | 2992 | 1973952.80 | 659.7436 |
| Regression on Error | 1 | 3286664.25 | 3286664.2507 |
| Factor A Adjusted for Average Error Regression | 5 | 99790.05 | 19958.0113 |
| Factor B Adjusted for Average Error Regression | 3 | 60942.88 | 20314.2947 |
| Interaction Adjusted for Average Error Regression | 15 | 330817.25 | 22054.4838 |

Normalized Litter Respiration Compartmentalized Into Three Seasons: Three-Way Analysis of Covariance

Factors: A = Vegetation type; B = Area; C = Season Fall, Wet, Spring
Variables: Mean temperature; normalized litter respiration

F Values: A X C = 50; B X C = 4.6

| Source | DS | SS | MS |
|---|---|---|---|
| Error | 2938 | 14.69 | .0050 |
| Factor A + Error | 2943 | 24.52 | .0083 |
| Factor B + Error | 2941 | 15.12 | .0051 |
| Factor C + Error | 2940 | 21.16 | .0072 |
| Regression on Error | 1 | 6.75 | 6.7581 |
| A Adjusted for Average Error Regression | 5 | 9.82 | 1.9655 |
| B Adjusted for Average Error Regression | 3 | 0.43 | 0.1433 |
| C Adjusted for Average Error Regression | 2 | 6.47 | 3.2362 |
| A X C Adjusted for Average Error Regression | 10 | 2.50 | 0.2508 |
| B X C Adjusted for Average Error Regression | 6 | 0.13 | 0.0229 |

Litter Weight: Two-Way Analysis of Variance

Factors: A = Vegetation type; B = Area
Variables: Normalized litter respiration; litter weight

F Values: A = 312.5; B = 1.4

| Source | DF | SS | MS |
|---|---|---|---|
| Factor A | 5 | 10425.00 | 2085.0133 |
| Factor B | 3 | 27.94 | 9.3153 |
| Interaction | 15 | 71.80 | 4.7867 |
| Error | 1176 | 7865.98 | 6.6888 |
| Total | 1199 | 18390.79 | --- |

Percent Douglas-Fir Needles: Two-Way
Analysis of Variance

Factors: A = Vegetation type; B = Area
Variables: Normalized litter respiration; percent Douglas-fir needles

F Values: A = 30.3; B = 0.9

| Source | DF | SS | MS |
|---|---|---|---|
| Factor A | 5 | 1239.91 | 247.9829 |
| Factor B | 3 | 22.88 | 7.6278 |
| Interaction | 15 | 118.56 | 7.9041 |
| Error | 216 | 1764.50 | 8.1690 |
| Total | 239 | 3145.85 | --- |

Litter Moisture: Two-Way Analysis of Variance

Factors: A = Vegetation type; B = Area
Variables: Normalized litter respiration; percent litter moisture

F Values: A = 3.40; B = 0.58

| Source | DF | | |
|---|---|---|---|
| Factor A | 5 | 6.37 | 1.2759 |
| Factor B | 3 | 6.48 | 2.1608 |
| Interaction | 15 | 5.99 | 3.9969 |
| Error | 1560 | 5.84 | 3.7457 |
| Total | 1583 | 5.97 | --- |

Litter weights estimated from moisture data (grams/$m^2$)

| Date | Type | | | | | |
|---|---|---|---|---|---|---|
| | H. discolor | A. circinatum | G. shallon | T. heterophylla | C. chrysophylla | P. munitum |
| Sep. 1, 1971 | 688 | 717 | 954 | 1102 | 1328 | 1576 |
| " 8 " | 638 | 730 | 1099 | 1129 | 1279 | 1615 |
| " " " | 724 | 817 | 985 | 1138 | 1561 | 1689 |
| " 18 " | 705 | 746 | 925 | 1128 | 1229 | 1591 |
| " 25 " | 699 | 774 | 917 | 1067 | 1316 | 1574 |
| Oct 2 " | 626 | 789 | 1140 | 1075 | 1342 | 1439 |
| " 16 " | 712 | 778 | 817 | 1078 | 1410 | 1582 |
| " 21 " | 750 | 771 | 973 | 1094 | 1450 | 1588 |
| " 28 " | 673 | 921 | 871 | 1046 | 1319 | 1774 |
| Nov 15 " | 752 | 840 | 864 | 1116 | 1301 | 1580 |
| Apr 25, 1972 | 711 | 695 | 873 | 979 | 1262 | 1511 |
| May 1 " | 680 | 696 | 761 | 969 | 1251 | 1470 |
| " 7 " | 634 | 784 | 856 | 1002 | 1335 | 1512 |
| " 14 " | 794 | 799 | 791 | 990 | 1220 | 1510 |
| " 20 " | 731 | 700 | 800 | 994 | 1219 | 1427 |
| " 27 " | 642 | 777 | 856 | 896 | 1123 | 1398 |
| June 3 " | 611 | 867 | 795 | 964 | 1091 | 1439 |
| " 10 " | 583 | 723 | 833 | 1056 | 1094 | 1211 |
| " 17 " | 715 | 732 | 832 | 908 | 1058 | 1296 |
| " 22 " | 650 | 664 | 755 | 933 | 1012 | 1459 |
| " 27 " | 730 | 772 | 814 | 994 | 1146 | 1631 |
| July 3 " | 736 | 649 | 873 | 1021 | 1296 | 1400 |
| Means | 690 | 760 | 886 | 1021 | 1263 | 1519 |