INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

U·M·I

University Microfilms International
A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
313/761-4700 800/521-0600

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Order Number 9419755

Latitudinal gradients in leaf litter decomposition in streams: Effects of leaf chemistry and temperature

Irons, John Gillam, III, Ph.D.

University of Alaska Fairbanks, 1993

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

LATITUDINAL GRADIENTS IN LEAF LITTER DECOMPOSITION IN STREAMS: EFFECTS OF LEAF CHEMISTRY AND TEMPERATURE

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

by

John G. Irons III, B.A., M.Sc.

Fairbanks, Alaska

December 1993

LATITUDINAL GRADIENTS IN LEAF LITTER DECOMPOSITION IN STREAMS: EFFECTS OF LEAF CHEMISTRY AND TEMPERATURE

by

John Gillam Irons III

RECOMMENDED:

Advisory Committee Chair

Department Head, Biology and Wildlife

APPROVED:

Dean, College of Natural Sciences

Dean of the Graduate School

December 7, 1993

Date

ABSTRACT

Autumnal leaf litter that falls into streams of forested regions forms a major source of energy for stream food webs. The processing of this litter has been studied for many years, and two generalizations have come from this research: 1) nitrogen concentration is positively correlated with breakdown rate, and 2) temperature is negatively correlated with breakdown rate. Along with investigators in Michigan and Costa Rica, I examined these generalizations by estimating breakdown rates of litter of ten tree species with widely varying nutritional quality along the latitudinal gradient of Costa Rica to Michigan to Alaska. At each site, litter processing experiments were done using leaves of the same ten tree species and the same methods in streams with similar character. We found that condensed tannin, a plant defense against herbivory, was more highly correlated (negatively) with breakdown rates than was nitrogen (positively correlated with breakdown), and 2) breakdown rate showed a complex response to water temperature (i.e., latitude). I propose a model of leaf litter breakdown in which the microbial contribution to litter breakdown is negatively correlated with latitude (i.e., temperature) and the invertebrate contribution to litter breakdown is positively correlated with latitude. In addition, I suggest that secondary compounds of low solubility, especially condensed tannin, should be considered along with nitrogen when evaluating a tree species for leaf litter quality.

TABLE OF CONTENTS

LATITUDINAL PATTERNS IN LEAF LITTER DECOMPOSITION:

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGMENTS

I thank the Institute of Arctic Biology and the Institute of Northern Forestry for logistical and financial assistance and the Chena Hot Springs Resort for access to the Monument Creek study site. I thank my advisory committee, Drs. J.P. Bryant, T.P. Clausen, P. Quang, and K. Van Cleve, and especially my committee chair, Dr. M.W. Oswood. My mother, Mrs. Gene Irons, and my sister, Kerry Irons, assisted in leaf litter collection. Other acknowledgments regarding specific aspects of the study are included in the relevant manuscripts.

OVERVIEW

Many studies in stream ecology have addressed the fate of leaves that fall into streams, and a considerable literature has accumulated (see manuscript I for literature review). Among the ideas currently held by stream ecologists about the controls of leaf litter decomposition are: 1) leaf litter processing is a three-stage process involving leaching, microbial degradation, and invertebrate ingestion, 2) different leaf species are processed at different rates, and 3) processing rates increase with increasing temperature. Studies of rates of leaf litter breakdown have generally been done at a given location (often in temperate regions) without regard to biogeographic patterns of microbial and invertebrate decomposers. Although nitrogen concentration in leaves has long been known to have a positive influence on decomposition rates, most previous studies have not considered the role that other physical or chemical characteristics of the leaf material might play in controlling the rates of leaf disappearance in streams. Furthermore, these physical and chemical characteristics are not static in time or space, either among tree species or among individuals of a single tree species. The evolutionary history and the relative "apparency" have influenced plant defenses against herbivores by altering the quality of their leaves as food. In addition, many plants have the ability to respond individualistically in ecological time through phenotypic changes in defenses in response to herbivory.

These variations in leaf quality (especially secondary metabolites with low solubility in water like condensed tannin) often affect the quality of leaf detritus to stream food webs.

This project was a collaborative study on latitudinal patterns in the decomposition of leaves of varying quality. The study was carried out simultaneously by five teams of investigators in five locations in North and Central America. In this dissertation, I present four manuscripts as separate sections. In the first, following an introduction and literature review, I include results and preliminary discussion of the Alaskan data. The next three sections are comprised of the three major papers documenting the results of a multi-investigator study of chemical and thermal controls on leaf litter decomposition in streams. Due to the nature of cross-site studies, there are several authors on these papers. The first paper (chapter II) documents the effects of leaf litter chemistry on mass loss rates of leaf litter, and although Dr. R.J. Stout is the first author, I had a major role in performing chemical analyses, conducting the Alaskan portion of the study, and writing an early version of the manuscript. In chapter III, I present the results of phenological analyses done only on the Alaskan samples, and in chapter IV, I discuss the role that temperature plays in leaf litter breakdown rates along a latitudinal gradient. Finally, in the conclusion section I construct a verbal model of the effects of leaf chemistry, invertebrate feeding, and temperature on the dynamics of leaf litter processing in streams. The appendix archives the raw data from the Alaskan portion of the study.

LEAF LITTER CHEMISTRY, MASS LOSS, AND MACROINVERTEBRATE COMMUNITY DYNAMICS DURING DECOMPOSITION OF NATIVE AND EXOTIC TREE SPECIES IN AN ALASKAN BOREAL FOREST STREAM

John G. Irons III[1,2]

---

[1] Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775-0180, USA.

[2] Institute of Northern Forestry, USDA Forest Service, 308 Tanana Drive, Fairbanks, AK, 99775-5500

INTRODUCTION

A major source of energy for stream communities of forested regions is leaf litter that falls from riparian trees in autumn (Cummins 1973, Minshall 1978). After reaching the stream, leaves undergo transformations that affect their quality as food for stream shredders. These changes include leaching of soluble substances from the leaves and colonization of the leaves by bacteria and fungi. Shredder insects then consume microbially colonized leaf detritus. Leaf characteristics (physical and chemical), microbial conditioning (species composition, abundance, and length of time), the shredder community (species composition and abundance) and the many interactions of these factors determine the rate at which leaves are processed in streams. These are discussed in more detail below.

LEACHING

Leaching is the first process by which mass is lost from leaves following entry into streams (Petersen and Cummins 1974, Triska and others 1975). Soluble compounds (e.g. low molecular weight carbohydrates, amino acids, hydrolyzable tannins) are readily leached within the first few days by running water (Suberkropp and others 1976): average 24 hour weight loss to leaching from leaves of many tree species is approximately 15% (Petersen and Cummins 1974), with some species over 20% (Petersen and Cummins 1974, Triska and Sedell 1976). However, some soluble sugars may remain in leaves (especially in poplar leaves) for substantially longer

(Chauvet 1987). Leaf leachate, which contributes to the dissolved organic carbon (DOC) pool, can be used directly by epilithic microbial communities in streams (Cummins and others 1972, Dahm 1981, Lush and Hynes 1978, Wetzel and Manny 1972). Although most of the mass loss attributable to leaching of red alder leaves occurrs in the first 48 hours, water color (generally thought to be caused by humic acids) increases linearly for 600 hours, suggesting that larger compounds are leached to the stream in small quantities over longer periods of time (Taylor and Adams 1986). In boreal streams, large molecular weight compounds (e.g. humic acids, tannins) seem to inhibit the ability of the microbes to use low molecular weight compounds ($<$1000 daltons), and contribute substantially to the epilithic metabolism (Ford and Lock 1987). Air-drying, oven-drying, or freezing may artificially increase leaching rates in some species (Bärlocher 1992, Chergui and Pattée 1992, Gessner 1991, Gessner and Schwoerbel 1989). In an earlier study in interior Alaska, birch, alder and willow leafpacks made from dried leaves lost about 15-20% of their original mass in 24 hours (Cowan and others 1983), and alder, birch, willow, and balsam poplar leaves all showed substantial reductions in condensed tannin (proanthocyanidin) concentrations following 24 hour leaching in the laboratory (J.G. Irons and J.P. Bryant, unpubl. data).

MICROBIAL COLONIZATION

Following a time lag (ca. one month), microbial colonization of the leaf surfaces occurs (Bärlocher and Kendrick 1975, Petersen and Cummins 1974), a process called conditioning. The rate of colonization and resulting microbial community composition depends on the species of riparian trees (Kaushik and Hynes 1971, Petersen and Cummins 1974, Suberkropp and Klug 1976). Bacterial and fungal (primarily aquatic hyphomycetes (Suberkropp and Klug 1976)) communities develop, and leaf nutrients (both concentration and absolute amount) increase (Bärlocher 1985, Iversen 1973). At peak fungal biomass, Gessner and Schwoerbel (1991) found that 9.2% of the alder leafpack-fungus complex was fungal biomass. It is currently believed that stream shredders obtain more of their nutrition from the microbial community than from the leaf tissue itself (Anderson and Sedell 1979, Cummins 1973, Cummins and Klug 1979, Kaushik and Hynes 1971, Petersen and Cummins 1974, Triska and others 1975). It appears that microbes (at least aquatic fungi) perform two major roles in the breakdown of leaf litter: 1) microbial production creates easily digested microbial biomass for shredder consumption, and 2) enzymes secreted by microbes break down indigestible leaf tissue into digestible subunits that may be used for microbial or shredder growth, a process known as conditioning (Bärlocher and Kendrick 1973).

Microbially colonized leaves show an increase in nitrogen and phosphorus concentrations within the first month of conditioning that has been attributed to the microbial community (Chauvet 1987, Iversen 1973, Kaushik and Hynes 1968, 1971, Mathews and Kowalczewski 1969, Meyer 1980, Triska and Buckley 1978, Triska and

Sedell 1976, Triska and others 1975). Much of the increased nitrogen is not contained in microbial biomass (Iversen 1973, Lawson and others 1984), but may be due to complexes of exogenous nitrogen and leaf polyphenols (Bärlocher and Kendrick 1975, Melillo and others 1984, Suberkropp and others 1976), or to the microbial secretions (exoenzymes) themselves (Iversen 1973).

SHREDDER DYNAMICS

Shredding macroinvertebrates have been identified as major contributors to the overall process of wood and leaf litter break-down in streams of forested regions (Anderson and others 1978, Barnes and others 1986, Benfield and Webster 1985, Cowan and Oswood 1984, Cowan and others 1983, Iversen 1975, Kaushik and Hynes 1971, Petersen and Cummins 1974, Sedell and others 1975, Triska and others 1975). However, other studies done in different habitats or at times other than autumn have shown no statistical correlation between shredder abundance and processing rates (Benfield and others 1977 (pasture), Mathews and Kowalczewski 1969 (large river), McArthur and others 1986 (summer), Meyer 1980 (1 mm mesh bags, which may exclude larger shredders), Reice 1978, Smith 1986 (tall-grass prairie), Tate and Gurtz 1986 (tall-grass prairie)). Most of these studies either excluded shredders, or were done in streams or rivers that had little of no shredder community as potential colonizers. Thus, shredders appear to have a large influence on the breakdown of riparian leaf litter (Anderson and Sedell 1979, Webster and Benfield 1986).

Microbial colonization is generally associated with increased shredder preference (Bärlocher and Kendrick 1973, Golladay and others 1983, Iversen 1975). Shredder consumption rates on alder leaves were stable (and low) for three weeks after inoculation, then began to increase (Anderson and Grafius 1975). Ingestion rates of a stonefly shredder were higher on conditioned leaves than on unconditioned leaves (Golladay and others 1983). Palatability to shredders varied with the species of aquatic hyphomycetes present; however, there was no correlation of consumption with nitrogen compounds, ATP, or enzymatic activity (Arsuffi and Suberkropp 1984, Suberkropp and others 1983). Not only are different species of fungi differentially preferred by shredders, but the shredders can discriminate between adjacent patches of different fungal species (Arsuffi and Suberkropp 1985). The spatial heterogeneity of leaves (e.g. the number of leaves of different tree species in close proximity) seems to increase the species diversity of the aquatic hyphomycetes that colonize them (Rossi and others 1983).

Shredders use leaf microbiota more efficiently than they do freshly shed leaves: assimilation efficiency for fungal mycelia ranged from 65-70%, compared to only 20% for uncolonized leaves (Bärlocher 1985). Conditioned leaves are assimilated better or more quickly (Bärlocher 1982, Golladay and others 1983, Grafius and Anderson 1979), invertebrate survival is better (Kostalos and Seymour 1976, Sutcliffe and others 1981, Willoughby and Sutcliffe 1976) and shredder growth rates are often higher (Anderson and Grafius 1975, Bärlocher and Kendrick 1973, Otto 1974) on leaves that have been conditioned in stream water. Alder leaves conditioned in the laboratory proved nutritionally inadequate for rearing *Clistoronia magnifica* (Trichoptera: Limnephilidae), when compared to diets of field-conditioned leaves and laboratory-conditioned leaves supplemented with enchytraeid worms or wheat (Anderson, N.H. and Cummins 1979). *Tipula abdominalis* (Diptera: Tipulidae) grow better on leaves inoculated with both fungi and bacteria than on leaves inoculated with only one species of fungi, and grow best on leaves of intermediate decompositional state (optimal conditioning) (Lawson and others 1984).

LEAF LITTER QUALITY

Microbes and shredders of stream ecosystems encounter a spectrum of leaf litter quality. Nitrogen (and presumably protein) concentrations in leaves of different tree species may differ. In addition to these variations in foliar nutrient concentrations, many plants have evolved chemical defenses (secondary compounds) against herbivory (e.g. Harborne 1988). Plant chemical defensive compounds having low solubility in water and which are not translocated out of leaves at abscision may be part of the suite of chemical characteristics faced by colonizing microbial and invertebrate decomposers. In this paper, I discuss condensed tannins, ubiquitous secondary compounds in woody plants, as a group of typical plant defensive compounds.

It has long been known that leaves of various tree species are differentially preferred by stream shredders (Benfield and Webster 1985, Cummins and Klug 1979, Irons and others 1988, Iversen 1974, Kaushik and Hynes 1971, Petersen and Cummins 1974, Vannote and Sweeney 1985). This effect may be partially due to differences among tree species in microbial conditioning (Iversen 1974), because different species of leaves are colonized by different species of fungi, and at different rates (Suberkropp and Klug 1976). However, it may also be due in part to the intrinsic chemistry of the leaves, either due to the positive influence of higher nutrient concentrations or the negative influence of secondary compounds (Irons and others 1988, Triska and others 1975). There is some evidence that foliar tannins can inhibit fungal invasion of living leaf tissue (Zucker 1983). In marine systems, phenolic compounds have been shown to inhibit decomposition both directly (by influencing microbes) and indirectly (by inhibiting grazers that eat microbes) (Harrison 1982). Thus, differing rates of microbial colonization and growth may be attributable in part to the concentration of secondary metabolites in the leaf litter. Irons and others (1988) showed that shredder preference for leaves of four species of trees was positively correlated with nitrogen concentration and negatively correlated with tannin concentration.

Although few stream ecologists have explicitly looked at the influence of condensed tannin on decomposition rates, inferences can be drawn by examining the literature of plant chemistry as well as that of litter processing in streams (Stout 1989). Alder (*Alnus* spp.) is a symbiotic nitrogen fixer, usually high in foliar nitrogen and low in foliar tannin concentrations (Chapin and Kedrowski 1983), is often the species with the highest processing (Chauvet 1987) and shredder growth rates, and is usually preferred over other species (Anderson and Grafius 1975, Irons and others 1988, Iversen 1974, Otto 1974, Petersen and Cummins 1974, Wallace and others 1970). Fresh summer alder leaves have higher nutrient concentrations (McArthur and others 1986), are processed faster and seem to be preferred over autumn shed alder leaves (Stout and Taft 1985, Stout and others 1985). Other species, high in tannins and low in foliar nitrogen (e.g. oak (*Quercus* spp.) and beech (*Fagus* spp.)) have decreased processing and shredder growth rates, and are less preferred by shredders (Iversen 1974, Kaushik and Hynes 1971, Mathews and Kowalczewski 1969). With respect to red alder, vine maple, bigleaf maple, and douglas fir, Triska and others (1975) found a positive correlation between the acid detergent cell wall fraction (soluble carbohydrates, soluble protein, organic acids, etc.) and processing rates, while they found negative correlations between processing rates and lignin, cellulose, and ash. Due to a high negative correlation between tannin and nitrogen levels, preferences for nitrogen or avoidance of tannin by microbes or shredders are not easily separated (Irons and others 1988).

Shredder growth rates are faster on diets of some leaf species than on others (Anderson and Cummins 1979, Anderson and Grafius 1975, Anderson and Sedell 1979, Iversen 1974, Otto 1974). *Tipula abdominalis* grows most rapidly on the species which it prefers (Vannote and Sweeney 1985). Although growth rates of *T.*

abdominalis are similar on basswood and hickory leaves, the efficiency of conversion of food to insect biomass on basswood leaves is twice that on hickory leaves (Anderson and Cummins 1979). *Potamophylax cingulatus* grows better in the laboratory on alder leaves than on beech leaves, while larvae growing in the stream show intermediate growth rates (Otto 1974).

Thus, it is apparent that high quality leaf litter that is high in nitrogen and low in tannin concentrations is processed rapidly, while low quality litter is processed more slowly. A continuum of fast-, medium-, and slow-rate leaves are necessary to sustain a population of shredders (Golladay and others 1983). This would provide a continuous supply of food through the insect life histories, rather than a sudden pulse of high quality food followed by famine, and would allow completion of the life cycles and maintenance of stable populations (Cummins and others 1989). Evidence from a pasture stream suggests that streams without this type of continuum in leaf processing rates have depauperate shredder communities (Benfield and others 1977).

In this paper, I describe foliar chemistry, mass loss patterns, and macroinvertebrate colonization dynamics during leaf litter decomposition in a subarctic Alaskan stream. The leaf species were chosen to represent a wide array of foliar chemistry (especially condensed tannin concentration) in order to provide leaf detritus of varying food quality to stream shredders. One group of species (mostly exotic species) was used to compare litter processing rates across gradients in litter chemistry and latitude (i.e. temperature) (chapter II, chapter IV), and the other group was used to determine the processing rates and macroinvertebrate community structure dynamics for a range of native Alaskan tree and shrub species (this chapter). Arsuffi and Suberkropp (1985) suggested that "fungal patchiness should be included as the primary level in the hierarchical arrangement of shredder resource heterogeneity." While recognizing that this is an important and poorly studied factor, I suggest that the chemical make-up of autumn-shed leaves, strongly influenced by the tree's history, affects both the ability of microbes to colonize leaf litter and the palatability of the litter to shredders, thus influencing overall rates of litter decomposition.

STUDY SITE

Monument Creek, a second order tributary of the Chena River approximately 115 km from Fairbanks (fig. I-1), was the site of the stream decomposition portion of this project. Monument Creek has a catchment area of approximately 74 km^2, rises at about 850 m above sea level, and the study site is about 14 km downstream from the source at an elevation of 380 m at 65°N latitude and 146°W longitude. Riparian vegetation includes willow (*Salix* spp.), alder (*Alnus crispa*), balsam poplar (*Populus balsamifera*), with occasional white spruce (*Picea glauca*) and black spruce (*P. mariana*). Monument Creek is the site of many previous studies (Anderson 1984, Buttimore and others 1984, Cowan 1983, Cowan and Oswood 1983, 1984, Cowan and others 1983, Howe 1981, Irons 1985, 1988, Irons and others 1989, Sonnichson 1982), which provide baseline and ancillary data. The nearby Chena Hot Springs

Resort offers outstanding logistical advantages, especially for winter sampling.

Streamwater and air temperatures were recorded continuously at Monument Creek between 7 October 1986 and 26 June 1989 on an Omnidata Easylogger (a flood in late June of 1989 damaged the datalogger and ended the temperature record). Water temperatures were recorded in mid-channel at the streambed surface and at depths of 10, 20, and 50 cm; streambed surface temperatures were used in these analyses. Details of the placement and calibration of the thermocouples were reported in Irons and others (1989). Thermocouples were scanned every 30 minutes, averaged for two hour intervals by the datalogger, and recorded onto a solid state chip. Thus, the record for each day consisted of 12 readings, each of which was the mean of four scans. From these data, daily means, minima, and maxima were calculated. Accumulated degree-days above 0°C were calculated by summing the daily means for each day of the 75 day study period.

METHODS

SPECIES AND SOURCES OF LEAVES

Leaves were obtained from a variety of regions in North and Central America, including tropical (Costa Rica), subtropical (North Carolina), temperate (New York and Michigan), and subarctic (Alaska) (table 1). Of two species selected from each region, one species was chosen to be high in condensed tannin and one species chosen to be low in condensed tannin as a measure of leaf litter quality (hereafter referred to as "high tannin" and "low tannin" species). These categories were based on the knowledge of the investigators, data from the literature, and in the case of Alaska, personal communications with J.P. Bryant, University of Alaska. Leaves from each location were sent to all other locations, and parallel decomposition studies were done on a latitudinal cline from Costa Rica to Fairbanks, Alaska. Only the Alaskan data are reported here.

At most sites, leaves were collected at abscision; however, due to early leaf-fall, leaves of the two Alaskan species were collected in winter from trees which had not lost their leaves the previous autumn. These were generally stump sprouts along unimproved roads that did not receive any salt or other road de-icer during the winter. Leaves from all sites were dried at 50°C after collection, then frozen at -25°C to reduce potential microbial contaminants. Although microbes in interior Alaska routinely face temperatures colder than this, I followed this protocol to be consistent with the other sites. Investigators at each of the above locations performed the same experiment in streams of similar depth, velocity, and water quality (see chapter II for more detailed description of sites and methods at the other locations).

In addition to the latitudinal comparisons, leaves of several other Alaskan tree species and treatments were included in this study. In order to obtain preliminary data on the effect of vertebrate (moose) browsing on foliar tannin and nitrogen, and hence on decomposition rates, we collected leaves from browsed and unbrowsed (by moose) stems of *Betula papyrifera* and *Salix alaxensis* and included them in our study. Because one investigator required a replacement batch of leaves of the Fairbanks species (*Alnus crispa* and *Salix alaxensis*), we collected senescent leaves from trees in autumn (September 1988) and included both sets in our study. Thus, we made browsed: unbrowsed comparisons for two tree species, and autumn-collected: winter-collected comparisons for two tree species (table 1).

Several additional Alaskan species were included in this study only: *Shepherdia canadensis*, *Ledum groenlandicum*, and *Salix pulcra* (table 1). All three species are common shrubs in interior Alaska and are known to be high in condensed tannin (J.P. Bryant, pers. comm.). Leaves were collected in September 1988. *Shepherdia canadensis* and *Salix pulcra* were collected at senescence, *Ledum groenlandicum* (an evergreen) leaves were green. Two species from Puerto Rico (*Sapium laurensce* and *Dacryodes excelsa*) were included in the studies at the other sites; however, I never received them and they were not included in this study.

PREPARATION OF LITTER BAGS AND LEAF PACKS

A coarse-meshed leaf litter bag technique was used to investigate processing rates in Monument Creek. Envelopes of 2 cm plastic mesh were constructed, each containing six pockets for the leaf packs. Each replicate consisted of three envelopes, for a total of 18 pockets. Species were randomly assigned to a location (i.e. pockets) in one of the three envelopes. The 25 replicates of each species were always placed in that location. Some of the Alaskan species (i.e. *Ledum*, *Shepherdia*, and *Salix* *pulcra*) have small leaves that do not lend themselves to litter bags with a 2 cm mesh: leafpacks of these species were placed in a second net bag (ca. 5 mm mesh) that was then placed inside the larger litter bags that went into the stream.

All leaves were oven dried at 50°C, then weighed into approximately 3 g leaf packs (range of approximately ±0.05 g, depending on the species). Leaves were placed into plastic Ziplock bags for storage until completion of the litter bags. When all leaves were weighed, they were hydrated by partially filling the bags with distilled, deionized water and sealing the top of the bag. Leaves were allowed to remain immersed in water until no longer brittle (approximately 20 minutes), at which time they were taken out of the plastic bags and put into their assigned pocket in the envelopes. Envelopes were stored in large plastic bags in a 1°C refrigerator until they were put into the stream.

PLACEMENT IN THE STREAM

Areas in the main current of Monument Creek were selected for moderate depths (30 to 50 cm) and velocities (approximately 0.3 m/s), and for the likelihood that they would remain unfrozen throughout the study period. Twenty five replicate sets of envelopes were fastened to the stream substrate with 2 cm hardwood dowels driven into the stream bottom. The trailing edges of the envelopes were weighted down with small rocks to prevent them from being lifted by the current. Envelopes were assigned random numbers, then placed in the stream starting with random number one at the upstream end of the site. Even numbers were placed with one species at the upstream end and odd numbers were placed with the same species at the downstream end to randomize any effect due to orientation.

For most species, five replicates were removed from the stream on each of five dates (with the exception of the last two dates, when one (day 56) and five (day 75) of fifteen envelopes were frozen in the ice. These dates were days 2, 14, 28, 56, and 75. Because *Trema* and *Acer* were known to disappear very rapidly at other locations (R.J. Stout, Michigan State University; C.R. Pringle, Cornell University; pers. comm.), these two species were collected on days 2, 7, 14, 28, and 56. Individual pockets were cut apart with scissors, and the net and remaining leaf material were placed into their original ziplock bag, and the bags placed into a cooler (to prevent freezing) for transport and storage back to the laboratory.

Plastic bags containing the leaf packs were stored in a 1°C cold room, and were processed as soon as feasible (maximum 3 d following removal from the stream). Packs were placed in enamel pans, and invertebrates and adhering organic and inorganic material was rinsed from leaves, the net, and the plastic bag with distilled, deionized water. Leaf packs were then oven dried at 50°C to constant weight, and invertebrates preserved in 80% ethanol for subsequent sorting, identifying, and enumeration. Following drying, leafpacks were weighed to the nearest 0.01 g. Leafpacks were then ground in a Wiley mill (mesh = 850μm) and 200 mg removed for chemical analysis (if more than 400 mg remained), while the remainder was combusted at 500°C for ash-free dry mass (AFDM) calculation. If less than 400 mg remained, all leaf material was used for AFDM estimation. Values that were more than two standard errors from the mean were considered outliers and were eliminated from statistical analyses (potential sources of error include loss of leaf material during handling, gain of organic material from drift, or laboratory error).

TANNIN ANALYSIS

Subsamples (74 - 76 mg) of each replicate were analyzed for tannin using the butanol-HCl reaction for proanthocyanidins described by Martin and Martin (1982) and modified by Bryant and others (1987), with quebracho tannin as a standard. Tannin concentration was determined colorimetrically on a Perkin-Elmer spectrophotometer at an absorbance wavelength of 550 nm. Data are reported as Quebracho equivalents (see Appendix). The calibration equation used to convert absorbance to Quebracho equivalents was determined empirically to be quadratic and was:

$$[TANNIN]=429.607\times(A_{550})-61.588\times(A_{550})^2 \quad r^2=0.999$$

where A_{550} is the absorbance at 550 nm and TANNIN is the amount of tannin in the sample in units of μg/0.3 ml (F ratio = 5513.383). The data were then converted to percent tannin in the remaining leaf material (by dry mass). Because condensed tannins found in different plant species, including Quebracho (a tropical shrub, the bark of which is high in tannin and often used as a standard), have different reactivities with this method (see below), the quebracho equivalent reported here should be used as a relative index, rather than as the true tannin concentration.

NUTRIENT ANALYSIS

Total Kjeldahl nitrogen and total phosphorus concentrations for two replicates collected on day 2 of stream processing were determined on a Technicon Autoanalyzer by a sulfuric/selenious acid digestion and colorimetric analysis with ferricyanide blue reaction for nitrogen and molybdate blue for phosphorus. These data were used as initial post-leaching values in latitudinal comparisons, as similar samples from Michigan were also analyzed by this technique at the same time. Subsequently, leaf packs removed from the stream after day 2 (those with enough remaining mass) were analyzed for total Kjeldahl nitrogen and phosphorus concentrations using a copper sulfate-hydrogen peroxide-sulfuric acid digestion, followed by colorimetric analyses on a Lachet Autoanalyzer.

MACROINVERTEBRATE ANALYSIS

Macroinvertebrates were sorted from detritus, identified to genus (species when possible), and enumerated using a Wild dissecting microscope. Chironomidae, however, were sorted only to family, although specimens representing the twelve most abundant morphologically distinct taxa were identified to genus. Estimates of relative proportions of the individual chironomid genera were made from ten randomly selected samples; however, individuals in each genus were not counted separately for all samples. Presence or absence of oligochaetes was noted: often these invertebrates were broken and could not be accurately counted. Keys used for insect identification were Edmunds and others (1976) for the mayflies (Ephemeroptera); Wiggins (1977) for the caddisflies (Trichoptera); Merritt and Cummins (1984), Oliver and others (1978), Simpson and Bode (1980), Bode (1983), and Wiederholm (1983) for true flies (Diptera); and Stewart and Stark 1988 for the stoneflies (Plecoptera).

Taxa were placed into functional feeding groups using published data from Cowan and others (1983), Howe (1981), and Irons (1988), and taxa not included in these works were assigned to functional groups using Merritt and Cummins (1984). Individuals of the representative chironomids were cleared in polyvinyl alcohol (BioQuip Co.), and gut contents were determined; although *Brillia* was present in Monument Creek and was ingesting coarse particulate organic matter (CPOM), it was a relatively small proportion of the chironomid fauna and all chironomids were classified as non-shredders.

Macroinvertebrate biomass was determined as ash-free dry mass (AFDM). Individuals were classified and sorted as shredders or non-shredders, and all members of each of these two categories were placed on a glass-fiber filter and dried to constant mass at 50°C (at least overnight), weighed, combusted at 500°C, and weighed again. Both total number and biomass (mg AFDM) of invertebrates were expressed on a per leafpack and a per gram of leaf tissue remaining basis.

RESULTS

I present the results of the thermal regime of Monument Creek and the foliar chemistry, mass loss, and macroinvertebrate community dynamics analyses for each species (and treatments within species) separately. Although presented as individual species, they are grouped into three categories. The first category includes the ten species, two from each of five locations, used in the latitudinal gradient analyses. The second group includes other species from Alaska that were included in the 1988 field season. These species were analyzed in several combinations, depending on the question posed. The third group consists of the two species, paper birch and feltleaf willow, that were used by Irons and others (1991) in a paper on the effects of moose browsing on birch leaf chemistry and hence decomposition rates in streams (willow data were not used in that analysis due to methodological problems). For each species I present a figure showing temporal patterns in foliar chemistry (condensed tannin, nitrogen, and phosphorus concentrations) and percent of leaf mass remaining after exposure of leaf material in the stream, and a second figure presenting the macroinvertebrate community dynamics through time. For some collection dates in the second and third groups, only shredders were sorted from the samples. I present estimates for non-shredders and total invertebrates graphically when available in the second group (to facilitate comparisons with leaf species in the first group), but only estimates of shredders for the third group. Regression equations are presented in the form $Y = b - (m*X)$ where X is the number of days of processing and Y is the percent AFDM remaining at time X: to convert to proportion remaining, divide the coefficients by 100.

THERMAL REGIME

Air temperature was below freezing during the entire period of the leaf litter breakdown study, 5 October - 19 December 1988 (fig. I-2), reaching a minimum daily mean of -34.0°C on 6 December 1988. The study began at the end of the summer season, and daily mean water temperature was initially 1.4°C on 5 October and fell to 0.25°C by 22 October. Water temperature remained at about 0.2°C throughout the remainder of the study; indeed, in the three years of data, 0.2°C was the normal temperature in winter when the streambed was not frozen. Monument Creek accumulated 912 degree-days above 0°C during the calendar year of 1988. During the decomposition study period, the stream accumulated 21.9 degree-days over the 75 day period. See Irons and Oswood (1992) for a detailed discussion of the thermal regime of Monument Creek.

SPECIES FROM COSTA RICA

Trema micrantha **(L.)**--The tree species from Costa Rica chosen to be low in tannin, *Trema micrantha*, was indeed low in tannin (fig. I-3). Tannin concentration was not different from 0.0% on any collection day. This species was initially very high in nitrogen concentration following 2 days and 7 days of exposure in the stream, followed by a sharp drop on day 14 to less that 1%. Nitrogen then increased until, on day 56, concentrations were about 3%. Phosphorus showed an initial increase between day 2 and day 7, and then declined to less than 0.1%. Unleached N and P values were unavailable. Mass loss in *Trema* was rapid: loss due to leaching for 48 hours was over 27%, and mass declined linearly after that (regression equation: $Y = 77.4 - (1.23*X)$). Estimated time for 50% mass loss was 23 days.

Macroinvertebrate numbers peaked on day 14 at about 230 per leafpack (fig. I-4), and stayed relatively constant subsequently; mean number of invertebrates was 135 (18% shredders and 82% non-shredders). Invertebrate biomass peaked on day 28 at about 30 mg per leafpack, declined on day 56, and was dominated by shredders (71% overall). When expressed on a per gram of leaf tissue remaining, density of invertebrates continued to rise as mass was lost from leafpacks, reaching about 1500 invertebrates per gram and 120 mg of invertebrates per gram of leaf tissue remaining on day 56.

Pithecellobium longifolium--The Costa Rican species thought to be high in tannin, *Pithecellobium longifolium*, had a post-leached condensed tannin concentration of about 11% (Quebracho equivalents) (fig. I-5). Tannin concentration gradually declined through time until, on day 75, concentration was 4%. Nitrogen concentration was initially 2.8% (post-leaching), increased to 4.6% on day 14, then gradually declined to 2.9% on day 75. Pre-leached values for tannin, N, and P concentrations were not available. Mass loss due to leaching was less than 4%, and mass loss due to other stream processes (e.g. microbial decomposition, invertebrate feeding) was slight (although statistically significant). There was a slight mass loss between days 14 and 28, but mass remained constant after day 28. The model which fit the mass loss data the best was a quadratic equation, but because linear regression was the best model overall, only that is reported here. The linear regression equation was $Y = 96.2 - (0.13*X)$, and the estimated time until 50% of the leaf material was gone was 462 days.

Macroinvertebrates, especially shredders, were rare on *Pithecellobium* leafpacks (fig. I-6): mean density of invertebrates was 113 (9% shredders, 91% non-shredders), while mean biomass was 6 mg per leafpack (53% shredders, 47% non-shredders). Because little mass was lost from leafpacks, mean density of invertebrates was only about 42 individuals and 2.3 mg per gram of leaf tissue remaining.

SPECIES FROM NORTH CAROLINA

***Cornus florida* L.**--Tannin concentrations in unleached flowering dogwood (*Cornus florida*) leaves were about 5.5%, declined to about 3% following leaching, then declined exponentially to very low levels (fig. I-7). Mean nitrogen concentration on a given sampling date remained relatively constant at the relatively low level of about 1.5% through the processing season, although there was high variability on day 56. Phosphorus concentration was low, with highest concentration of about 0.05% on day 2 and day 75. *Cornus* lost about 25% mass due to leaching, which was followed by little mass loss over the next 12 days. After day 14, mass was lost steadily (regression equation: Y = 75.6 - (0.66*X)). Estimated number of days until 50% of leaf mass was gone was 37 days. Like *Pithecellobium*, the mass loss curve for *Cornus* was best fit by a quadratic equation (based on F values); only linear regression coefficients are reported here (see below).

The number of macroinvertebrates per leafpack continued to increase through the study to a peak of about 550 (15% shredders, 85% non-shredders) on day 75 (fig. I-8), and the mean number per leafpack (263) was dominated by non-shredders (86%). Invertebrate biomass (mean = 19 mg), however, was dominated by shredders (63%), and peaked at 45 mg on day 56 rather than day 75. Both number and biomass per gram of leaf tissue remaining increased as mass was reduced, with non-shredders again dominating numbers and shredders dominating biomass.

***Quercus falcata* Michx.**--Tannin concentration in unleached southern red oak (*Q. falcata*) leaves was about 15% (Quebracho equivalents) (fig. I-9). Leaching dropped the concentration to about 12% over 48 hours, and concentration declined gradually to about 8.6% on day 75. Nitrogen concentration was low following leaching (about

1.6%) and declined gradually to about 1.0% on day 75. Phosphorus showed a slight rise between day 2 and day 14 to a peak of 0.1%, then declined to virtually negligible levels by day 75. Mass loss was slight, both due to leaching and other stream processes, with over 80% of the original mass remaining after 75 days in Monument Creek. The linear regression equation was Y = 89.4 - (0.08*X) and estimated time until 50% remaining was estimated at 394 days.

Macroinvertebrate numbers were low (mean of 158 per leafpack) and dominated by non-shredders (88%) (fig. I-10). Macroinvertebrate biomass was also low (mean of 7.2 mg), and although shredders were slightly more abundant than non-shredders (54%), this was much lower than for most other species. Compared with other species, numbers and biomass per gram of leaf tissue remaining was very low (61 individuals and 2.8 mg per gram).

SPECIES FROM NEW YORK

***Acer saccharum* Marshall**--Sugar maple (*Acer saccharum*) leaves were low in tannin following leaching (about 3%), and declined slightly through the study period to less than 2% (unleached tannin concentration could not be determined due to a shortage of leaf material) (fig. I-11). Nitrogen concentrations remained relatively constant at about 2.5% over the first 14 days, then decreased to about 1.7%. Phosphorus fluctuated around 1% through the study. For this species, day 75 was eliminated and day 7 was added because it was felt that decomposition rate would be so fast that there would be nothing left by the last day of sampling (R.J. Stout, Mich. State Univ., pers. comm.). However, several other species in Alaska actually lost more mass by day 56 (e.g. both *Alnus* species); at the temperate and tropical sites, mass loss rate for this species was much greater. Linear regression equation for mass loss was $Y = 83.7 - (0.90*X)$, and estimated time until 50% of the mass was remaining was 37 days.

Macroinvertebrate colonization of *Acer* leaves continued through the 56 day study period, reaching a peak of 782 per leafpack on day 56 (mean of 314, 13% of which were shredders), while biomass peaked at 65 mg (88% shredders) per leafpack (mean of 20 mg, 66% shredders). On a per gram of leaf tissue remaining, invertebrates peaked at 924 individuals and 75 mg per gram of leaf remaining (fig. I-12).

***Fagus grandifolia* Ehrh.**--American beech (*Fagus grandifolia*) had relatively high concentrations (about 11% quebracho equivalents) of condensed tannin in unleached leaves, which declined exponentially until on day 75 it was just over 2% (fig. I-13). Nitrogen concentration showed a strange pattern: from about 2% following leaching, it dropped sharply to less than 1% on day 14, then steadily increased to about 2.6% on day 75. Phosphorus concentration remained constant at less than 0.1% throughout the study. Mass loss due to leaching was about 10%, followed by very little loss until after day 56 (the high variability on day 75 was due to one leaf pack with a mass remaining of only 26%). Linear regression equation for mass loss through time was $Y = 92.3 - (0.32*X)$, and estimated time to 50% mass remaining was 141 days.

Numbers of invertebrates peaked on day 56 at 619 individuals per leafpack (14%) shredders, and mean number was 344 (11%) shredders (fig. I-14). Biomass also peaked on day 56 at 34 mg per leafpack (71% shredders), with a mean of 14.3 mg (53% shredders). On a per gram of leaf tissue remaining basis, number of individuals increased to a maximum of 314 (mean of 157) and biomass increased to 21.1 mg (mean of 7.2 mg) on day 75.

SPECIES FROM MICHIGAN

***Alnus rugosa* (Du Roi) Spreng.**--Tannin concentrations in tag alder (*Alnus rugosa*), the species from Michigan chosen to be low in tannin, were in the low to moderate range, starting at about 5% and declining exponentially to about 2% on day 28 (fig. I-15). On days 56 and 75, there was not enough leaf material left for either tannin or nitrogen analyses. Nitrogen declined from about 3 to 2.5%: alders are nitrogen-fixing plants and might be expected to be relatively high in N concentration. Phosphorus remained constant at just under 0.1% for the samples in which there was enough mass remaining for analysis. Mass loss due to leaching was about 20%, following by a 26 day period of little mass loss, then a substantial loss of mass by day 56, and virtually no remaining mass on day 75. Estimated time for 50% mass loss was 32 days, and the regression equation for mass loss was $Y = 91.6 - (1.27*X)$.

Macroinvertebrate numbers increased until day 28, when they reached a peak of 361 individuals per leafpack, while the mean density was 173 per leafpack (14% shredders) (fig. I-16). Biomass also peaked on day 28 at 28.6 mg per leafpack (87% shredders) and mean biomass was 173 mg per leafpack. Because the low amount of leaf biomass remaining on day 75 (0.6%) resulted in extremely high numbers and biomass of invertebrates per gram leaf tissue remaining, they are not shown in figure I-16. The estimated number and biomass including day 75 were 15,811 individuals (mean of 2343) and 2,199 mg (mean of 354 mg), while the estimates excluding day 75 were 669 individuals (mean of 239) and 34.7 mg (mean of 16.7 mg) per gram of leaf tissue remaining.

***Quercus rubra* L.**--Northern red oak (*Quercus rubra*), the species from Michigan chosen to be in the high tannin group, started with relatively high levels in unleached leaves, but then lost much of it due to leaching (fig. I-17). Following the leaching, tannin loss was exponential, with concentrations on day 75 less than 2%. Nitrogen showed a substantial increase, from about 2% (post-leaching) to about 3% on day 14, then concentrations remained essentially constant until day 75. Phosphorus remained constant at just over 0.1% throughout the study. This species showed very little mass loss due to leaching, less than 4%, then mass declined linearly to about 67% on day 75. The linear regression equation for mass loss was $Y = 97.8 - (0.44*X)$, and estimated time to 50% remaining was 119 days.

Macroinvertebrate numbers were relatively low, peaking at 353 on day 56, with a mean of 181 (15% shredders) (fig. I-18). Biomass of invertebrates peaked on day 75 at 41.8 mg, 91% of which was shredder biomass (mean of 15.5 mg): this biomass was made up primarily of a few large limnephilid caddisflies. On a per gram basis, both numbers and biomass were relatively low, peaking at 172 individuals (mean of 80) and 21 mg (mean of 7.3 mg) per gram of leaf tissue remaining.

SPECIES FROM ALASKA

***Alnus crispa* (Ait.) Pursh**--Temporal patterns in mass loss, chemistry, and macroinvertebrate abundance in leafpacks green alder (*Alnus crispa*), the Alaskan species chosen for the low tannin group (fig. I-19), were similar to those in tag alder (*Alnus rugosa*) from Michigan. Insufficient leaf material remained on days 56 and 75 for chemical analyses. Tannin concentrations were low, but more variable with time than in tag alder (the regression was not significant). Nitrogen was a bit lower on day 2 (2%), but increased to about 3% by day 14. Phosphorus showed a slight increase with time to about 0.12%. Mass loss also showed similar patterns to *A. rugosa*, with leaching loss about 23%, little mass loss early in the study period, a sharp drop between days 28 and 56, and virtually nothing left on day 75. Linear regression equation for mass loss was $Y = 86.9 - (1.22*X)$, and estimated time until 50% mass remaining was 31 days.

Macroinvertebrates showed a unimodal distribution, with peak numbers at 316 individuals on day 28 and a mean of 185, 19% of which were shredders (fig. I-20). Biomass peaked on day 56 at 31.7 mg per leafpack, and mean biomass was 16.2 mg per leafpack. Like tag alder, there was only about 0.6% AFDM remaining on day 75, making estimates of numbers and biomass per gram of leaf tissue remaining meaningless, and these estimates were not included in figure I-20. The overall means with including day 75 in the calculations (10658 individuals and 927 mg per gram of leaf material remaining on this collection date) were 2131 individuals and 927 mg, and excluding day 75 were 425 individuals and 43 mg per gram of leaf tissue.

***Salix alaxensis* (Anderss.) Cov.**--Concentration of tannin in unleached leaves collected in winter from unbrowsed feltleaf willow saplings (*Salix alaxensis*), the Alaskan species in the high tannin group, were about 9.9% (Quebracho equivalents) (fig. I-21). However, 48 hours of leaching in Monument Creek reduced the concentration to 3.2%, which was the largest loss of tannin of any of the ten species used in the latitudinal study. The willow leaves used in this study were picked from trees in winter, and were found to be much lower in tannin than leaves picked in autumn at the time of normal abscision (see below). This may be due to differing inherent chemistry in leaves that do not abscise in autumn or to leaching which may have occurred from the dead leaves still remaining on the tree. The large tannin loss moved *S. alaxensis* from the "high tannin" group into the "low tannin" group (in an *a posteriori* sense). Nitrogen increased from 1.8% on day 2 to 2.4% on day 28, then declined to 1.2% on day 75. Phosphorus remained below 0.1% through the 75 days. Mass loss due to leaching was about 20%, and, like the two alder species, mass loss showed a time period of slow decomposition for the first 28 days, then a faster mass loss to about 10% remaining on day 75. Linear regression equation for mass loss was Y = 91.4 - (1.02*X), and estimated time until 50% mass remaining was 41 days.

Macroinvertebrate densities were fairly high, peaking on day 28 at 570 (15% shredders), with a mean of 326 individuals per leafpack (fig. I-22). Biomass peaked on day 56 at 37.1 mg (79% shredders), with a mean of 20.5 mg per leafpack. When compared to leaf mass remaining, invertebrate numbers on *S. alaxensis* leaves peaked at 1141 individuals (mean of 400) and 95.9 mg (mean of 30.2 mg) per gram of leaf tissue remaining.

ALASKAN SPECIES: A RANGE OF LITTER QUALITY

I also tested several additional Alaskan species with a wide range of inherent leaf litter quality. Due to insufficient funding and time, only shredder macroinvertebrates were sorted from approximately half of these samples. Unfortunately, the samples in which all invertebrates were sorted were not randomly or systematically selected so that an estimate of total number and biomass cannot be calculated for each sampling date. Hence, in the succeeding figures, although total numbers and biomass of invertebrates are shown and discussed for some collection dates, only number and biomass of shredders are used in statistical analyses.

***Ledum groenlandicum* Oeder**--*Ledum groenlandicum* (=*Ledum palustre* ssp. *groenlandicum*) is an evergreen shrub in the heath family (Ericaceae) known as Labrador Tea. This is the only species for which we used green leaves. The small (ca. 30 - 40 mm in length, 5 mm in width) leaves were too small to be held by the 2 cm mesh used for the litter bags, so I placed them in a bag of smaller mesh (ca. 5 mm) within the larger-meshed litter bags. *Ledum* had the highest concentration of condensed tannin in its leaves of any species used in this study. Unleached leaves had a concentration of over 37% dry mass (quebracho equivalents), and post-leached leaves had 18% (fig. I-23). There was a steady decline during processing that approximated an exponential decay, with concentration on day 75 approximately 5%. Nitrogen concentration started relatively low at about 1.5% in unleached leaves, then climbed to almost 4% on day 28, declining to less than 2% on day 75. Phosphorus was not dynamic. Mass loss due to leaching was about 9%, and further mass loss was relatively slight, with a final mass remaining of about 70% on day 75. The linear regression equation for mass loss was $Y = 90.0 - (0.37*X)$, and the estimated time until 50 percent mass was remaining was 100 days.

Macroinvertebrate numbers were high in *Ledum* (fig. I-24). On day 75, the mean number of invertebrates was 1044 per leafpack (109 of which were shredders), and mean biomass was 42 mg (30 mg of shredders). Mean number of shredders for the whole study was 58.7, and biomass was 12.6. Due to the extremely slow decomposition rates, the mean number of shredders was only 28.8 and biomass was

6.3 mg per gram of leaf material remaining. I suspect that both the number (especially small chironomids) and biomass of invertebrates was artificially enhanced by the use of a fine-meshed (ca. 5 mm) bag inside a coarse-meshed bag (ca 20 cm), as well as the large amount of leaves needed to make 3 g. This combination created a large amount of surface area with many interstices of appropriate size for aquatic invertebrates, and I feel that most were using *Ledum* leafpacks as habitat rather than as food.

***Salix planifolia* Pursh ssp. *pulcra* (Cham.) Argus**--*Salix planifolia* ssp. *pulcra*, often referred to as just *Salix pulcra* or diamondleaf willow, is a small (ca. 1-2 m in height) willow found commonly in arctic and alpine tundra. It is rich in condensed tannin, with unleached leaf concentrations about 36% (quebracho equivalents), post-leached leaf concentrations about 27%, and concentrations declining exponentially to virtually zero with exposure in the stream (fig. I-25). Indeed, leafpacks continued to be visibly leaching a brown substance through day 28. Nitrogen concentration was moderate in unleached leaves, and increased with time to about 3% on day 75. Phosphorus showed a small drop due to leaching, then remained relatively constant through time at just over 0.1%. *S. pulcra* showed a large (over 30%) drop in mass due to leaching. After a 26 day period of slight mass loss, the rate picked up, and mass remaining on day 75 was about 15%. The linear regression equation for mass loss was $Y = 73.3 - (0.71*X)$, and the estimated time until 50% mass loss was 33 days.

Macroinvertebrate density was relatively high on *S. pulcra*. Total number of invertebrates on leafpacks on day 75 was 603 (90 shredders), and was probably higher on day 56 (based on shredder numbers) (fig. I-26). Biomass of shredders was high: on day 56 there was 68 mg of shredder biomass (total is not available), the highest average for any collection date for any species. Mean biomass was 31 mg for the entire study period. Due to the relatively large amount of mass loss and the high numbers of invertebrates, total number (3004, 502 of which were shredders) and biomass (160 mg, 127 mg of which was shredders) of invertebrates per gram leaf tissue remaining was the highest of any species in the 1988 field season, with the exception of *Alnus rugosa* and *A. crispa* (winter-picked leaves), which had too little mass remaining to be meaningful.

***Shepherdia canadensis* (L.) Nutt.**--*Shepherdia canadensis* (buffaloberry or soapberry) is a low (ca. 0.5 m) shrub in the family found in the understory of deciduous stands in the boreal forest of Alaska (Viereck and others 1992). Although *S. canadensis* twigs are extremely high in condensed tannin concentration (J.P. Bryant, pers. comm.), concentrations in the unleached leaves were less than 15%, concentrations in leached leaves were about 10%, and leaching continued through the study period to a concentration of 1% on day 75 (fig. I-27). Nitrogen concentration showed no appreciable leaching (concentration of about 1.9% for leached and unleached leaves), but a substantial decrease to about 1% on day 28, then an increase back to 2% on day

75. Phosphorus remained relatively constant at about 0.7% throughout the study. Almost 30% of the mass of the leafpacks was lost due to leaching, and mass decreased linearly thereafter to 25% on day 75. The linear regression equation for mass loss was Y = 76.8 - (0.69*X), and time to 50% mass remaining was 38 days.

Like *Ledum* and *Salix pulcra*, *Shepherdia* leafpacks were colonized by relatively high numbers of macroinvertebrates (fig. I-28). The mean total number of invertebrates on day 75 was 592, with 75 of those being shredders, and the mean number of shredders over the 75 day period was 57.7. Shredder biomass peaked on day 56, with 37.7 mg, almost identical to the total number on day 75, which had 17 mg shredders. There were 862 individuals and 55 mg of invertebrates per gram of leaf material remaining on day 75, and an overall mean of 51.3 and 14.7 mg.

***Alnus crispa* (Ait.) Pursh (autumn-picked leaves)**--Green alder (*Alnus crispa*) leaves, picked from the shrubs at senescence in the autumn, had very little condensed tannin (fig. I-29). Initial pre-leached tannin concentration was about 2% and fell to less than 1% for the duration of the study period. Although tannin concentration was low, this species has a phenolic secondary metabolite called pinosylvin (first isolated from *Pinus sylvestris*, Scots Pine) that deters browsing by snowshoe hare (Bryant and others 1983). Nitrogen concentrations in leached leafpacks (day 2) were about 2.4% and increased to 3.1% on day 28, then declined to about 1% by day 75. Phosphorus concentrations remained below 0.1% throughout the study. Mass loss due to leaching and handling was about 15%, followed by a relatively slow mass loss phase for 26 days, then a gradual increase in processing rate to an end-point of about 20% of the original mass remaining on day 75. Linear regression equation was Y = 95.3 - (0.83*X). Estimated time until 50% of the mass was processed was 57 days.

The highest number of macroinvertebrates per leafpack was 363 on day 75 (48 were shredders), when the total biomass was 20.4 mg (14.5 mg was shredders) (fig. I-30). On day 56, however, shredder biomass peaked at 25.8 mg, when there were 78 shredders per leafpack. Shredder density peaked at 132 individuals and 45.5 mg per gram leaf material remaining.

ALASKAN SPECIES: BROWSED VERSUS UNBROWSED COMPARISON

***Salix alaxensis* (Anderss.) Cov. (autumn-picked leaves from unbrowsed trees)**--Feltleaf willow leaves picked from the trees at the time of autumn senescence had much higher concentrations of condensed tannin than did the leaves picked in mid-winter (used in the latitudinal gradient portion of this study). Unleached leaves had a concentration of about 30% (quebracho equivalents), which immediately dropped to about 15% during leaching (fig. I-31). There was a subsequent exponential decline to about 1% on day 56 (there was too little mass remaining on day 75 for chemical analyses). Nitrogen showed an initial increase during the leaching phase, then stayed relatively constant at about 1.3% for the rest of the study period. Phosphorus was essentially constant for the entire study and about 0.1%. Mass remaining showed a sharp drop due to leaching (about 30%), then a gradually increasing rate to an endpoint of about 15% on day 75. The linear regression equation was Y = 75.2 - (0.77*X), and the estimated time to 50% mass remaining was 32 days.

Macroinvertebrate densities were relatively low on leafpacks of autumn-picked, unbrowsed feltleaf willow leaves (fig. I-32). Shredder numbers peaked on day 56 at 70, and the highest total number estimated was 219 on day 75 (41 were shredders). Mean shredder number per leafpack was 33.3 for the 75 day period. Mean shredder biomass was 12.4 mg, and peak biomass was on day 28, with a mean of 21.8 mg. Shredders were estimated to have a mean of 42 individuals (peak of 127 on day 75) and 17.3 mg (peak of 61.2 mg on day 75) per gram of leaf material remaining.

***Salix alaxensis* (Anderss.) Cov. (autumn-picked leaves from browsed branches)--** Tannin concentrations in leafpacks of *S. alaxensis* were high initially, but declined rapidly through time (fig. I-33). Concentrations in unleached leaves were over 30% (quebracho equivalents), but dropped to about 18% following leaching, to 5% after 14 days in the stream, and to near 1% on days 28 and 56. Nitrogen concentration in unleached leaves was about 1.4%, dropped to 1.0% after leaching, and increased slightly after that. Phosphorus showed a drop from 0.2% to 0.07% following leaching, and remained constant after that. Leafpacks lost over 30% mass due to leaching, remained relatively constant for the next 26 days, then lost mass to an endpoint of about 15% mass remaining on day 75. The linear regression equation for mass loss was Y = 76.1 - (0.80*X), and estimated time to 50% mass remaining was 33 days.

Shredder numbers were similar to those found in *S. alaxensis* leafpacks from unbrowsed trees (fig. I-34). Overall means were 32.5 individuals per leafpack and 44 individuals per gram of leaf tissue remaining, with peak numbers on day 56 at 74 individuals per leafpack. Biomass was slightly higher in the leafpacks from browsed branches, with means of 16.1 mg per leafpack, and 24.1 mg and per gram of leaf tissue remaining, with the peak also on day 56 at 35.1 mg of shredder per leafpack.

***Betula papyrifera* Marsh. var. *humilis* (Reg.) Fern. & Raup (from unbrowsed trees)**--Alaska paper birch leaves had relatively high condensed tannin concentration (fig. I-35). Unleached leaves had a concentration of about 19%, and two days of leaching caused an increase in tannin to about 22% (not an actual increase in the amount of tannin: mass was lost at a faster rate than tannin, causing the appearance of an increase). After the peak on day 2, tannin concentration declined exponentially to about 1% on days 56 and 75. Nitrogen concentration increased linearly from about 0.9% in unleached leafpacks to about 1.4% on day 75. Unlike most other species, phosphorus showed a sharp drop due to leaching, from about 0.55% to just over 0.1%, but remained relatively constant thereafter. Leaf mass dropped about 13% due to leaching, and declined to about 22% mass remaining on day 75. The linear regression equation for mass loss was Y = 91.9 - (0.99*X), and estimated time until

50% mass was left was 42 days.

Shredders peaked in numbers (mean of 99) and biomass (mean of 40.1 mg) on day 56, while the largest estimated totals were 471 individuals (62 shredders) and 21.6 mg (11.5 mg shredders) on day 75 (fig. I-36). Mean shredder densities were 45 individuals and 17 mg per leafpack. On a per gram of leaf material remaining basis, the mean shredder number was 53 and biomass was 19.5 mg.

***Betula papyrifera* Marsh. var. *humilis* (Reg.) Fern. & Raup (from browsed branches)**--Paper birch leaves from branches that had been browsed within the previous two years had initial condensed tannin concentrations of about 19%, similar to those from unbrowsed trees (fig. I-37). Leaching, however, caused a drop in tannin concentration to about 4%, a drop not seen in leaves from unbrowsed trees. ^{13}C NMR spectra of condensed tannin purified from leaves collected from browsed and unbrowsed trees were identical (T.P. Clausen and J.G. Irons III, unpublished data). Differences in leachability were likely due to differences in leaf thickness, wax content, or cell wall characteristics. Nitrogen concentration in unleached leaves was about 1.7%, dropped to 1.3% following leaching, and increased slightly to 1.4% on day 56. Phosphorus concentration in birch leaves from browsed branches, like those from unbrowsed trees, exhibited a substantial drop due to leaching, from 0.7% to 0.1%, and remained relatively constant thereafter. Mass loss due to leaching was slightly greater than in leaves from unbrowsed trees (19%), but mass loss patterns were similar until days 56 and 75, when leaves from browsed branches lost significantly more mass than did leaves from unbrowsed trees. Linear regression equation of mass loss through time was Y = 91.1 - (1.21*X), and time until 50% of the mass was gone was 34 days. Effects of foliar chemistry on mass loss rates in birch leaves from browsed and unbrowsed trees are discussed in Irons and others (1991).

Shredder numbers and biomass in birch leafpacks from browsed branches were similar to those from unbrowsed trees, with means of 40 individuals and 15.6 mg per leafpack (fig. I-38). Peak numerical abundance was on day 56, with 63 shredders, and peak biomass was on day 28 with 40.1 mg of shredders per leafpack. Mean shredder abundance was 78.5 individuals and 29.6 mg per gram of leaf tissue remaining.

DISCUSSION

The tree species chosen for this study provided a continuum in leaf litter quality. Condensed tannin and nitrogen concentrations had negative and positive relationships with leaf litter quality, respectively, and appear to provide a two-dimensional index of litter quality. Tannin concentrations (based on quebracho equivalents) ranged from a high of 37% in unleached green *Ledum* leaves and 26.5% following leaching on day 2 in *Salix pulcra* to concentrations indistinguishable from zero in *Trema*. Nitrogen concentrations following leaching ranged from 2.96% in

Trema to 0.8% in unbrowsed *Betula*, and the largest range within a species was found in *Trema*, which had 4.7% on day 7 and 0.7% on day 14. Phosphorus dynamics showed no dramatic differences among species or through time.

There was also a continuum of processing rates of leafpacks of these species (table 2). Visual inspection of the mass loss curves suggested that the negative exponential model of decomposition may not be the most appropriate for this data set. I tested negative exponential, linear, and quadratic models of mass loss. In no species was the negative exponential model the best fit (based on F ratios): a linear fit was best in 13 species and quadratic was best in 5 species (table 2). The slowest rates of decomposition were found in the high tannin species of *Pithecellobium*, *Quercus falcata*, and *Q. rubra*. While *Q. falcata* was low in nitrogen concentration, both *Q. rubra* and *Pithecellobium* had relatively high concentrations. Thus, foliar condensed tannin concentrations may have an important role in controlling leaf litter decomposition rates in streams. The relative importance of tannin and nitrogen in determining leaf litter decomposition rates for some of theses species were discussed in chapter II.

Macroinvertebrate community structure and colonization did not follow the expected patterns of an increasing proportion of shredders through time and the highest abundance and biomass of shredders on species of high nitrogen and low tannin concentrations. Indeed, the highest mean shredder biomass on any collection date was found on the species with the highest post-leaching tannin concentration

(*Shepherdia*). I feel that this is an artifact induced by the need for a second, small-meshed net bag in order to contain the small leaves of *Ledum*, *Shepherdia*, and *Salix pulcra*. The combination of many small leaves required to make up 3 g and the double nets needed to hold the small leaves provided a large amount of leaf and net surface area for invertebrate colonization. The extremely slow mass loss suggests that most of invertebrates, including shredders, were using these leafpacks primarily as habitat and not as a food source. The relationship between litter quality, macroinvertebrate abundance and biomass, and leaf litter mass loss in Monument Creek was discussed in more detail in chapter III.

Alaskan streams are generally cold: Monument Creek accumulated 973 degree-days above zero Celcius in 1987 and 912 degree-days in 1988 (Irons and Oswood 1992). Because temperature has been implicated as an important controlling variable in leaf litter decomposition rates in streams (Webster and Benfield 1986), one would expect that rates in Alaska would be among the slowest. However, decomposition rates of alder in Monument Creek in a previous study were rapid (Cowan and others 1983), and other studies have shown high rates of mass loss in cold streams (Mutch and Davies 1984, Short and others 1980). The processing rates reported here span the gamut from extremely slow (e.g. *Ledum*, *Pithecellobium*) to relatively rapid (e.g. *Trema* and the *Alnus* species). While these rates are consistent with those found for similar species in temperate regions (eg. Petersen and Cummins 1974), when expressed on a per degree-day basis, they are among the fastest reported in the literature (chapter IV).

Food webs in stream ecosystems that depend on leaf litter as an important energy source are inextricably linked to the nearby terrestrial ecosystem of the riparian zone. The leaf litter provided to the stream by riparian vegetation is often of a wide range of quality as food for stream shredders. Golladay and others (1983) and Cummins and others (1989) suggested that this range of litter quality provides a continuous supply of food to stream shredders through time, and that the presence of poor quality leaf litter (i.e. slowly decomposing species) provide food for and allow the existence of a spring-summer shredder community. Spring-summer decomposers, either invertebrate shredders (Cowan and others 1983) or microbial decomposers (Buttimore and others 1984), do not seem to be present in Monument Creek; however, the presence of slowly decomposing species may allow late-winter shredders such as the limnephilid caddisfly *Onocosmoecus unicolor* (Irons 1988) to maintain a viable population. Thus, the presence of a continuum of leaf litter quality such as that reported here, partially determined by leaf chemistry, may be important for maintaining stream food webs that include vertebrate predators such as pacific salmon and arctic grayling.

ACKNOWLEDGEMENTS

Funding for this project was provided by the National Science Foundation Taiga Forest Long Term Ecological Research grant BSR-8702629, with additional assistance from the Institute of Northern Forestry (Aquatic/Land Interaction Program) and the Institute of Arctic Biology. I thank the Chena Hot Springs Resort for access to the Monument Creek study site via their airstrip and the colleagues listed in Table 1 for providing leaf material. Field help was provided by J. Johnson, D. Kennedy, S. Peek, and M. Wagener. S. Kennedy sewed the litter bags, K. Frisby and R. Stafford performed the tannin analysis, and Lori Moilinan and Allen Doyle performed the nitrogen analysis. E. Gabrielson, S. Peek, and S. Tuccio helped with macroinvertebrate sorting and biomass determination. Early versions of this manuscript were improved with help from Drs. J. Bryant, T. Clausen, J. Craven, M. Oswood, P. Quang, and K. Van Cleve.

LITERATURE CITED

Anderson, N.H.; Cummins, K.W. 1979. Influences of diet on the life histories of aquatic insects. Journal of the Fisheries Research Board of Canada. 36: 335-342.

Anderson, N.H.; Grafius, E. 1975. Utilization and processing of allochthonous material by stream Trichoptera. Verh. Int. Verein. Limnol. 19: 3083-3088.

Anderson, N.H.; Sedell, J.R. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Annual Review of Entomology. 24: 351-377.

Anderson, N.H.; Sedell, J.R.; Roberts, L.M.; [and others]. 1978. The role of aquatic invertebrates in processing of wood debris in coniferous forest streams. American Midland Naturalist. 100: 64-82.

Anderson, P.R. 1984. Seasonal changes in attached algae in two Alaskan subarctic streams. M.Sc. Thesis. University of Alaska Fairbanks.

Arsuffi, T.L.; Suberkropp, K. 1984. Leaf processing capabilities of aquatic hyphomycetes: interspecific differences and influence on shredder feeding preferences. Oikos. 42: 144-154.

Arsuffi, T.L.; Suberkropp, K. 1985. Selective feeding by stream caddisfly (Trichoptera) detritivores on leaves with fungal-colonized patches. Oikos. 45: 50-58.

Bärlocher, F. 1982. The contribution of fungal enzymes to the digestion of leaves by Gammarus fossarum Koch (Amphipoda). Oecologia. 52: 1-4.

Bärlocher, F. 1985. The role of fungi in the nutrition of stream invertebrates. Botanical Journal of the Linnean Society. 91: 83-94.

Bärlocher, F. 1992. Effects of drying and freezing autumn leaves on leaching and colonization by aquatic hyphomycetes. Freshwater Biology. 28: 1-7.

Bärlocher, F.; Kendrick, B. 1973. Fungi in the diet of *Gammarus pseudolimnaeus* (Amphipoda). Oikos. 24: 295-300.

Bärlocher, F.; Kendrick, B. 1975. Leaf-conditioning by microorganisms. Oecologia. 20: 359-362.

Barnes, J.R.; McArthur, J.V.; Cushing, C.E. 1986. Effect of excluding shredders on leaf litter decomposing in two streams. Great Basin Naturalist. 46: 204-207.

Benfield, E.F.; Webster, J.R. 1985. Shredder abundance and leaf breakdown in an Appalachian Mountain stream. Freshwater Biology. 15: 113-120.

Benfield, E.F.; Jones, D.S.; Patterson, M.F. 1977. Leaf pack processing in a pastureland stream. Oikos. 29: 99-103.

Bode, R.W. 1983. Larvae of North American *Eukiefferiella* and *Tuetenia* (Diptera: Chironomidae. Bulletin of the New York State Museum 452:1-40.

Bryant, J.P.; Wieland, G.D.; Reichardt, P.B.; [and others]. 1983. Pinosylvin methyl ether deters snowshoe hare feeding on green alder. Science. 222: 1023-1025.

Bryant, J.P.; Clausen, T.P.; Reichardt, P.B.; [and others]. 1987. Effect of nitrogen fertilization upon the secondary chemistry and nutritional value of quaking aspen (*Populus tremuloides* Michx.) leaves for the large aspen tortrix (*Choristoneura conflictana* (Walker)). Oecologia. 73: 513-517.

Buttimore, C.A.; Flanagan, P.W.; Cowan, C.A.; [and others]. 1984. Microbial activity during leaf decomposition in an Alaskan subarctic stream. Holarctic Ecology. 7: 104-110.

Chapin, F.S., III; Kedrowski, R.A. 1983. Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. Ecology. 64: 376-391.

Chauvet, E. 1987. Changes in the chemical composition of alder, poplar, and willow leaves during decomposition in a river. Hydrobiologia. 148: 35-44.

Chergui, H.; Pattée, E. 1992. Processing of fresh and dry *Salix* leaves in a Moroccan river system. Acta Oecologia. 13: 291-298.

Cowan, C.A. 1983. Phenology of detritus input, storage and processing in an Alaskan subarctic stream. M.Sc. Thesis. University of Alaska Fairbanks.

Cowan, C.A.; Oswood, M.W. 1983. Input and storage of benthic detritus in and Alaskan subarctic stream. Polar Biology. 2: 35-40.

Cowan, C.A.; Oswood, M.W. 1984. Spatial and seasonal associations of benthic macroinvertebrates and detritus in an Alaskan subarctic stream. Polar Biology. 3: 211-215.

Cowan, C.A.; Oswood, M.W.; Buttimore, C.A.; [and others]. 1983. Processing and macroinvertebrate colonization of detritus in and Alaskan subarctic stream. Holarctic Ecology. 6: 340-348.

Cummins, K.W. 1973. Trophic relations of aquatic insects. Annual Review of Entomology. 18: 183-206.

Cummins, K.W.; Klug, M.J. 1979. Feeding ecology of stream invertebrates. Annual Review of Ecology and Systematics. 10: 147-172.

Cummins, K.W.; Klug, M.J.; Wetzel, R.G.; [and others]. 1972. Organic enrichment with leaf leachate in experimental lotic ecosystems. BioScience. 22(12): 719-722.

Cummins, K.W.; Wilzbach, M.A.; Gates, D.M.; [and others]. 1989. Shredders and riparian vegetation. BioScience. 39: 24-30.

Dahm, C.N. 1981. Pathways and mechanisms for removal of dissolved organic carbon from leaf leachate in streams. Canadian Journal of Fisheries and Aquatic Sciences. 38: 68-76.

Edmunds, G.F., Jr.; Jensen, S.L.; Berner, L. 1976. The mayflies of North and Central America. University of Minnesota Press, Minneapolis.

Ford, T.E.; Lock, M.A. 1987. Epilithic metabolism of dissolved organic carbon in boreal forest rivers. Microbial Ecology. 45: 89-97.

Gessner, M.O. 1991. Differences in processing dynamics of fresh and dried leaf litter in a stream ecosystem. Freshwater Biology. 26: 387-398.

Gessner, M.O.; Schwoerbel, J. 1989. Leaching kinetics of fresh leaf litter with implications for the current concept of leaf processing in streams. Archive fur

Hydrobiologia. 115(1): 81-90.

Gessner, M.O.; Schwoerbel, J. 1991. Fungal biomass associated with decaying leaf litter in a stream. Oecologia. 87: 602-603.

Golladay, S.W.; Webster, J.R.; Benfield, E.F. 1983. Factors affecting food utilization by a leaf shredding aquatic insect: leaf species and conditioning time. Holarctic Ecology. 6: 157-162.

Grafius, E.; Anderson, N.H. 1979. Population dynamics, bioenergetics, and role of *Lepidostoma quercina* Ross (Trichoptera: Lepidostomatidae) in an Oregon woodland stream. Ecology. 60: 433-441.

Harborne, J.B. 1988. Phytochemical ecology. Academic Press, New York. (check date)

Harrison, P.G. 1982. Control of microbial growth and of Amphipod grazing by water-soluble compounds from leaves of *Zostera marina*. Marine Biology. 67: 225-230.

Howe, A.L. 1981. Life histories and community structures of Ephemeroptera and

Plecoptera in two Alaskan subarctic streams. M.Sc. Thesis. University of Alaska Fairbanks.

Irons, J.G., III. 1985. The life histories and community structure of the caddisflies (Trichoptera) of two Alaskan subarctic streams. M.Sc. Thesis. University of Alaska Fairbanks.

Irons, J.G., III. 1988. Life history patterns and trophic ecology of Trichoptera in two Alaskan (U.S.A.) subarctic streams. Canadian Journal of Zoology. 66(6): 1258-1265.

Irons, J.G., III; Oswood, M.W. 1992. Seasonal temperature patterns in an arctic and two subarctic Alaskan (USA) headwater streams. Hydrobiologia. 237: 147-157.

Irons, J.G., III; Oswood, M.W.; Bryant, J.P. 1988. Consumption of leaf detritus by a stream shredder: influence of tree species and nutrient status. Hydrobiologia. 160: 53-61.

Irons, J.G., III; Ray, S.R.; Miller, L.K.; [and others]. 1989. Spatial and seasonal patterns of streambed water temperatures in an Alaskan subarctic stream. In Woessner, W.W.; Potts, D.F., eds. Symposium proceedings on headwaters hydrology. June 1989, Missoula, MT. Bethesda, MD: Am. Water Res. Assoc.: 381-390.

Irons, J.G., III; Bryant, J.P.; Oswood, M.W. 1991. Effects of moose browsing on decomposition rates of birch leaf litter in a subarctic stream. Canadian Journal of Fisheries and Aquatic Sciences. 48(3): 442-444.

Iversen, T. 1973. Decomposition of autumn-shed beech leaves in a springbrook and its significance for the fauna. Archive fur Hydrobiologia. 72: 305-312.

Iversen, T.M. 1974. Ingestion and growth in *Sericostomata personatum* (Trichoptera) in relation to the nitrogen content of ingested leaves. Oikos. 25: 278-282.

Iversen, T.M. 1975. Disappearance of autumn-shed beech leaves placed in bags in small streams. Verh. Int. Verein. Limnol. 19: 1687-1692.

Kaushik, N.K.; Hynes, H.B.N. 1968. Experimental study on the role of autumn-shed leaves in aquatic environments. Journal of Ecology. 56: 229-243.

Kaushik, N.K.; Hynes, H.B.N. 1971. The fate of the dead leaves that fall into streams. Archive fur Hydrobiologia. 68: 465-515.

Kostalos, M; Seymour, R.L. 1976. Role of microbial enriched detritus in the nutrition of *Gammarus minus* (Amphipoda). Oikos. 27: 512-516.

Lawson, D.L.; Klug, M.J.; Merritt, R.W. 1984. The influence of the physical, chemical, and microbiological characteristics of decomposing leaves on the growth of the detritivore *Tipula abdominalis* (Diptera: Tipulidae). Canadian Journal of Zoology. 62: 2339-2343.

Lush, D.L.; Hynes, H.B.N. 1978. The uptake of dissolved organic matter by a small spring stream. Hydrobiologia. 60: 271-275.

Martin, J.S.; Martin, M.M. 1982. Tannin assays in ecological studies: Lack of correlation between phenolics, proanthocyanidins and protein-precipitating constituents in mature foliage of six oak species. Oecologia. 54: 205-211.

Mathews, C.P.; Kowalczewski, A. 1969. The disappearance of leaf litter and its contribution to production in the River Thames. Journal of Ecology. 57: 543-555.

McArthur, J.V.; Leff, L.G.; Kovacic, D.A.; [and others]. 1986. Green leaf decomposition in coastal plain streams. Journal of Freshwater Ecology. 3: 553-558.

Melillo, J.M.; Naiman, R.J.; Aber, J.D.; [and others]. 1984. Factors controlling mass loss and nitrogen dynamics of plant litter decaying in northern streams. Bulletin of Marine Science. 35: 341-356.

Merritt, R.W.; Cummins, K.W. 1984. An introduction to the aquatic insects of North America, 2nd edition. Kendall/Hunt Publ. Co., Dubuque.

Meyer, J.L. 1980. Dynamics of phosphorus and organic matter during leaf decomposition in a forest stream. Oikos. 34: 44-53.

Minshall, G.W. 1978. Autotrophy in stream ecosystems. BioScience. 28: 767-771.

Mutch, R.A.; Davies, R.W. 1984. Processing of willow leaves in two Alberta Rocky Mountain streams. Holarctic Ecology. 7: 171-176.

Oliver, D. R., McClymont, D. and Roussel, M.E. 1978. A key to some larvae of Chironomidae (Diptera) from the Mackenzie and Porcupine River watersheds. Fisheries and Environmment Canada, Fisheries and Marine Service Technical Report Number 791:1-73.

Otto, C. 1974. Growth and energetics in a larval population of *Potamophylax* *cingulatus* (Steph.) (Trichoptera) in a south Swedish stream. Journal of Animal Ecology. 43: 339-361.

Petersen, R.C.; Cummins, K.W. 1974. Leaf processing in a woodland stream. Freshwater Biology. 4: 343-368.

Reice, S.R. 1978. Role of detritivore selectivity in species-specific litter decomposition in a woodland stream. Verh. Int. Verein. Limnol. 20: 1396-1400.

Rossi, L.; Fano, E.A.; Basset, A.; [and others]. 1983. An experimental study of a microfungal community on plant detritus in a Mediterranean woodland stream. Mycologia. 75: 887-896.

Sedell, J.R.; Triska, F.J.; Triska, N.S. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams: I. Weight loss and associated invertebrates. Verh. Int. Verein. Limnol. 19: 1617-1627.

Short, R.A.; Canton, S.P.; Ward, J.V. 1980. Detrital processing and associated macroinvertebrates in a Colorado mountain stream. Ecology. 61: 727-732.

Simpson, K.W.; Bode, R.W. 1980. Common larvae of Chironomidae (Diptera) from the New York state streams and rivers with particular reference to the fauna of artificial substrates. Bulletin of the NewYork State Museum 439:1-105.

Smith, D.L. 1986. Leaf litter processing and the associated invertebrate fauna in a tallgrass prairie stream. American Midland Naturalist. 116: 78-86.

Sonnichson, S.K. 1982. Ecology of slimy sculpin (*Cottus cognatus*) in the Chena River, Alaska. Univ. Alaska, Fairbanks, AK.

Stewart, K.W.; Stark, B.P. 1988. Nymphs of North American stonefly genera (Plecoptera). The Entomological Society of America, .

Stout, R.J. 1989. Effects of condensed tannins on leaf processing in mid-latitude and tropical streams: a theoretical approach. Canadian Journal of Fisheries and Aquatic Sciences. 46: 1097-1106.

Stout, R.J.; Taft, W.H. 1985. Growth patterns of a chironomid shredder on fresh and senescent Tag Alder leaves in two Michigan streams. Journal of Freshwater Ecology. 3: 147-153.

Stout, R.J.; Taft, W.H.; Merritt, R.W. 1985. Patterns of macroinvertebrate colonization on fresh and senescent alder leaves in two Michigan streams. Freshwater Biology. 15: 573-580.

Suberkropp, K.; Klug, M.J. 1976. Fungi and bacteria associated with leaves during processing in a woodland stream. Ecology. 57: 707-719.

Suberkropp, K.; Godshalk, G.L.; Klug, M.J. 1976. Changes in the chemical composition of leaves during processing in a woodland stream. Ecology. 57: 720-727.

Suberkropp, K.; Arsuffi, T.L.; Anderson, J.P. 1983. Comparison of degradative ability, enzyme activity, and palatability of aquatic hyphomycetes grown on leaf litter. Applied and Environmental Microbiology. 46: 237-244.

Sutcliffe, D.W.; Carrick, T.R.; Willoughby, L.G. 1981. Effects of diet, body size, age and temperature on growth rates in the amphipod *Gammarus pulex*. Freshwater Biology. 11: 183-214.

Tate, C.M.; Gurtz, M.E. 1986. Comparison of mass loss, nutrients, and invertebrates associated with elm leaf litter decomposition in perennial and intermittent reaches of tallgrass prairie streams. Southwestern Naturalist. 31: 511-

520.

Taylor, R.L.; Adams, P.W. 1986. Red alder leaf litter and streamwater quality in western Oregon. Water Resources Bulletin. 22: 629-635.

Triska, F.J.; Buckley, B.M. 1978. Patterns of nitrogen uptake and loss in relation to litter disappearance and associated invertebrate biomass in six streams of the Pacific Northwest, U.S.A. Verh. Int. Verein. Limnol. 20: 1324-1332.

Triska, F.J.; Sedell, J.R. 1976. Decomposition of four species of leaf litter in response to nitrate manipulation. Ecology. 57: 783-792.

Triska, F.J.; Sedell, J.R.; Buckley, B. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams: II. Biochemical and nutrient changes. Verh. Int. Verein. Limnol. 19: 1628-1639.

Vannote, R.L.; Sweeney, B.W. 1985. Larval feeding and growth rate of the stream cranefly Tipula abdominalis in gradients of temperature and nutrition. Proceedings of the Academy of Natural Science of Philadelphia. 137: 119-128.

Viereck, L.A.; Dyrness, C.T.; Batten, A.R.; [and others]. 1992. The Alaska vegetation classification. USDA Forest Service General Technical Report PNW-GTR-286, Portland, OR.

Wallace, J.B.; Woodall, W.R.; Sherberger, F.F. 1970. Breakdown of leaves by feeding of *Peltoperla maria* nymphs (Plecoptera: Peltoperlidae). Annals of the Entomological Society of America. 63: 562-567.

Webster, J.R.; Benfield, E.F. 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics. 17: 567-594.

Wetzel, R.G.; Manny, B.A. 1972. Decomposition of dissolved organic carbon and nitrogen compounds from leaves in an experimental hard-water stream. Limnology and Oceanography. 17(6): 927-931.

Wiederholm, T. (ed.) 1983. Chironomidae of the Holarctic Region, keys and diagnosis. Part 1. Larvae. Ent. Scand. Suppl. 19:1-457.

Wiggins, G.B. 1977. Larvae of the North American caddisfly genera (Trichoptera). Univ. Toronto Press, Toronto.

Willoughby, L.G.; Sutcliffe, D.W. 1976. Experiments on feeding and growth of the amphipod Gammarus pulex (L.) related to its distribution in the River Duddon. Freshwater Biology. 6: 577-586.

Zucker, W.V. 1983. Tannins: does structure determine function? An ecological perspective. American Naturalist. 121: 335-365.

Table I-1. Species, location of origin, and collecting investigator of leaves used in analysis of latitudinal patterns of leaf litter processing rates. Leaf litter quality (QUAL) is tabulated as species high in condensed tannin concentration (H) or species low in tannin concentration (L). The Alaskan species were chosen to provide a range of tannin concentrations, hence they are not listed as high or low in tannin.

SPECIES	COMMON NAME	FAMILY	QUAL	COLLECTION LOCATION	INVESTIGATOR
Pithecellobium longifolium (H. & B.) Standley	Sotacaballo	Leguminosae	H	Costa Rica	C.M. Pringle
Trema micrantha (L.) Blume	Capulía	Ulmaceae	L	Costa Rica	C.M. Pringle
Cornus florida L.	Flowering Dogwood	Cornaceae	L	North Carolina	S.R. Reice
Quercus falcata Michx.	Southern Red Oak	Fagaceae	H	North Carolina	S.R. Reice
Acer saccharum Marshall	Sugar Maple	Aceraceae	L	New York	W.H. McDowell
Fagus grandifolia Ehrh.	American Beech	Fagaceae	H	New York	W.H. McDowell
Alnus rugosa (Du Roi) Spreng.	Tag Alder	Betulaceae	L	Michigan	R.J. Stout
Quercus rubra L.	Northern Red Oak	Fagaceae	H	Michigan	R.J. Stout
Alnus crispa (Ait.) Pursh	Green Alder	Betulaceae	L	Alaska	J.G. Irons, M.W. Oswood
Salix alaxensis (Anderss.) Cov.	Feltleaf Willow	Salicaceae	H	Alaska	J.G. Irons, M.W. Oswood
Ledum groenlandicum Oeder	Labrador Tea	Ericaceae		Alaska	J.G. Irons, M.W. Oswood
Salix planifolia Pursh. spp. *pulcra* (Cham.) Argus	Diamondleaf Willow	Salicaceae		Alaska	J.G. Irons, M.W. Oswood
Shepherdia canadensis (L.) Nutt.	Buffaloberry	Elaeagnaceae		Alaska	J.G. Irons, M.W. Oswood
A. crispa (autumn-picked)	Green Alder	Betulaceae		Alaska	J.G. Irons, M.W. Oswood
S. alaxensis (no-browse)	Feltleaf Willow	Salicaceae		Alaska	J.G. Irons, M.W. Oswood
Salix alaxensis (browsed)	Feltleaf Willow	Salicaceae		Alaska	J.G. Irons, M.W. Oswood
Betula papyrifera Marsh. var. *humulis* (Reg.) Fern. & Raup (no-browse)	Alaska Paper Birch	Betulaceae		Alaska	J.G. Irons, M.W. Oswood
Betula papyrifera (browsed)	Paper Birch	Betulaceae		Alaska	J.G. Irons, M.W. Oswood

Table I-2. Coefficients and F ratios for three models of the change in leaf litter mass through time for leaves placed in Monument Creek in autumn of 1988. Abbreviations: LIN = linear regression, EXP = exponential decay (data were log-transformed), QUAD = quadratic equation. Locations of origin are CR = Costa Rica, NC = North Carolina, NY = New York State, MI = Michigan, and AK = Alaska. H and L correspond to the *a priori* "high" and "low" tannin concentration groups. Species are arranged in order of latitude within the *a priori* tannin groups.

			Coefficients of Decay						
SPECIES	ORIG	H/L	LIN	F	EXP	F	QUAD X	QUAD X^2	F
Pithecellobium	CR	H	-0.0012	21.0	-0.0006	20.5	-0.0048	+0.00005	26.6
Quercus falcata	NC	H	-0.0018	21.4	-0.0009	22.5	-0.0019	0.00000	24.8
Fagus grandifolia	NY	H	-0.0031	12.6	-0.0019	10.9	+0.0024	-0.00008	8.4
Quercus rubra	MI	H	-0.0041	502.9	-0.0023	469.1	-0.0056	+0.00002	284.6
Salix alaxensis	AK	H	-0.0097	157.6	-0.0066	135.8	-0.0033	-0.00009	196.6
Trema micrantha	CR	L	-0.0109	189.1	-0.0081	182.9	+0.0008	-0.00003	260.6
Cornus florida	NC	L	-0.0057	58.5	-0.0042	80.1	-0.0015	-0.00008	386.7
Acer saccharum	NY	L	-0.0084	96.4	-0.0053	94.0	+0.0018	-0.00018	435.8
Alnus rugosa	MI	L	-0.0127	195.1	-0.0098	188.9	-0.0079	-0.00006	122.4
Alnus crispa	AK	L	-0.0121	373.0	-0.0099	327.3	-0.0124	0.00000	209.4
Ledum groenlandicum	AK		-0.0037	57.7	-0.0021	53.4	-0.0069	+0.0000	33.0
Salix pulcra	AK		-0.0071	286.6	-0.0049	257.0	-0.0050	-0.0000	153.6
Shepherdia canadensis	AK		-0.0069	393.2	-0.0047	338.9	-0.0052	-0.0000	206.4
A. crispa (autumn-picked)	AK		-0.0083	79.6	-0.0055	57.9	+0.0029	-0.0001	87.4
S. alaxensis (no-browse)	AK		-0.0077	225.2	-0.0054	173.1	-0.0018	-0.0001	203.7
Salix alaxensis (browsed)	AK		-0.0080	233.1	-0.0057	199.2	-0.0018	-0.0001	260.0
Betula papyrifera (no-browse)	AK		-0.0099	192.3	-0.0066	146.2	-0.0084	-0.0000	93.0
Betula papyrifera (browsed)	AK		-0.0121	217.6	-0.0086	192.8	-0.0100	-0.0000	105.8

FIGURE CAPTIONS

Figure I-1--Location of the study site showing Monument Creek, the stream site for the decomposition portion of the study.

Figure I-2--Air and water temperatures at Monument Creek for the 75 day decomposition study period in 1988.

Figure I-3--Condensed tannin, nitrogen, and phosphorus concentrations in leaf litter, and percent ash-free dry mass remaining through time for *Trema micrantha* from Costa Rica following processing in Monument Creek, Alaska. Error bars are one standard error of the mean, and unapparent error bars are hidden by the symbol.

Figure I-4--Mean number of invertebrates per leaf, mean invertebrate biomass per leafpack, mean number of invertebrates per gram of leaf material remaining, and mean biomass of invertebrates per gram of *Trema micrantha* leaf material remaining following processing in Monument Creek, Alaska. Error bars are one standard error of mean total number or biomass of invertebrates, and unapparent error bars are hidden by the symbol.

Figure I-5--Condensed tannin, nitrogen, and phosphorus concentrations in leaf litter, and percent ash-free dry mass remaining through time for *Pithecellobium longifolium* from Costa Rica following processing in Monument Creek, Alaska. Error bars are one standard error of the mean, and unapparent error bars are hidden by the symbol.

Figure I-6--Mean number of invertebrates per leaf, mean invertebrate biomass per leafpack, mean number of invertebrates per gram, and mean biomass of invertebrates per gram of leaf material remaining of *Pithecellobium longifolium* leaf material remaining following processing in Monument Creek, Alaska. Error bars are one standard error of mean total number or biomass of invertebrates, and unapparent error bars are hidden by the symbol.

Figure I-7--Condensed tannin, nitrogen, and phosphorus concentrations in leaf litter, and percent ash-free dry mass remaining through time for *Cornus florida* from North Carolina following processing in Monument Creek, Alaska. Error bars are one standard error of the mean, and unapparent error bars are hidden by the symbol.

Figure I-8--Mean number of invertebrates per leaf, mean invertebrate biomass per leafpack, mean number of invertebrates per gram, and mean biomass of invertebrates per gram of leaf material remaining of *Cornus florida* leaf material remaining following processing in Monument Creek, Alaska. Error bars are one standard error of mean total number or biomass of invertebrates, and unapparent error bars are hidden by the symbol.

Figure I-9--Condensed tannin, nitrogen, and phosphorus concentrations in leaf litter, and percent ash-free dry mass remaining through time for *Quercus falcata* from North Carolina following processing in Monument Creek, Alaska. Error bars are one standard error of the mean, and unapparent error bars are hidden by the symbol.

Figure I-10--Mean number of invertebrates per leaf, mean invertebrate biomass per leafpack, mean number of invertebrates per gram, and mean biomass of invertebrates per gram of leaf material remaining of *Quercus falcata* leaf material remaining following processing in Monument Creek, Alaska. Error bars are one standard error of mean total number or biomass of invertebrates, and unapparent error bars are hidden by the symbol.

Figure I-11--Condensed tannin, nitrogen, and phosphorus concentrations in leaf litter, and percent ash-free dry mass remaining through time for *Acer saccharum* from New York following processing in Monument Creek, Alaska. Error bars are one standard error of the mean, and unapparent error bars are hidden by the symbol.

Figure I-12--Mean number of invertebrates per leaf, mean invertebrate biomass per leafpack, mean number of invertebrates per gram, and mean biomass of invertebrates per gram of leaf material remaining of *Acer saccharum* leaf material remaining following processing in Monument Creek, Alaska. Error bars are one standard error of mean total number or biomass of invertebrates, and unapparent error bars are hidden by the symbol.

Figure I-13--Condensed tannin, nitrogen, and phosphorus concentrations in leaf litter, and percent ash-free dry mass remaining through time for *Fagus grandifolia* from New York following processing in Monument Creek, Alaska. Error bars are one standard error of the mean, and unapparent error bars are hidden by the symbol.

Figure I-14--Mean number of invertebrates per leaf, mean invertebrate biomass per leafpack, mean number of invertebrates per gram, and mean biomass of invertebrates per gram of leaf material remaining of *Fagus grandifolia* leaf material remaining following processing in Monument Creek, Alaska. Error bars are one standard error of mean total number or biomass of invertebrates, and unapparent error bars are hidden by the symbol.

Figure I-15--Condensed tannin, nitrogen, and phosphorus concentrations in leaf litter, and percent ash-free dry mass remaining through time for *Alnus rugosa* from Michigan following processing in Monument Creek, Alaska. Error bars are one standard error of the mean, and unapparent error bars are hidden by the symbol.

Figure I-16--Mean number of invertebrates per leaf, mean invertebrate biomass per leafpack, mean number of invertebrates per gram of leaf material remaining, and mean biomass of invertebrates per gram of *Alnus rugosa* leaf material remaining following processing in Monument Creek, Alaska. Numbers and biomass per gram of leaf remaining on day 75 are not shown due to the low amount of mass remaining (0.6%), denoted by an asterisk. Error bars are one standard error of mean total number or biomass of invertebrates, and unapparent error bars are hidden by the symbol.

Figure I-17--Condensed tannin, nitrogen, and phosphorus concentrations in leaf litter, and percent ash-free dry mass remaining through time for *Quercus rubra* from Michigan following processing in Monument Creek, Alaska. Error bars are one standard error of the mean, and unapparent error bars are hidden by the symbol.

Figure I-18--Mean number of invertebrates per leaf, mean invertebrate biomass per leafpack, mean number of invertebrates per gram of leaf material remaining, and mean biomass of invertebrates per gram of *Quercus rubra* leaf material remaining following processing in Monument Creek, Alaska. Error bars are one standard error of mean total number or biomass of invertebrates, and unapparent error bars are hidden by the symbol.

Figure I-19--Condensed tannin, nitrogen, and phosphorus concentrations in leaf litter, and percent ash-free dry mass remaining through time for *Alnus crispa* from Alaska following processing in Monument Creek, Alaska. Error bars are one standard error of the mean, and unapparent error bars are hidden by the symbol.

Figure I-20--Mean number of invertebrates per leaf, mean invertebrate biomass per leafpack, mean number of invertebrates per gram of leaf material remaining, and mean biomass of invertebrates per gram of *Alnus crispa* leaf material remaining following processing in Monument Creek, Alaska. Numbers and biomass per gram of leaf remaining on day 75 are not shown due to the low amount of mass remaining (0.6%), denoted by an asterisk. Note that the range on the y axis for the biomass per gram panel is greater than for other species. Error bars are one standard error of mean total number or biomass of invertebrates, and unapparent error bars are hidden by the symbol.

Figure I-21--Condensed tannin, nitrogen, and phosphorus concentrations in leaf litter, and percent ash-free dry mass remaining through time for *Salix alaxensis* from Costa Rica following processing in Monument Creek, Alaska. Error bars are one standard error of the mean, and unapparent error bars are hidden by the symbol.

Figure I-22--Mean number of invertebrates per leaf, mean invertebrate biomass per leafpack, mean number of invertebrates per gram of leaf material remaining, and mean biomass of invertebrates per gram of *Salix alaxensis* leaf material remaining following processing in Monument Creek, Alaska. Error bars are one standard error of mean total number or biomass of invertebrates, and unapparent error bars are hidden by the symbol.

Figure I-23--Condensed tannin, nitrogen, and phosphorus concentrations in leaf litter, and percent ash-free dry mass remaining through time for *Ledum groenlandicum* from Alaska following processing in Monument Creek, Alaska. Error bars are one standard error of the mean, and unapparent error bars are hidden by the symbol.

Figure I-24--Mean number of invertebrates per leaf, mean invertebrate biomass per leafpack, mean number of invertebrates per gram of leaf material remaining, and mean biomass of invertebrates per gram of *Ledum groenlandicum* leaf material remaining following processing in Monument Creek, Alaska. Error bars are one standard error of mean total number or biomass of invertebrates, and unapparent error bars are hidden by the symbol.

Figure I-25--Condensed tannin, nitrogen, and phosphorus concentrations in leaf litter, and percent ash-free dry mass remaining through time for *Salix pulcra* from Alaska following processing in Monument Creek, Alaska. Error bars are one standard error of the mean, and unapparent error bars are hidden by the symbol.

Figure I-26--Mean number of invertebrates per leaf, mean invertebrate biomass per leafpack, mean number of invertebrates per gram of leaf material remaining, and mean biomass of invertebrates per gram of *Salix pulcra* leaf material remaining following processing in Monument Creek, Alaska. Error bars are one standard error of mean total number or biomass of invertebrates, and unapparent error bars are hidden by the symbol.

Figure I-27--Condensed tannin, nitrogen, and phosphorus concentrations in leaf litter, and percent ash-free dry mass remaining through time for *Shepherdia canadensis* from Alaska following processing in Monument Creek, Alaska. Error bars are one standard error of the mean, and unapparent error bars are hidden by the symbol.

Figure I-28--Mean number of invertebrates per leaf, mean invertebrate biomass per leafpack, mean number of invertebrates per gram of leaf material remaining, and mean biomass of invertebrates per gram of *Shepherdia canadensis* leaf material remaining following processing in Monument Creek, Alaska. Error bars are one standard error of mean total number or biomass of invertebrates, and unapparent error bars are hidden by the symbol.

Figure I-29--Condensed tannin, nitrogen, and phosphorus concentrations in leaf litter, and percent ash-free dry mass remaining through time for *Alnus crispa* (autumn-picked leaves) from Alaska following processing in Monument Creek, Alaska. Error bars are one standard error of the mean, and unapparent error bars are hidden by the symbol.

Figure I-30--Mean number of invertebrates per leaf, mean invertebrate biomass per leafpack, mean number of invertebrates per gram of leaf material remaining, and mean biomass of invertebrates per gram of *Alnus crispa* (autumn-picked leaves) leaf material remaining following processing in Monument Creek, Alaska. Error bars are one standard error of mean total number or biomass of invertebrates, and unapparent error bars are hidden by the symbol.

Figure I-31--Condensed tannin, nitrogen, and phosphorus concentrations in leaf litter, and percent ash-free dry mass remaining through time for *Salix alaxensis* (leaves picked from unbrowsed trees) from Alaska following processing in Monument Creek, Alaska. Error bars are one standard error of the mean, and unapparent error bars are hidden by the symbol.

Figure I-32--Mean number of invertebrates per leaf, mean invertebrate biomass per leafpack, mean number of invertebrates per gram of leaf material remaining, and mean biomass of invertebrates per gram of *Salix alaxensis* leaf material remaining following processing in Monument Creek, Alaska. Error bars are one standard error of mean total number or biomass of invertebrates, and unapparent error bars are hidden by the symbol.

Figure I-33--Condensed tannin, nitrogen, and phosphorus concentrations in leaf litter, and percent ash-free dry mass remaining through time for *Salix alaxensis* (leaves picked from previously browsed branches) from Alaska following processing in Monument Creek, Alaska. Error bars are one standard error of the mean, and unapparent error bars are hidden by the symbol.

Figure I-34--Mean number of invertebrates per leaf, mean invertebrate biomass per leafpack, mean number of invertebrates per gram of leaf material remaining, and mean biomass of invertebrates per gram of *Salix alaxensis* (leaves picked from previously browsed branches) leaf material remaining following processing in Monument Creek, Alaska. Error bars are one standard error of mean total number or biomass of invertebrates, and unapparent error bars are hidden by the symbol.

Figure I-35--Condensed tannin, nitrogen, and phosphorus concentrations in leaf litter, and percent ash-free dry mass remaining through time for *Betula papyrifera* (leaves picked from unbrowsed trees) from Alaska following processing in Monument Creek, Alaska. Error bars are one standard error of the mean, and unapparent error bars are hidden by the symbol.

Figure I-36--Mean number of invertebrates per leaf, mean invertebrate biomass per leafpack, mean number of invertebrates per gram of leaf material remaining, and mean biomass of invertebrates per gram of *Betula papyrifera* (leaves picked from unbrowsed trees) leaf material remaining following processing in Monument Creek, Alaska. Error bars are one standard error of mean total number or biomass of invertebrates, and unapparent error bars are hidden by the symbol.

Figure I-37--Condensed tannin, nitrogen, and phosphorus concentrations in leaf litter, and percent ash-free dry mass remaining through time for *Betula papyrifera* (leaves picked from previously browsed branches) from Alaska following processing in Monument Creek, Alaska. Error bars are one standard error of the mean, and unapparent error bars are hidden by the symbol.

Figure I-38--Mean number of invertebrates per leaf, mean invertebrate biomass per leafpack, mean number of invertebrates per gram of leaf material remaining, and mean biomass of invertebrates per gram of *Betula papyrifera* leaf material remaining following processing in Monument Creek, Alaska. Error bars are one standard error of mean total number or biomass of invertebrates, and unapparent error bars are hidden by the symbol.

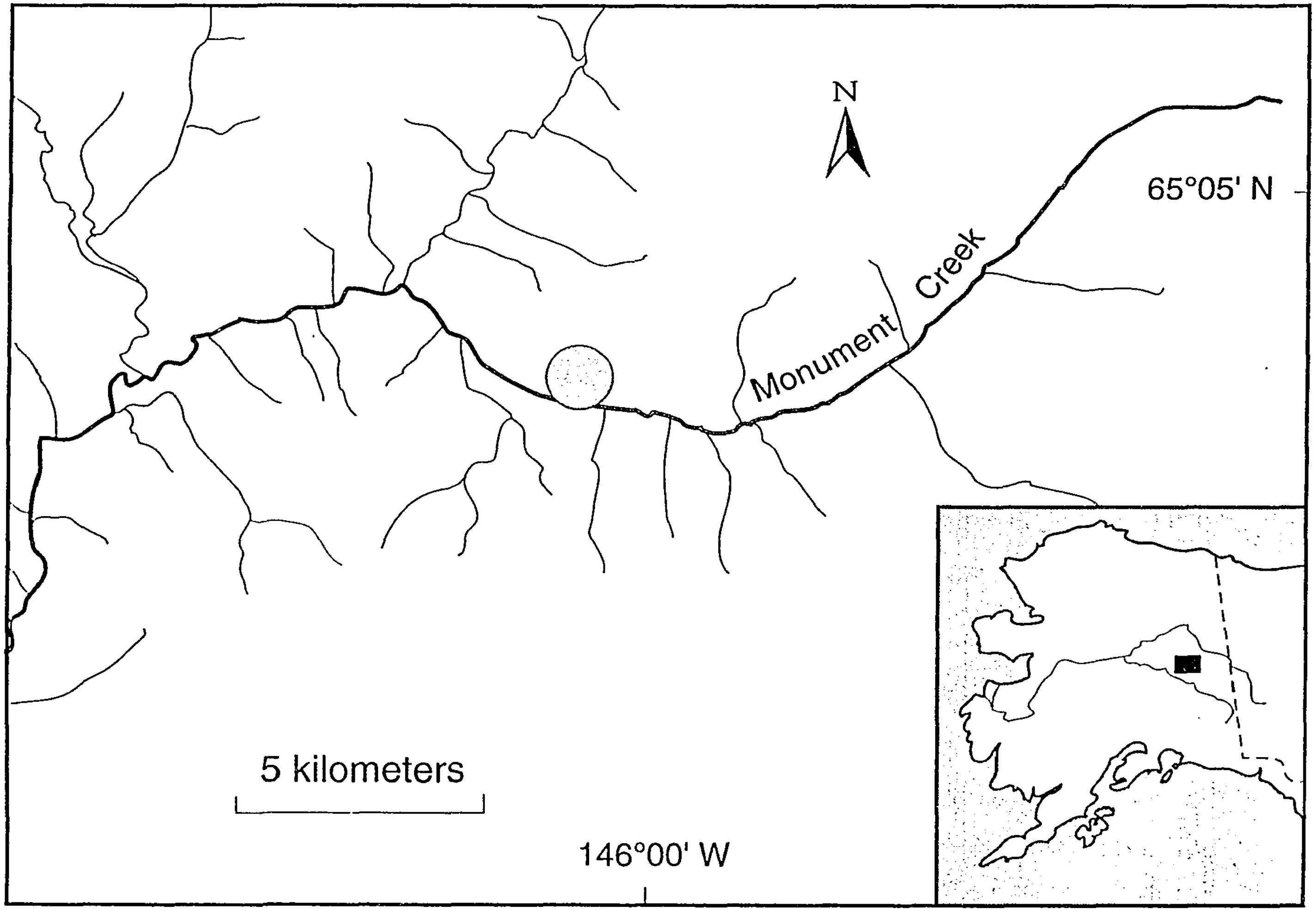
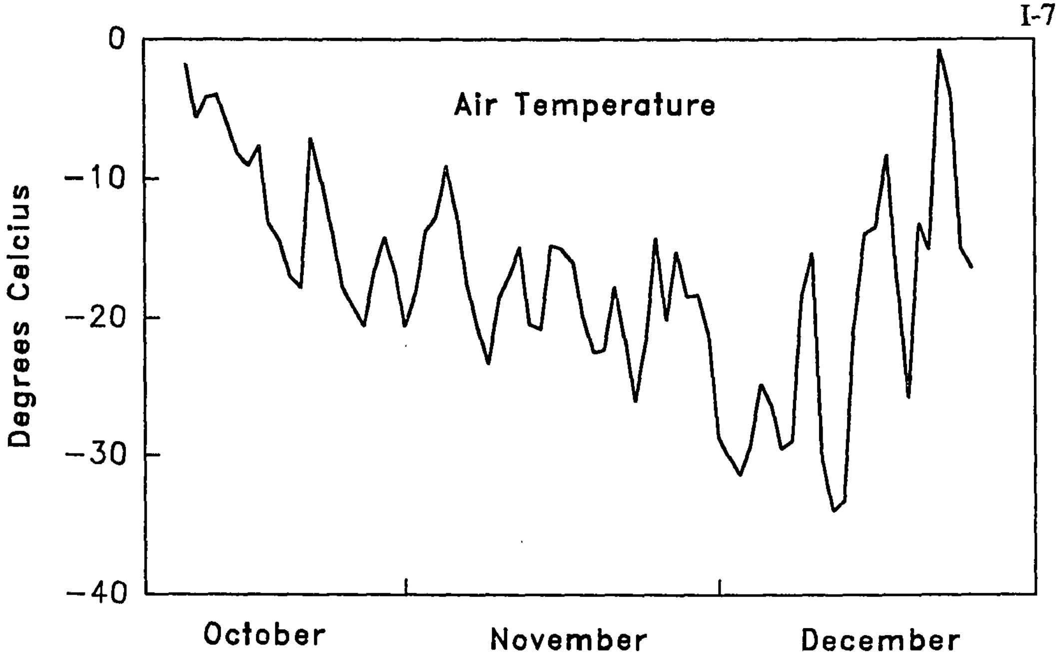


Figure I-1


Air Temperature
0
−10
−20
−30
−40
Degrees Celcius
October
November
December

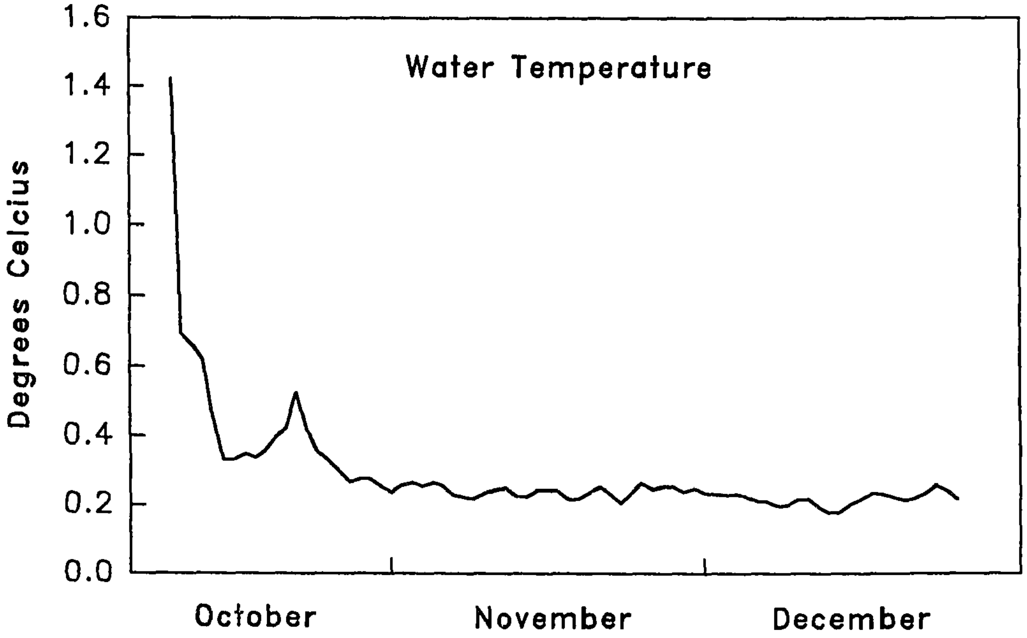

Water Temperature
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Degrees Celcius
October
November
December

Figure I-2

Trema micrantha

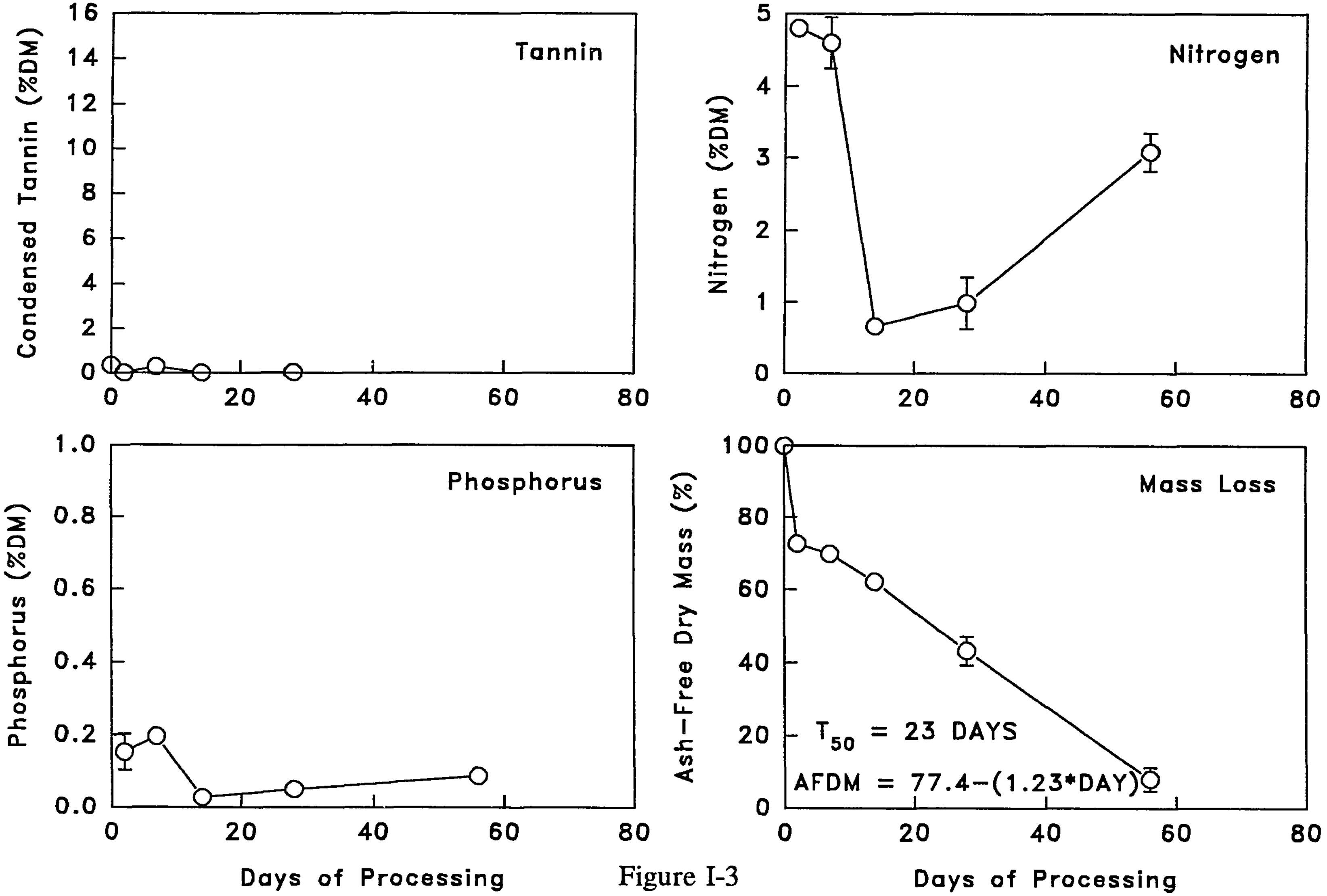


Figure I-3

Trema micrantha

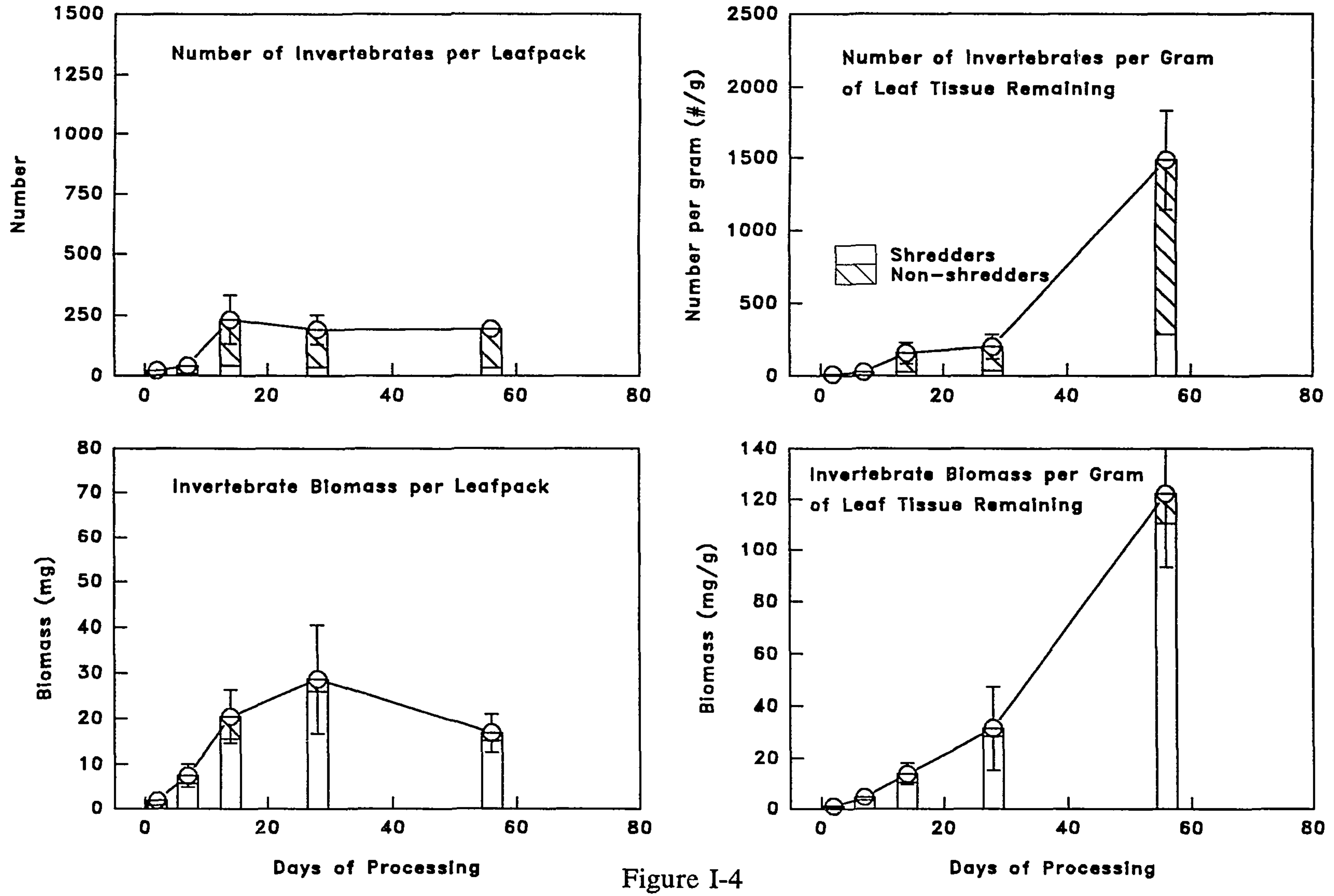


Figure I-4

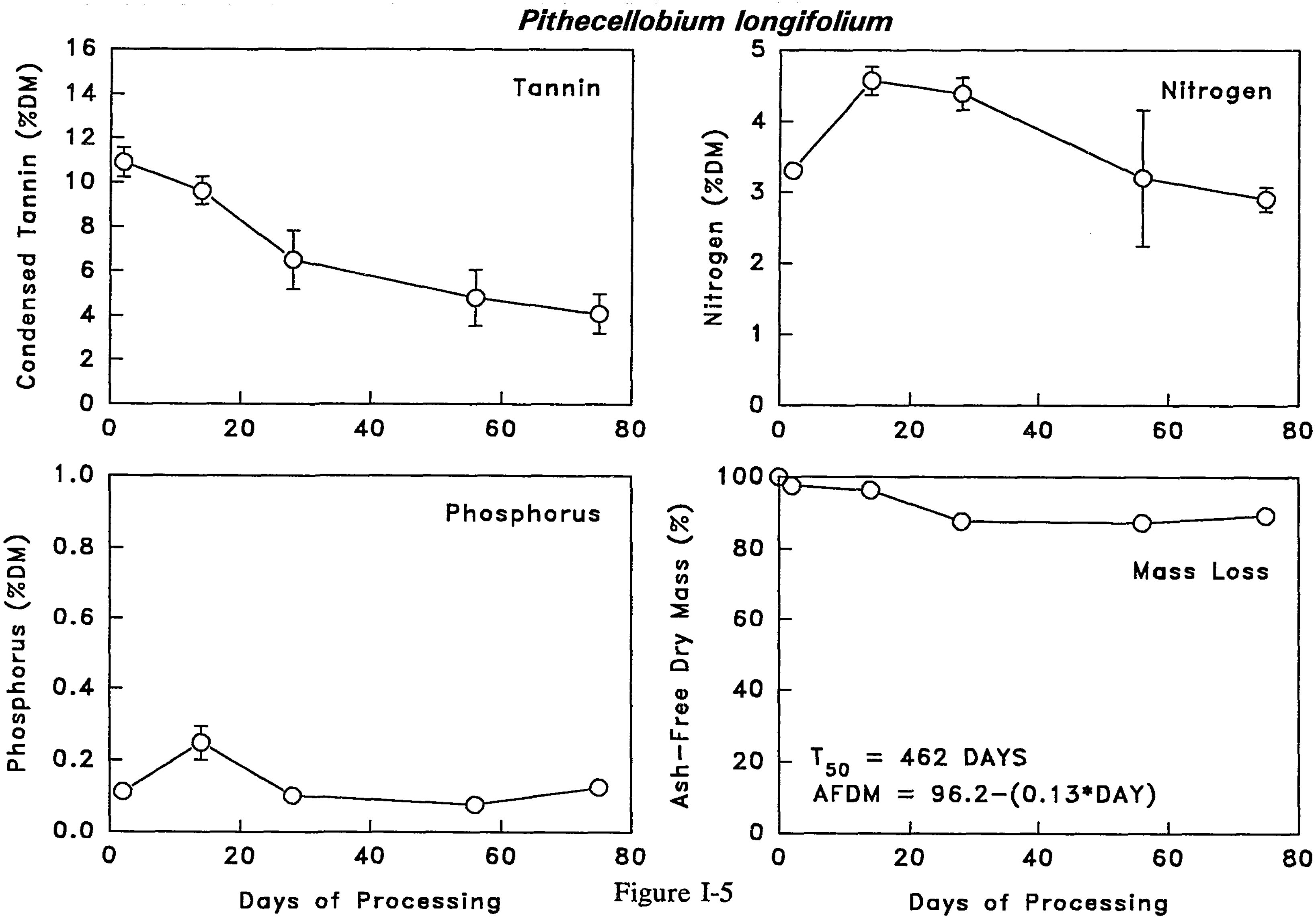

Pithecellobium longifolium
Tannin
Condensed Tannin (%DM)
0
2
4
6
8
10
12
14
16
Nitrogen
Nitrogen (%DM)
0
1
2
3
4
5
Phosphorus
Phosphorus (%DM)
0.0
0.2
0.4
0.6
0.8
1.0
Mass Loss
Ash-Free Dry Mass (%)
0
20
40
60
80
100
T_{50} = 462 DAYS
AFDM = 96.2-(0.13*DAY)
0
20
40
60
80
Days of Processing
Days of Processing

Figure I-5

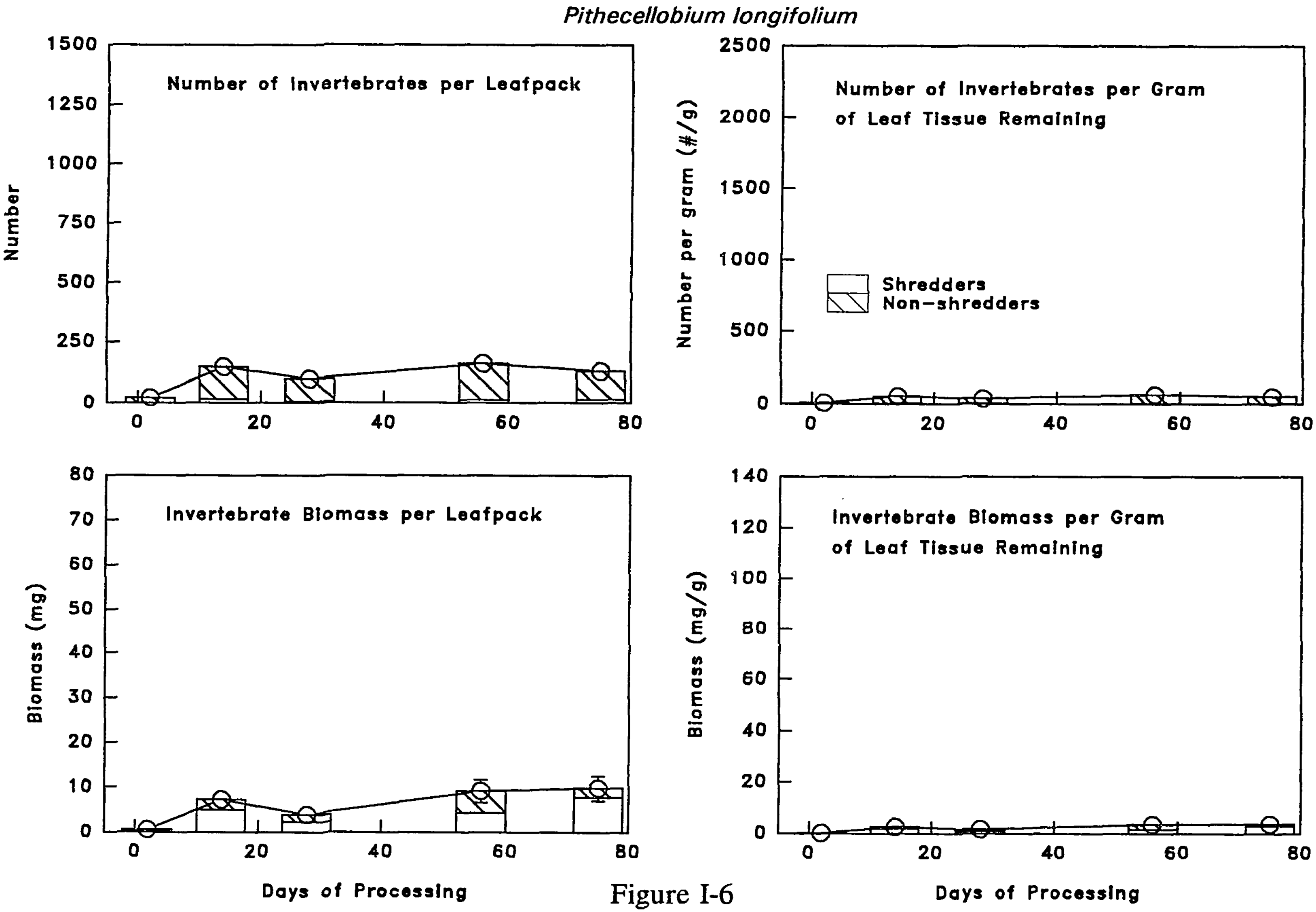

Pithecellobium longifolium
Number of Invertebrates per Leafpack
Number
1500
1250
1000
750
500
250
0
0
20
40
60
80
Number of Invertebrates per Gram of Leaf Tissue Remaining
Number per gram (#/g)
2500
2000
1500
1000
500
0
Shredders
Non-shredders
Invertebrate Biomass per Leafpack
Biomass (mg)
80
70
60
50
40
30
20
10
Invertebrate Biomass per Gram of Leaf Tissue Remaining
Biomass (mg/g)
140
120
100
Days of Processing
Days of Processing

Figure I-6

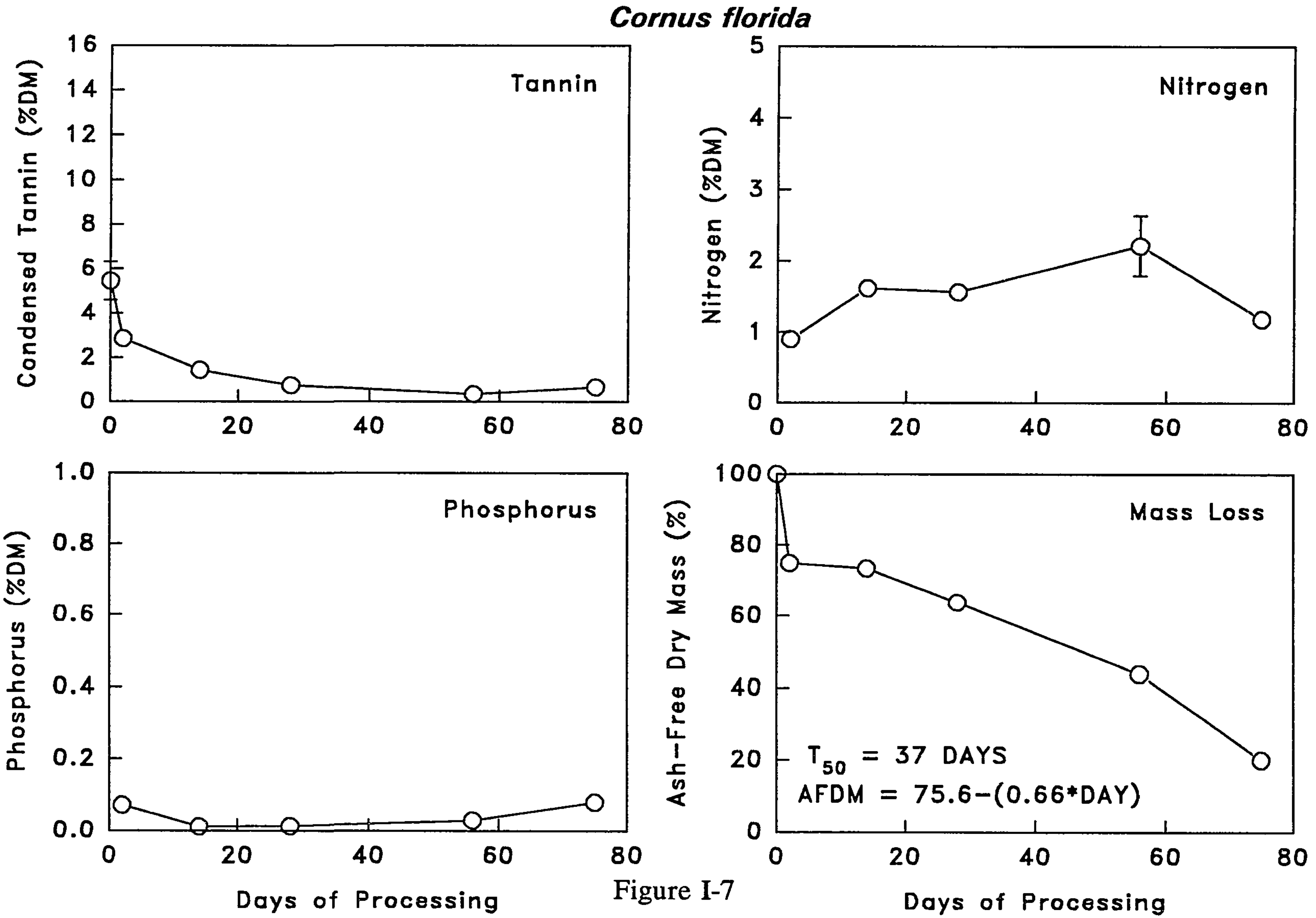

Cornus florida
Tannin
Condensed Tannin (%DM)
0
2
4
6
8
10
12
14
16
0
20
40
60
80
Nitrogen
Nitrogen (%DM)
0
1
2
3
4
5
0
20
40
60
80
Phosphorus
Phosphorus (%DM)
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
Days of Processing
Mass Loss
Ash-Free Dry Mass (%)
0
20
40
60
80
100
T50 = 37 DAYS
AFDM = 75.6-(0.66*DAY)
0
20
40
60
80
Days of Processing

Figure I-7

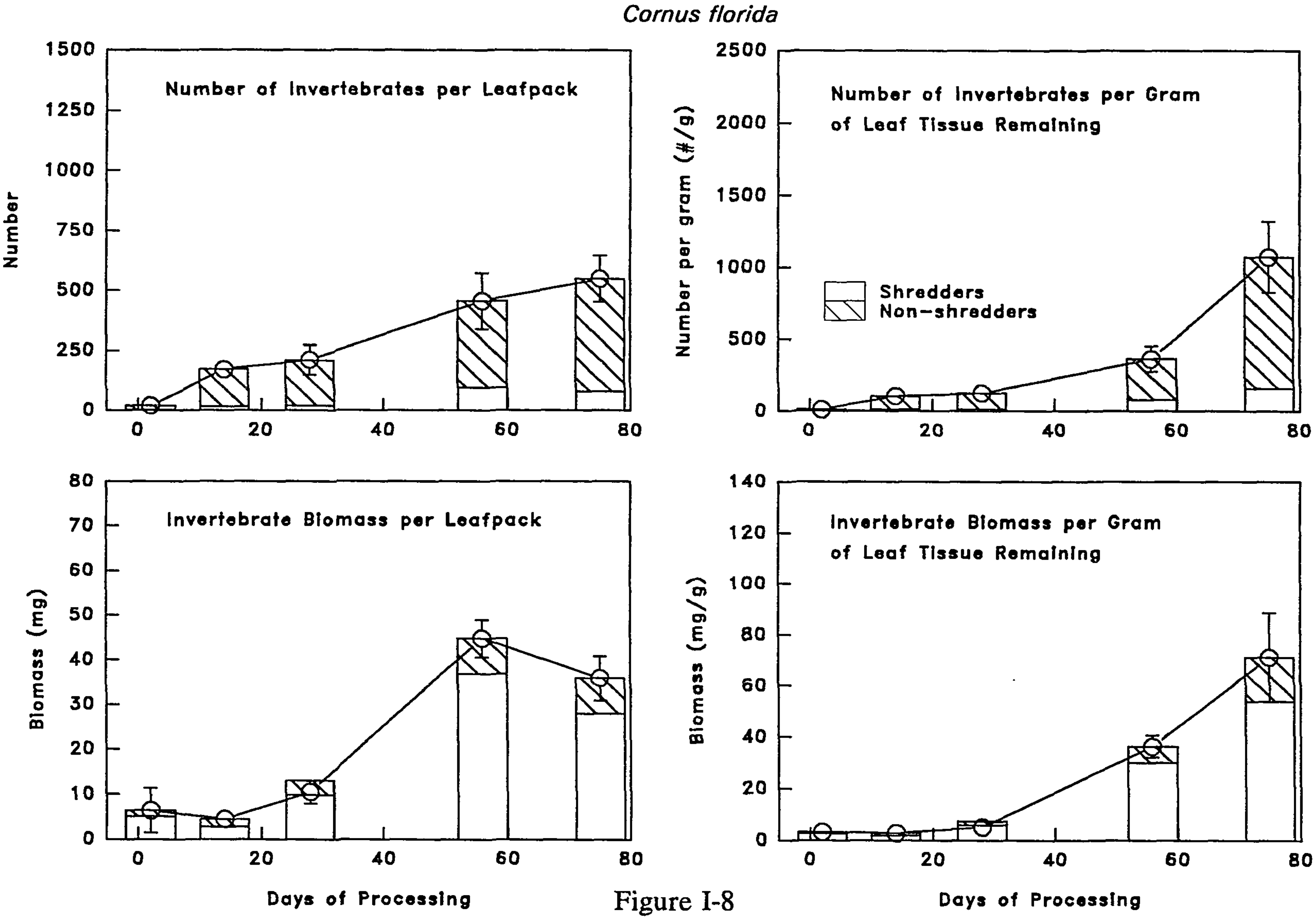

Cornus florida
Number of Invertebrates per Leafpack
Number
0
250
500
750
1000
1250
1500
Number of Invertebrates per Gram
of Leaf Tissue Remaining
Number per gram (#/g)
0
500
1000
1500
2000
2500
Shredders
Non-shredders
Invertebrate Biomass per Leafpack
Biomass (mg)
0
10
20
30
40
50
60
70
80
Invertebrate Biomass per Gram
of Leaf Tissue Remaining
Biomass (mg/g)
0
20
40
60
80
100
120
140
0
20
40
60
80
Days of Processing
Days of Processing

Figure I-8

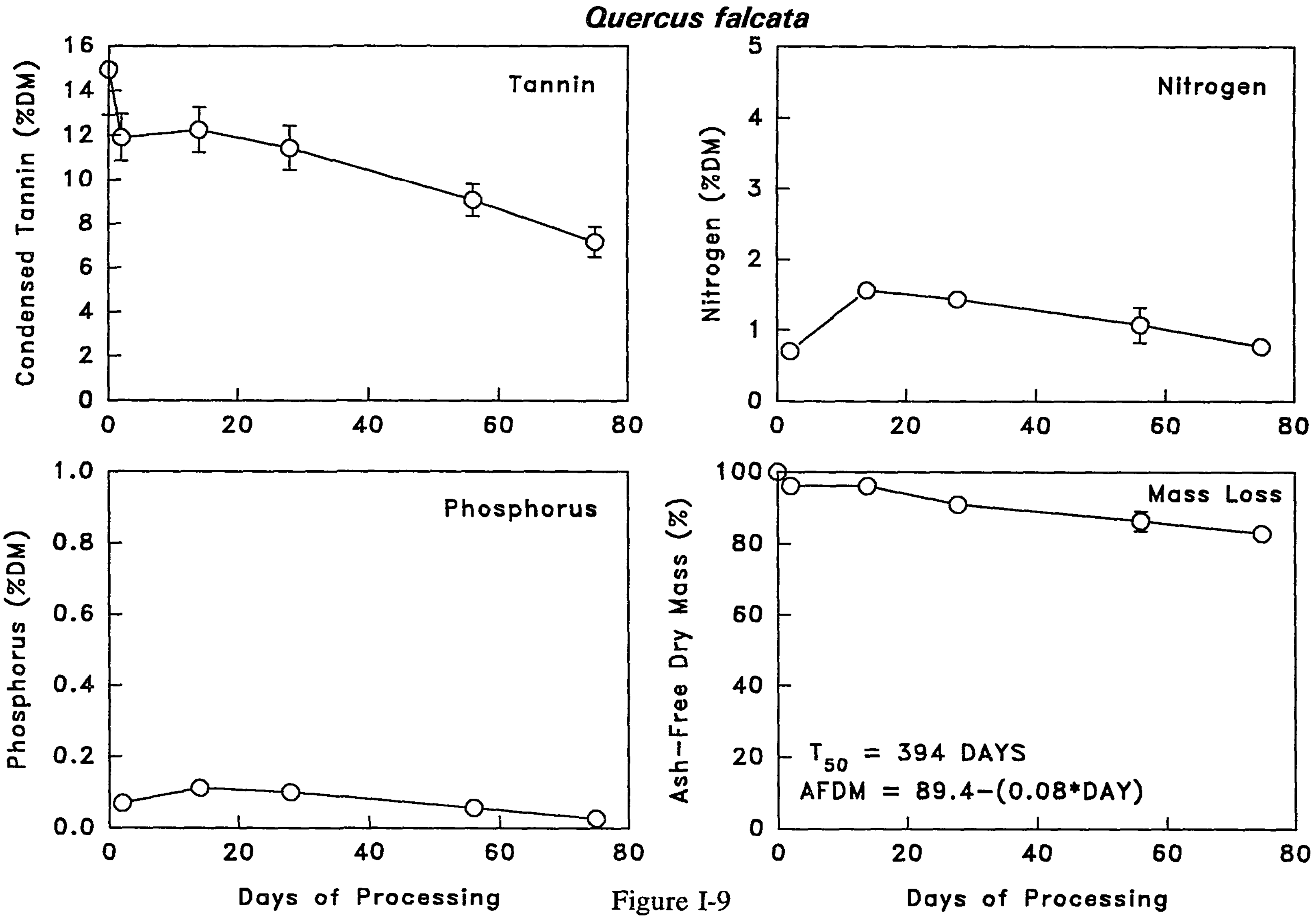

Quercus falcata
Tannin
Condensed Tannin (%DM)
0
2
4
6
8
10
12
14
16
Nitrogen
Nitrogen (%DM)
0
1
2
3
4
5
Phosphorus
Phosphorus (%DM)
0.0
0.2
0.4
0.6
0.8
1.0
Mass Loss
Ash-Free Dry Mass (%)
0
20
40
60
80
100
T50 = 394 DAYS
AFDM = 89.4-(0.08*DAY)
0
20
40
60
80
Days of Processing
Days of Processing

Figure I-9

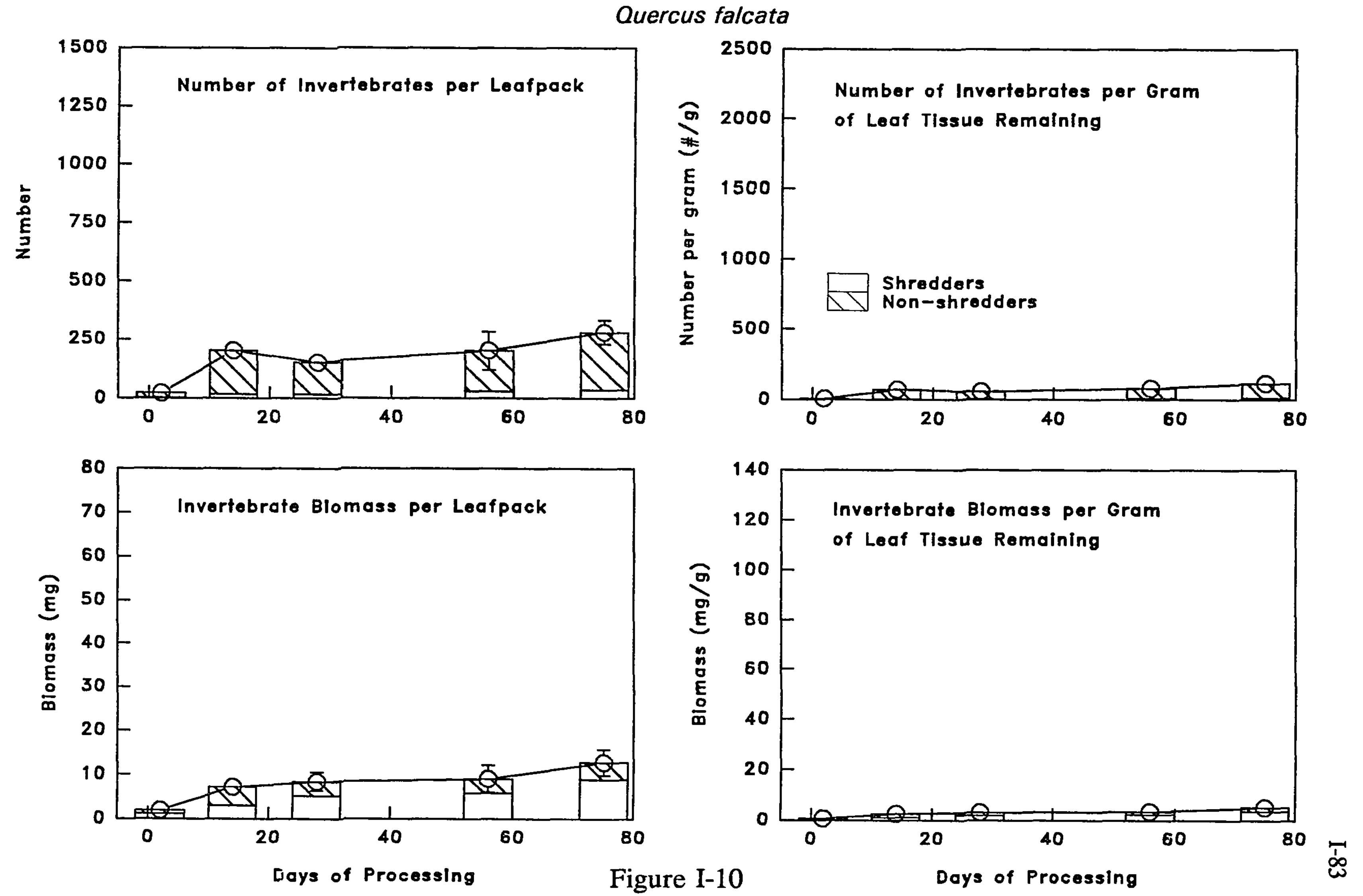

Quercus falcata
Number of Invertebrates per Leafpack
Number
1500
1250
1000
750
500
250
0
0
20
40
60
80
Number of Invertebrates per Gram
of Leaf Tissue Remaining
Number per gram (#/g)
2500
2000
1500
1000
500
0
Shredders
Non-shredders
Invertebrate Biomass per Leafpack
Biomass (mg)
80
70
60
50
40
30
20
10
0
Days of Processing
Invertebrate Biomass per Gram
of Leaf Tissue Remaining
Biomass (mg/g)
140
120
100
80
60
40
20
0
Days of Processing

Figure I-10

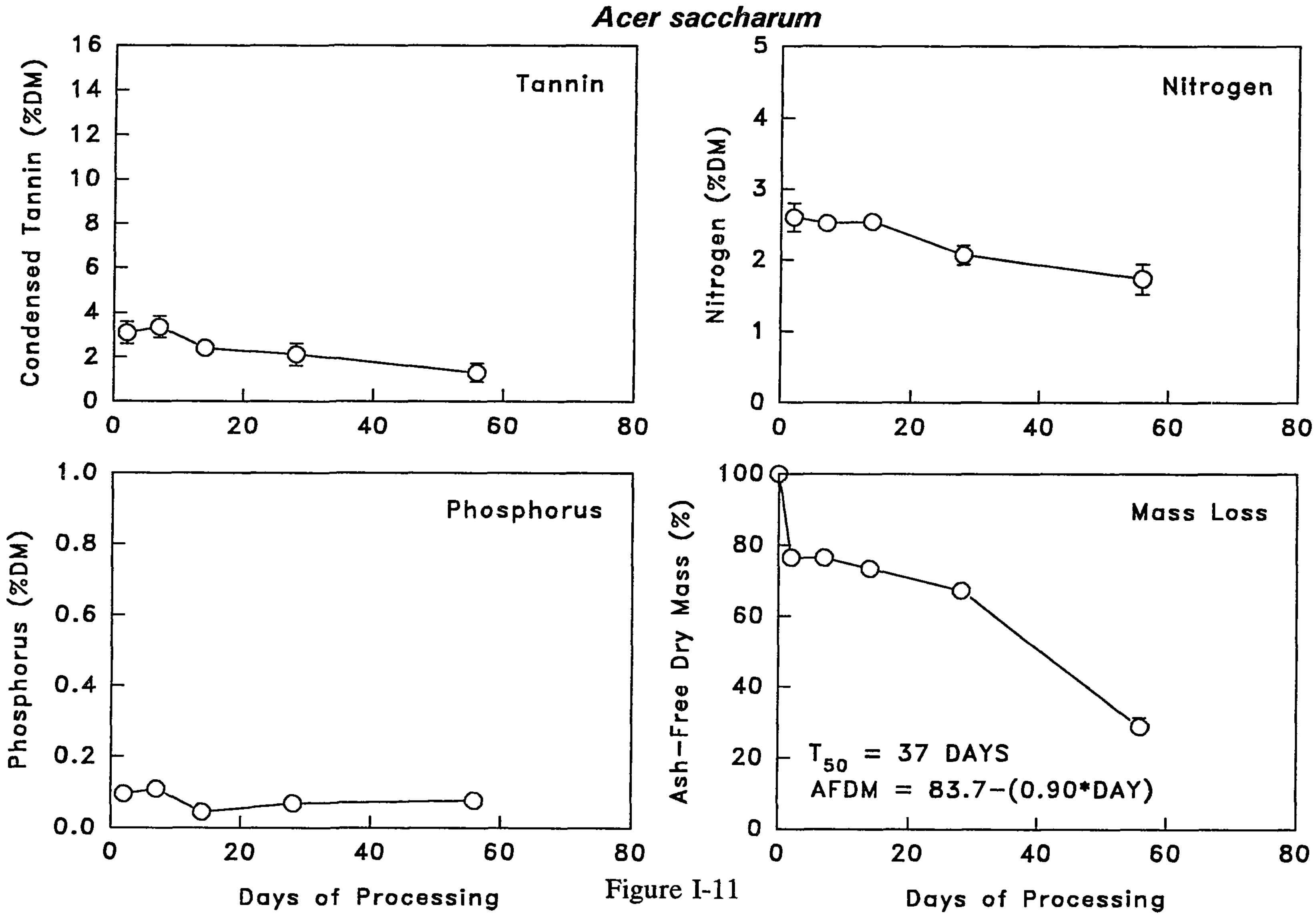

Acer saccharum
Tannin
Condensed Tannin (%DM)
0
2
4
6
8
10
12
14
16
0
20
40
60
80
Nitrogen
Nitrogen (%DM)
0
1
2
3
4
5
0
20
40
60
80
Phosphorus
Phosphorus (%DM)
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
Days of Processing
Mass Loss
Ash-Free Dry Mass (%)
0
20
40
60
80
100
T_{50} = 37 DAYS
AFDM = 83.7-(0.90*DAY)
0
20
40
60
80
Days of Processing

Figure I-11

Acer saccharum

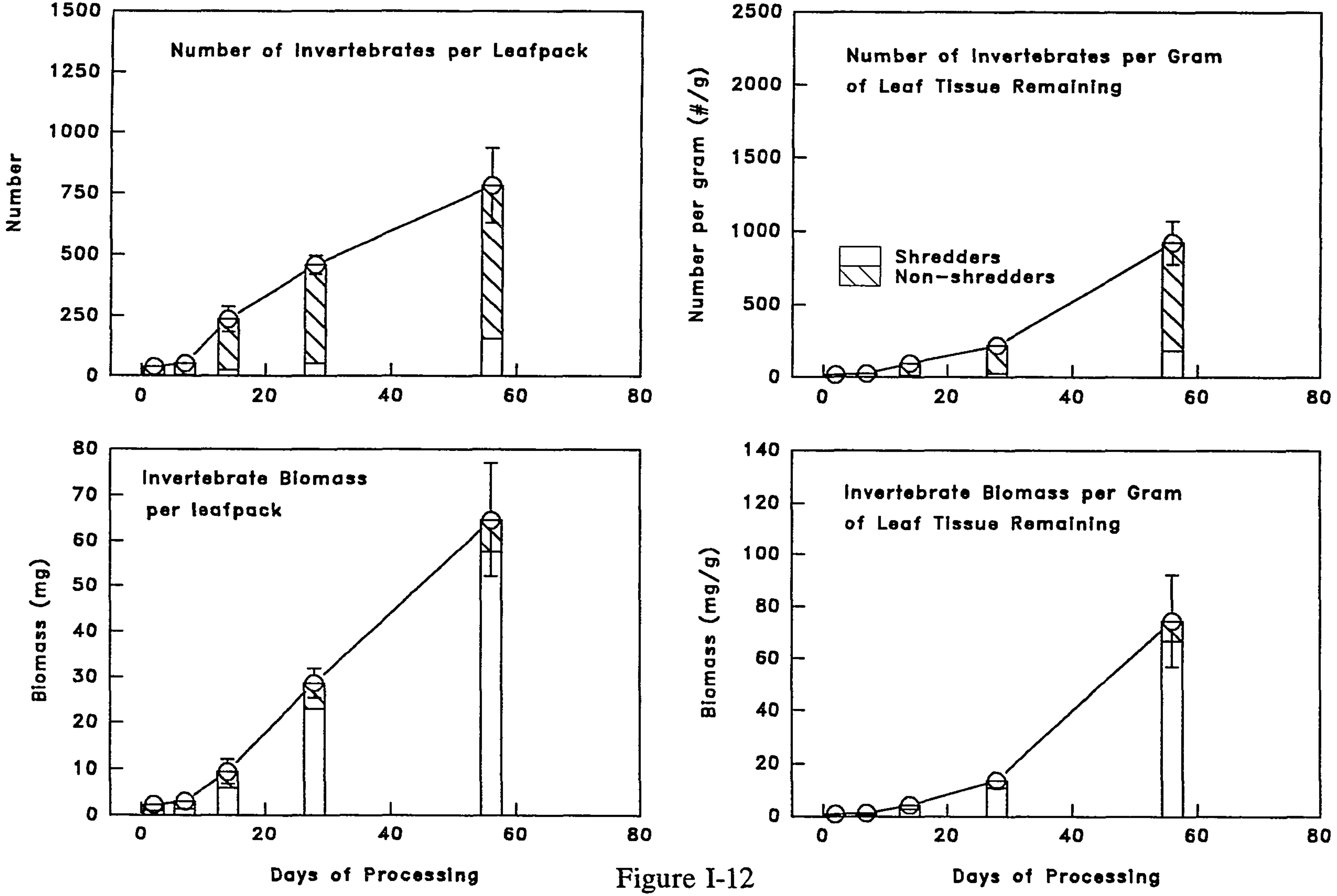


Figure I-12

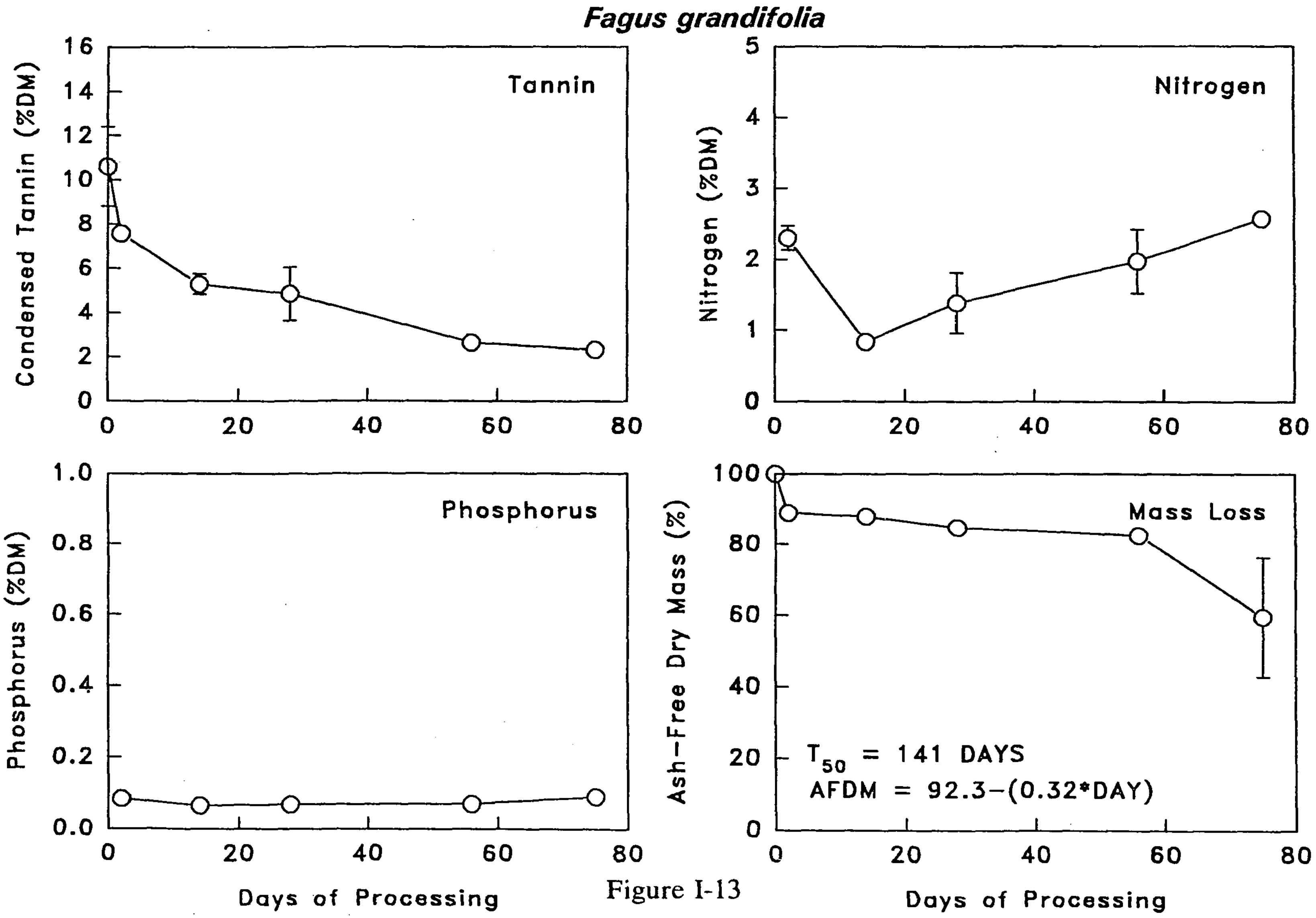

Fagus grandifolia
Tannin
Condensed Tannin (%DM)
0
2
4
6
8
10
12
14
16
Nitrogen
Nitrogen (%DM)
0
1
2
3
4
5
Phosphorus
Phosphorus (%DM)
0.0
0.2
0.4
0.6
0.8
1.0
Mass Loss
Ash-Free Dry Mass (%)
0
20
40
60
80
100
T_{50} = 141 DAYS
AFDM = 92.3-(0.32*DAY)
0
20
40
60
80
Days of Processing
Days of Processing

Figure I-13

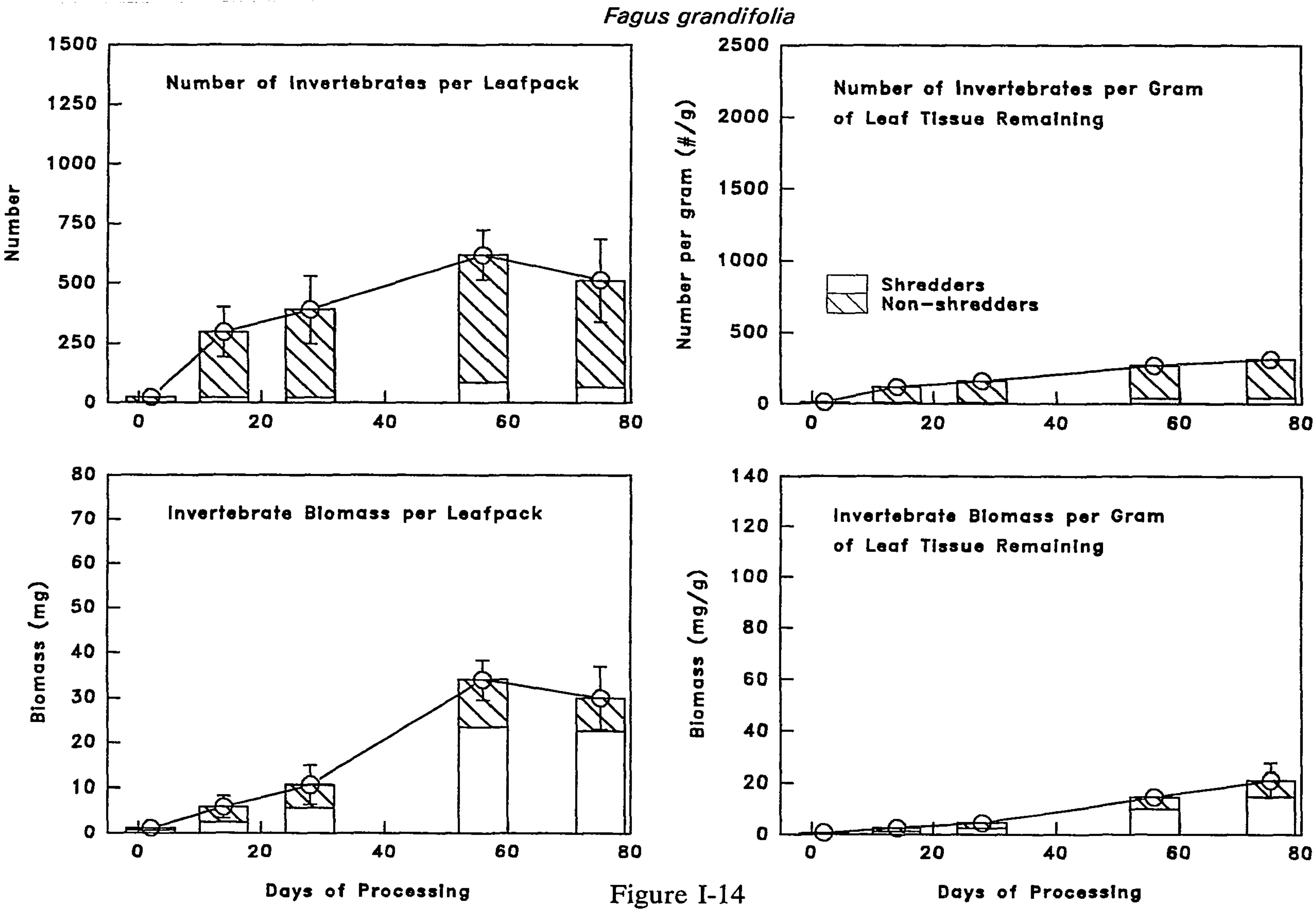

Fagus grandifolia
Number of Invertebrates per Leafpack
Number
1500
1250
1000
750
500
250
0
0
20
40
60
80
Number of Invertebrates per Gram
of Leaf Tissue Remaining
Number per gram (#/g)
2500
2000
1500
1000
500
0
Shredders
Non-shredders
Invertebrate Biomass per Leafpack
Biomass (mg)
80
70
60
50
40
30
20
10
0
Days of Processing
Invertebrate Biomass per Gram
of Leaf Tissue Remaining
Biomass (mg/g)
140
120
100
80
60
40
20
0
Days of Processing

Figure I-14

Alnus rugosa

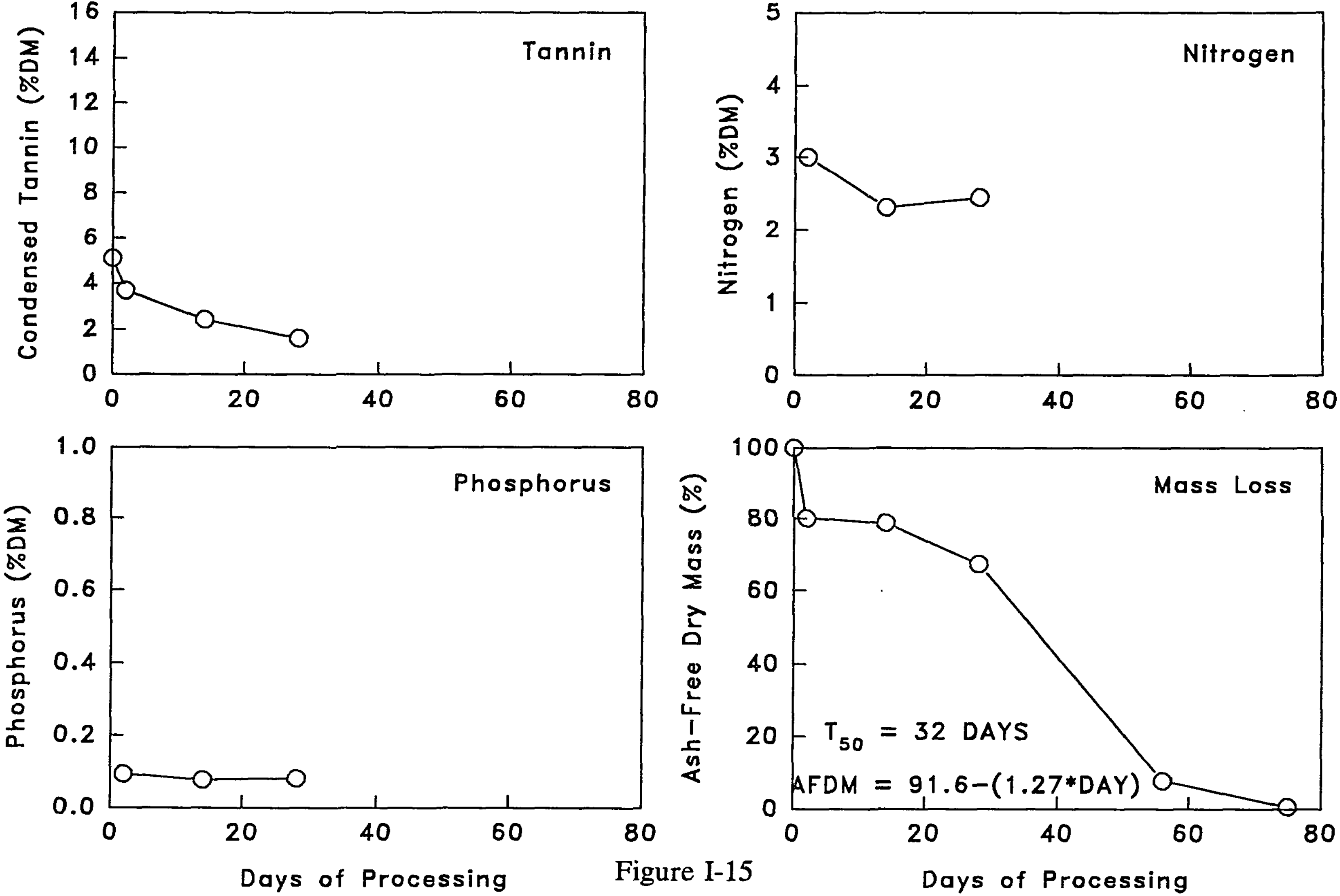


Figure I-15

Alnus rugosa

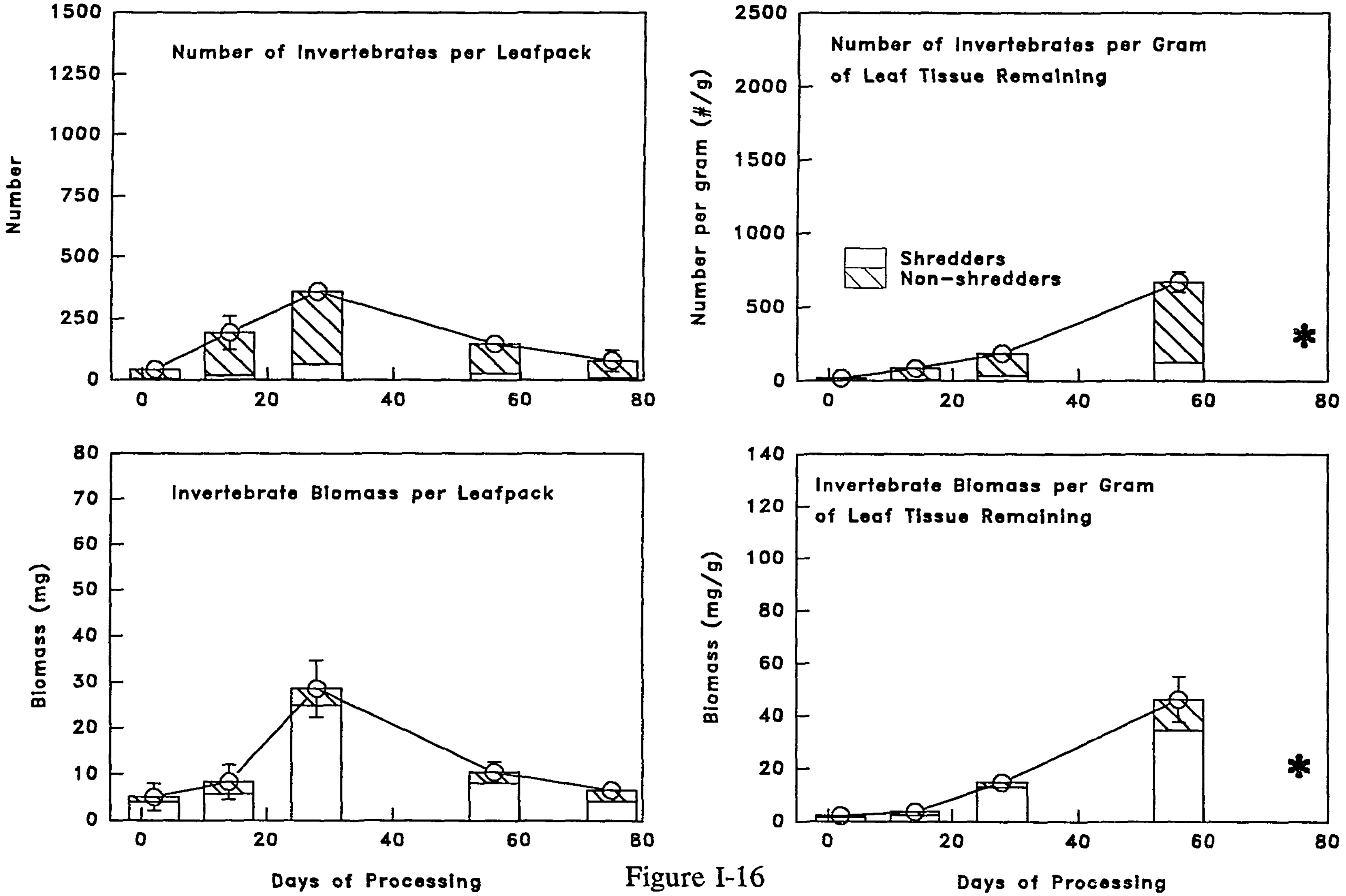


Figure I-16

Quercus rubra

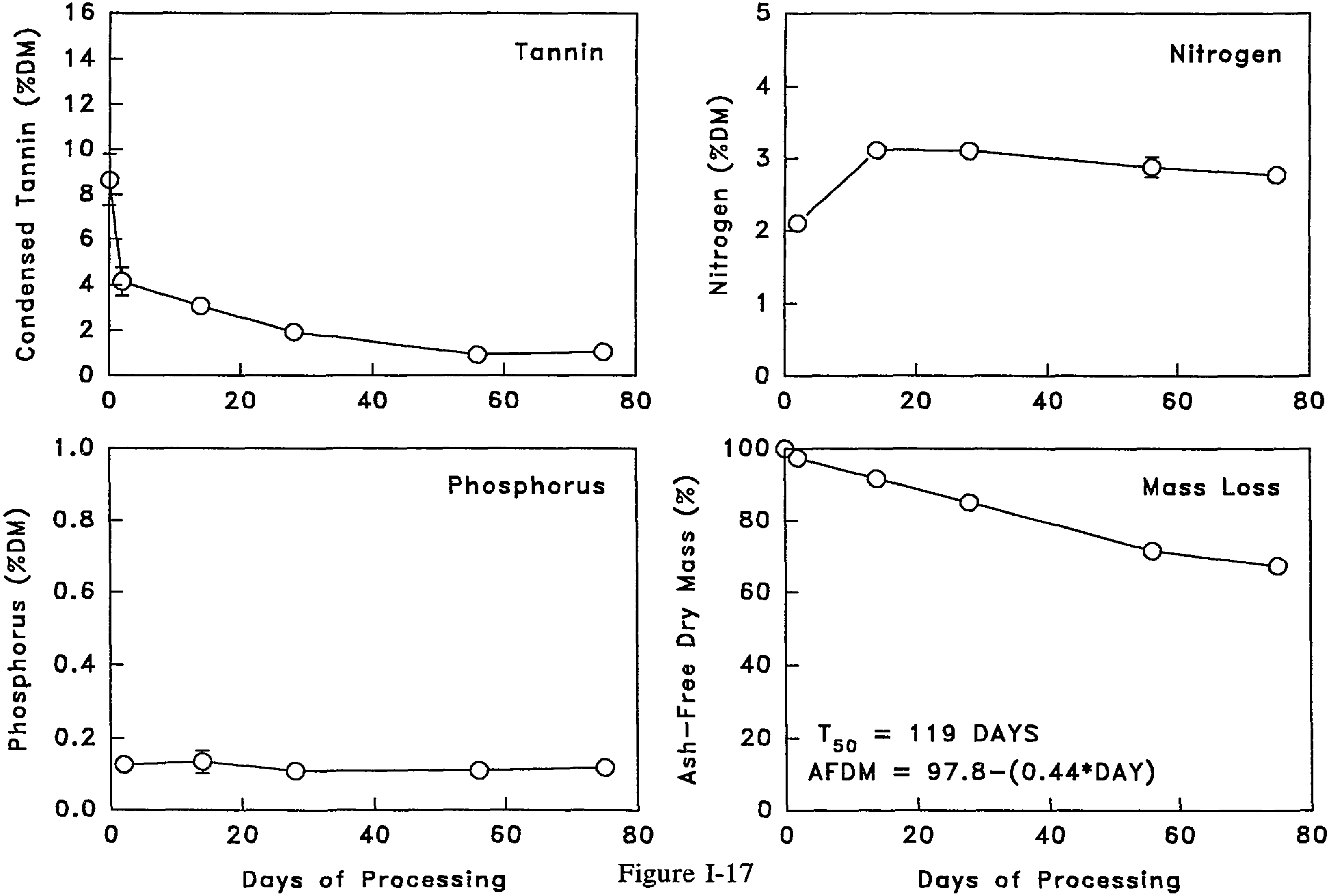


Figure I-17

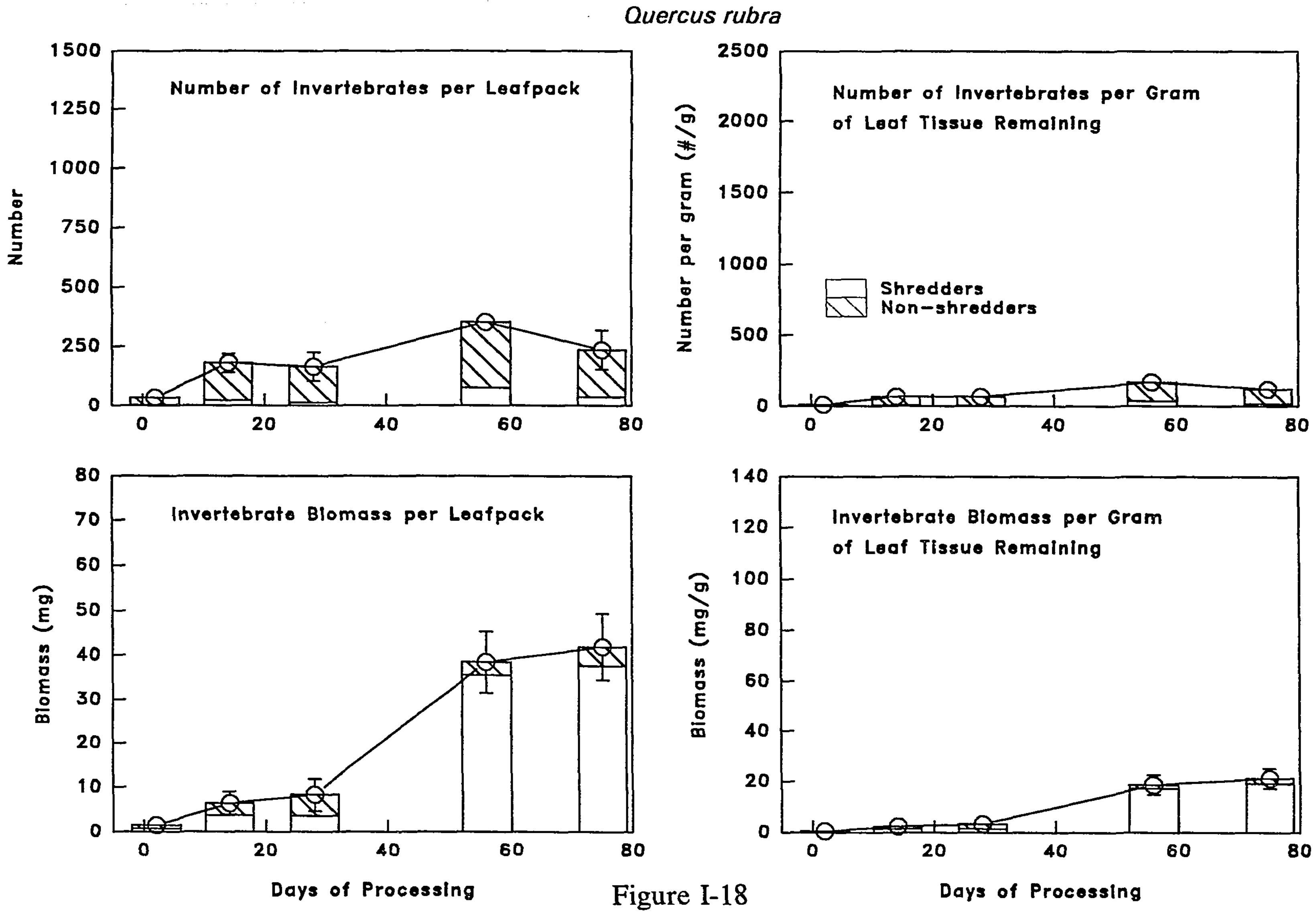

Quercus rubra
Number of Invertebrates per Leafpack
Number
1500
1250
1000
750
500
250
0
20
40
60
80
Number of Invertebrates per Gram of Leaf Tissue Remaining
Number per gram (#/g)
2500
2000
1500
1000
500
Shredders
Non-shredders
Invertebrate Biomass per Leafpack
Biomass (mg)
70
60
50
30
10
Invertebrate Biomass per Gram of Leaf Tissue Remaining
Biomass (mg/g)
140
120
100
Days of Processing

Figure I-18

***Alnus crispa* (winter-picked leaves)**

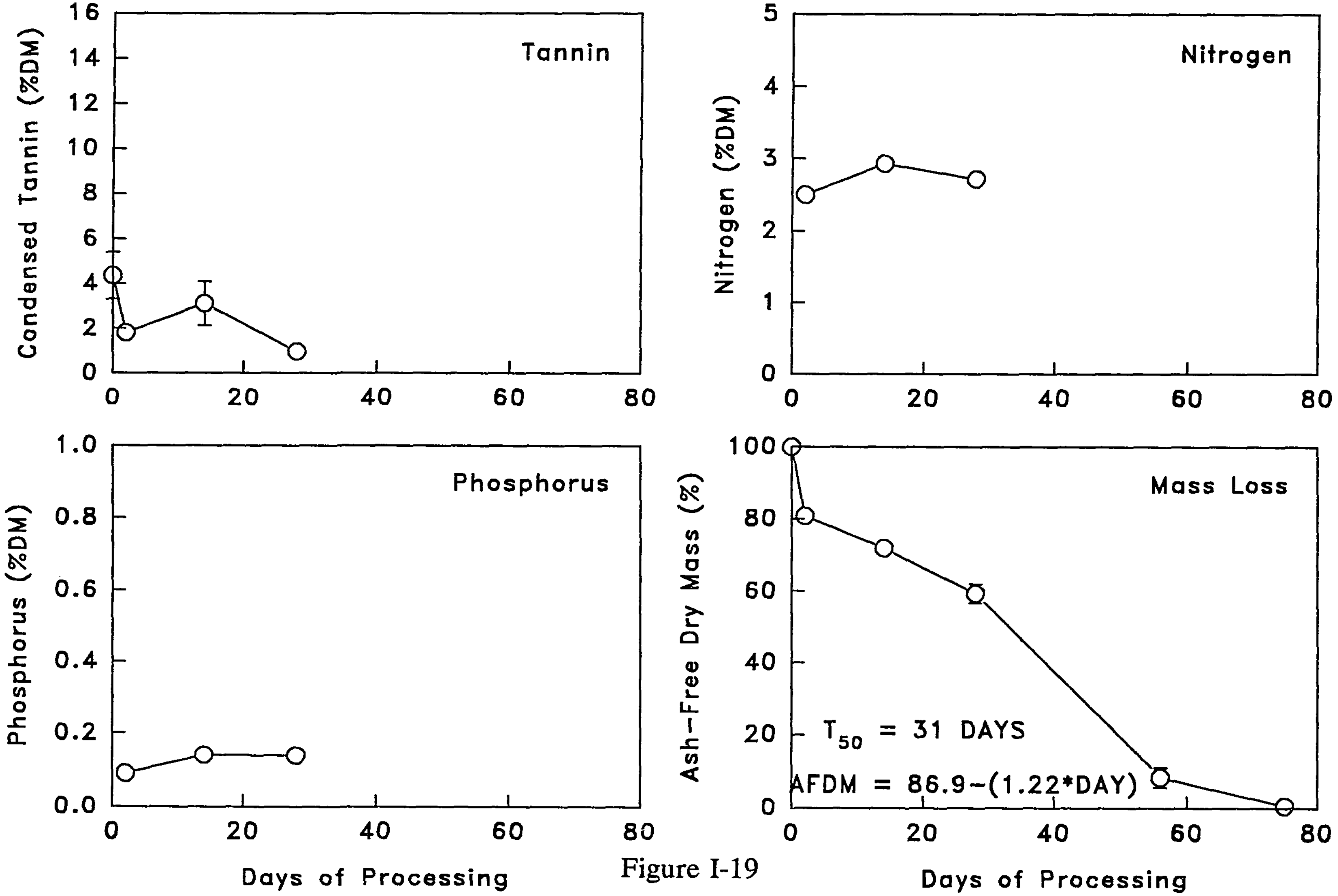


Figure I-19

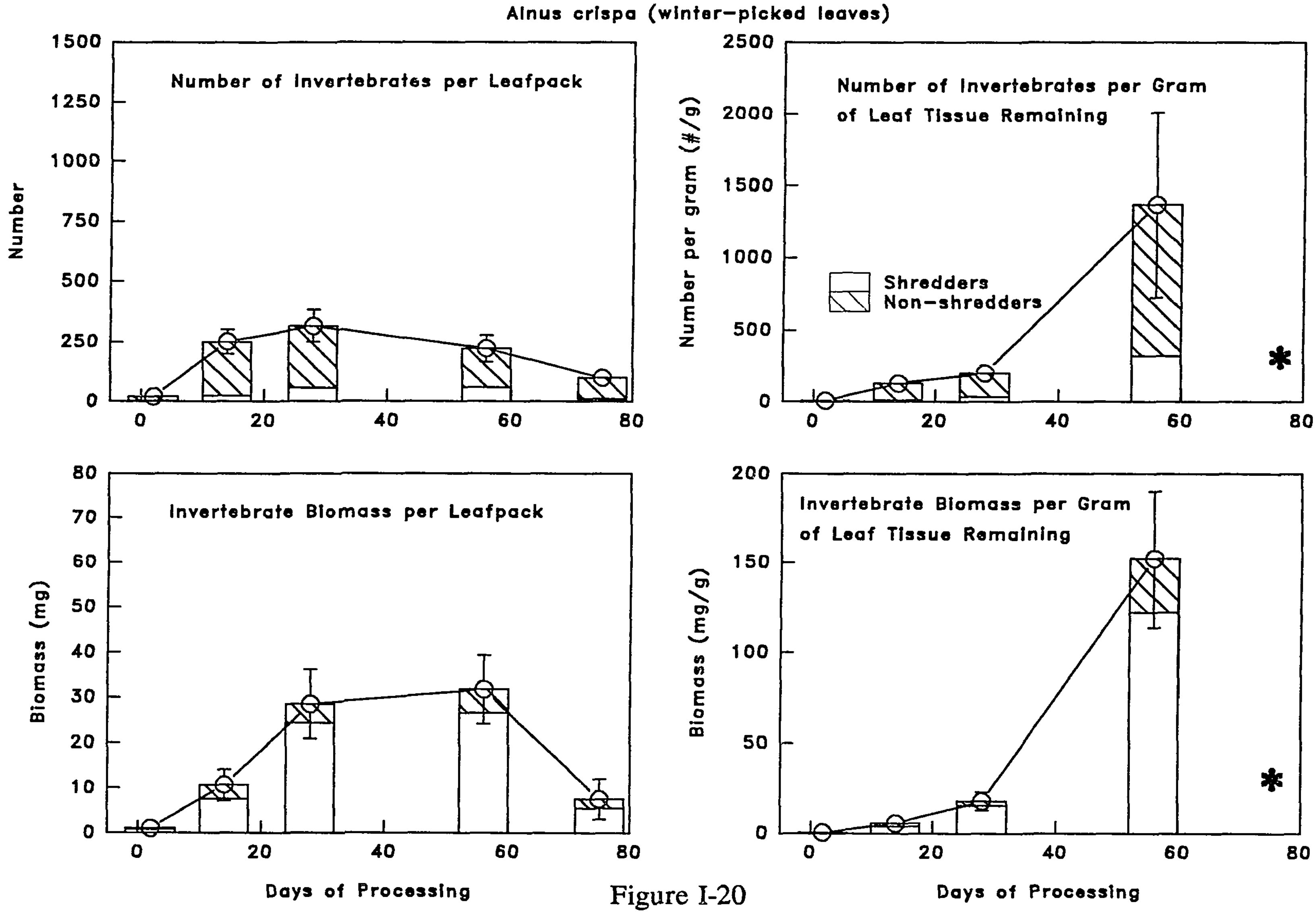

Alnus crispa (winter-picked leaves)
Number of Invertebrates per Leafpack
Number
1500
1250
1000
750
500
250
0
0
20
40
60
80
Number of Invertebrates per Gram of Leaf Tissue Remaining
Number per gram (#/g)
2500
2000
1500
1000
500
0
Shredders
Non-shredders
*
Invertebrate Biomass per Leafpack
Biomass (mg)
80
70
60
50
40
30
20
10
0
Days of Processing
Invertebrate Biomass per Gram of Leaf Tissue Remaining
Biomass (mg/g)
200
150
100
50
0
*
Days of Processing

Figure I-20

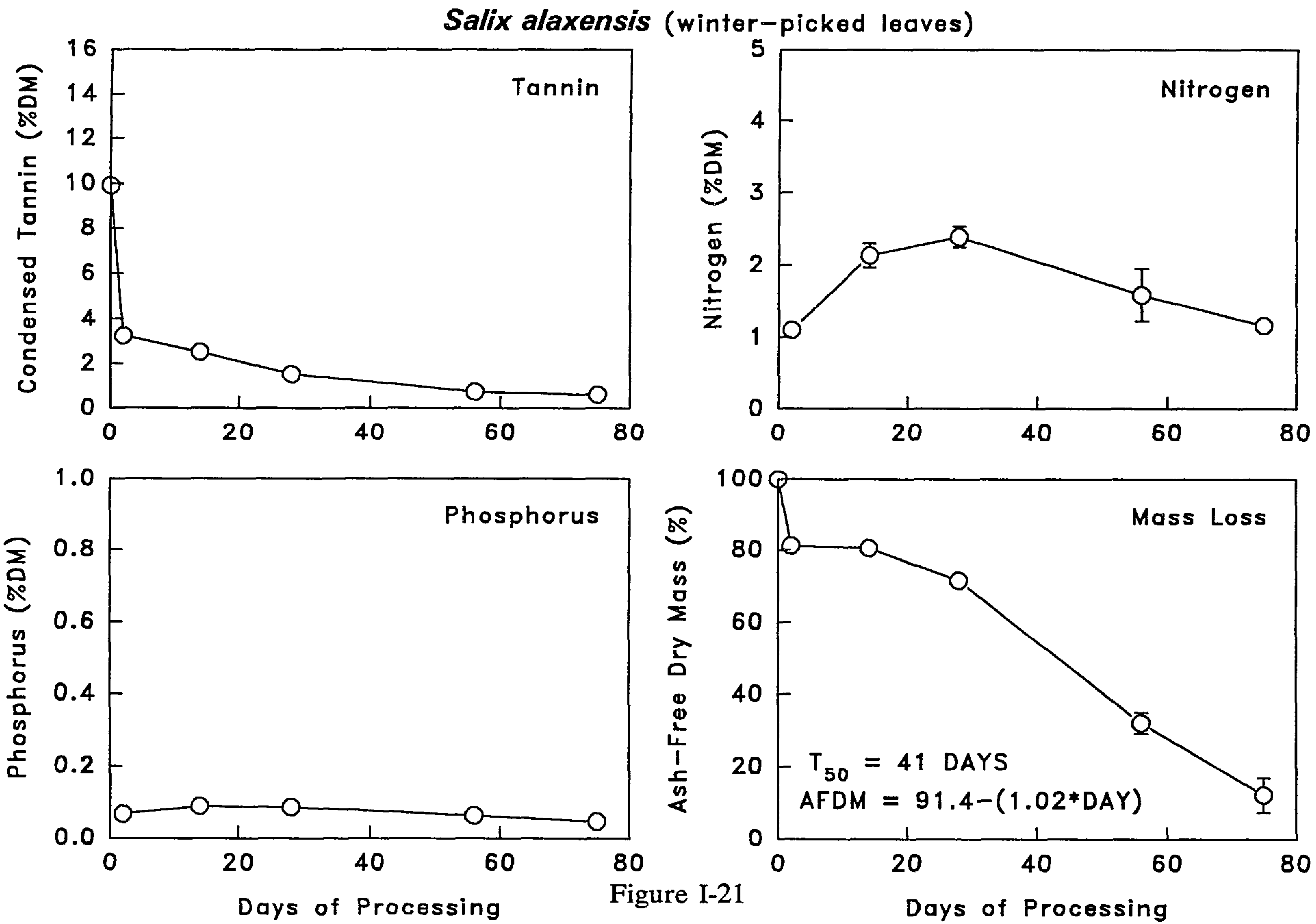

Salix alaxensis (winter-picked leaves)
Tannin
Condensed Tannin (%DM)
0
2
4
6
8
10
12
14
16
Nitrogen
Nitrogen (%DM)
0
1
2
3
4
5
Phosphorus
Phosphorus (%DM)
0.0
0.2
0.4
0.6
0.8
1.0
Mass Loss
Ash-Free Dry Mass (%)
0
20
40
60
80
100
T_{50} = 41 DAYS
AFDM = 91.4-(1.02*DAY)
0
20
40
60
80
Days of Processing

Figure I-21

Salix alaxensis (winter-picked leaves)

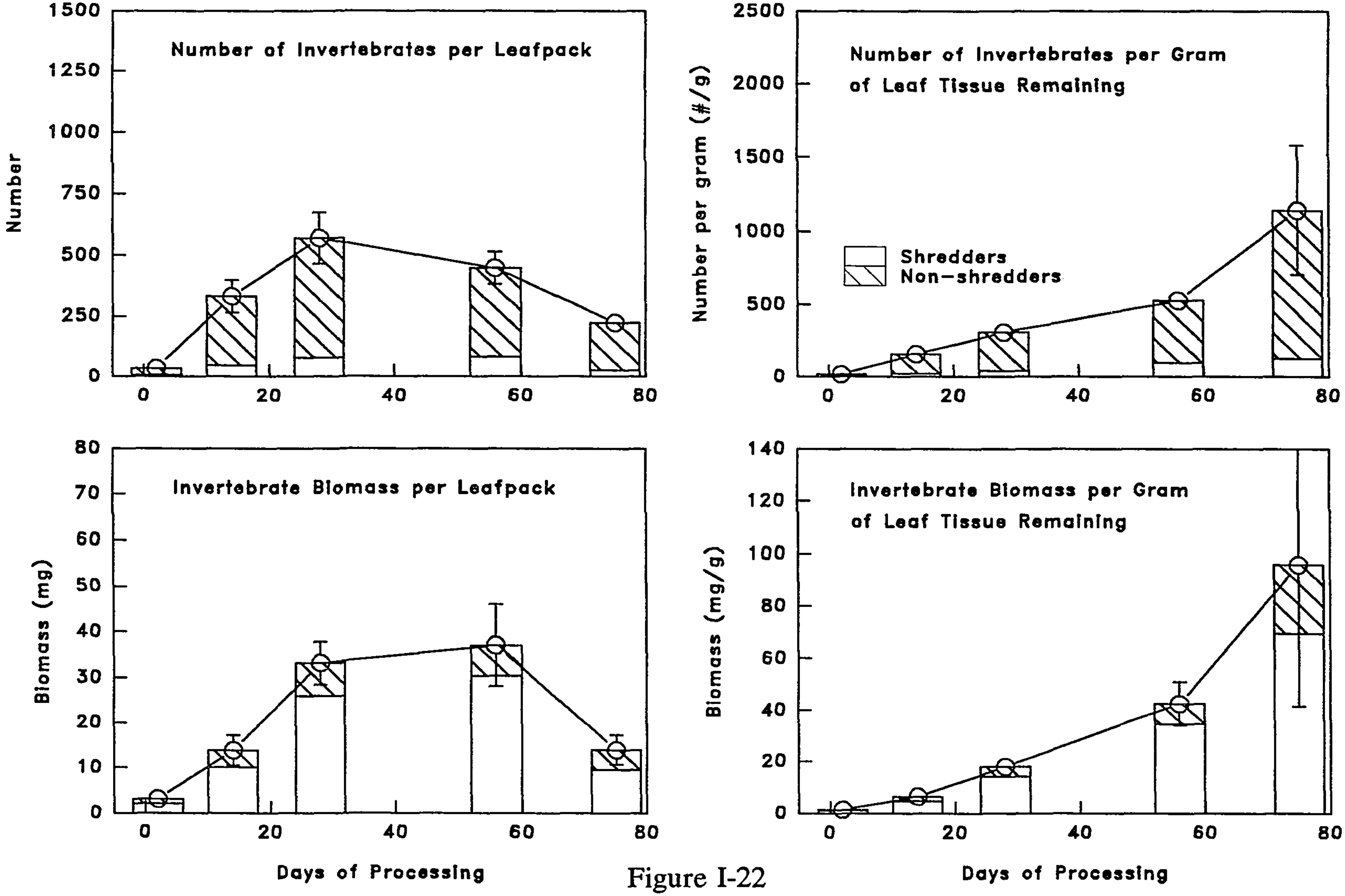


Figure I-22

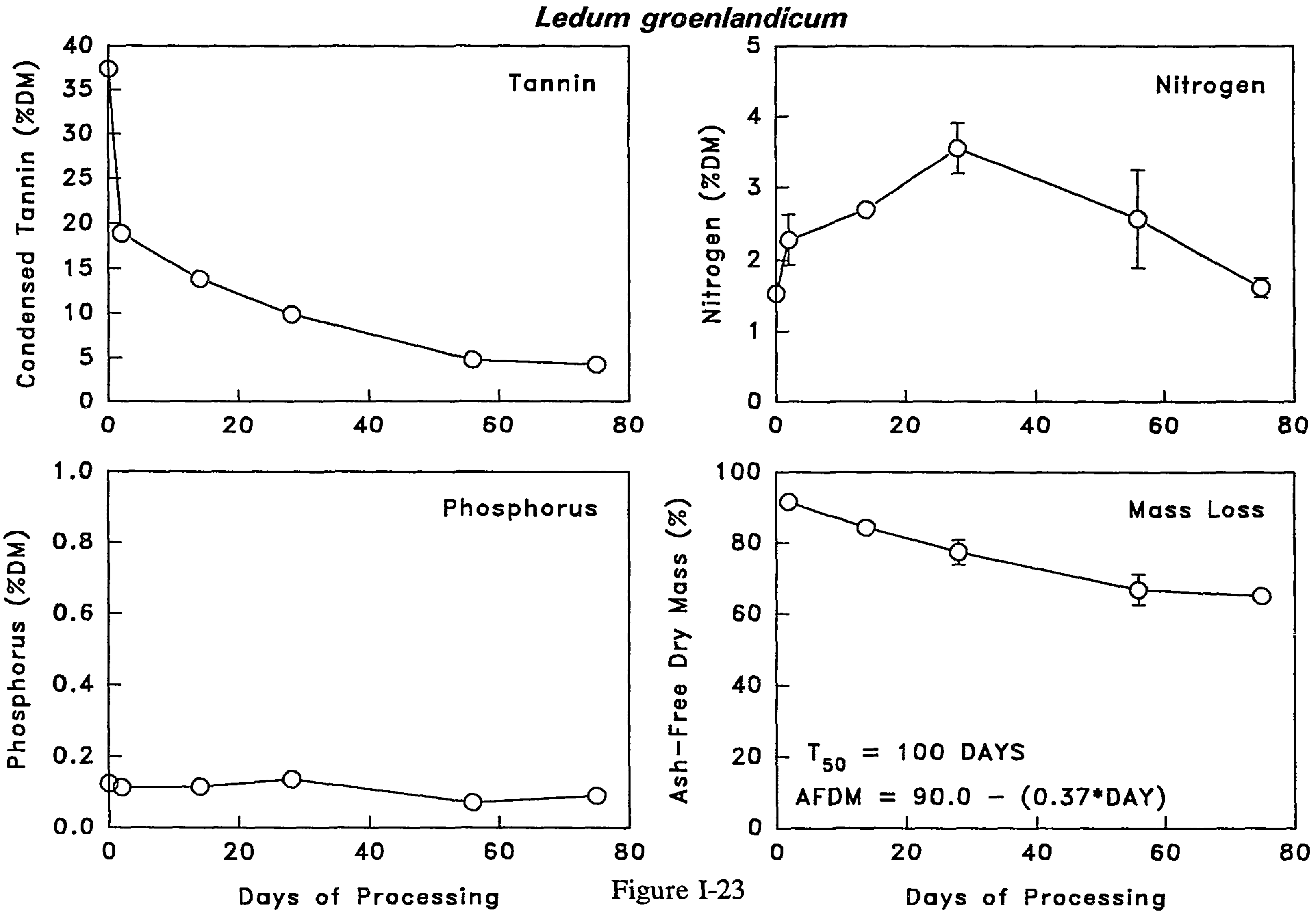

Ledum groenlandicum
Tannin
Condensed Tannin (%DM)
0
5
10
15
20
25
30
35
40
Nitrogen
Nitrogen (%DM)
0
1
2
3
4
5
Phosphorus
Phosphorus (%DM)
0.0
0.2
0.4
0.6
0.8
1.0
Mass Loss
Ash-Free Dry Mass (%)
0
20
40
60
80
100
T_{50} = 100 DAYS
AFDM = 90.0 - (0.37*DAY)
0
20
40
60
80
Days of Processing
Days of Processing

Figure I-23

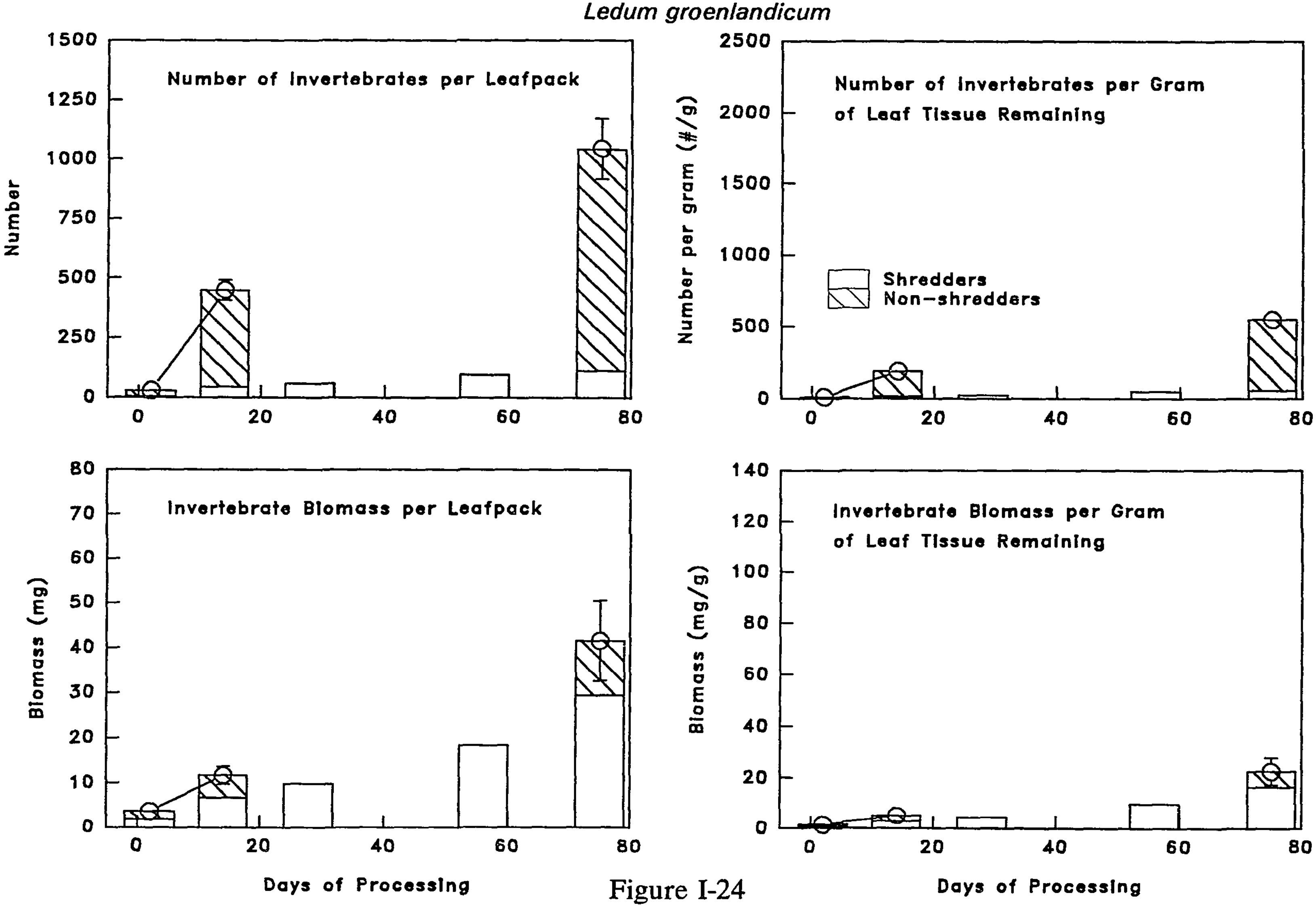

Ledum groenlandicum
Number of Invertebrates per Leafpack
Number
1500
1250
1000
750
500
250
0
0
20
40
60
80
Number of Invertebrates per Gram of Leaf Tissue Remaining
Number per gram (#/g)
2500
2000
1500
1000
500
0
Shredders
Non-shredders
Invertebrate Biomass per Leafpack
Biomass (mg)
80
70
60
50
40
30
20
10
0
Invertebrate Biomass per Gram of Leaf Tissue Remaining
Biomass (mg/g)
140
120
100
80
60
40
20
0
Days of Processing
Days of Processing

Figure I-24

Salix pulcra

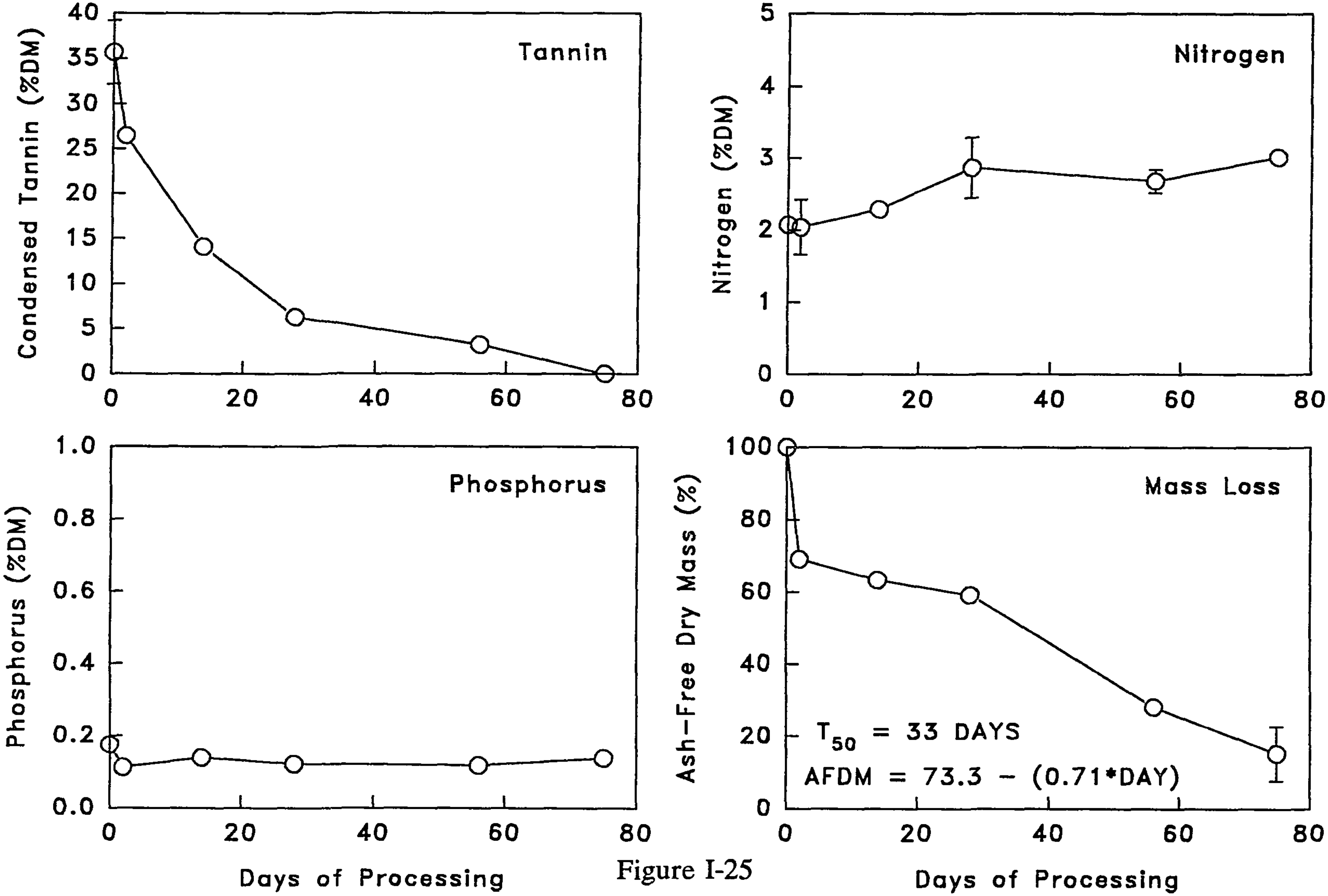


Figure I-25

Salix pulcra

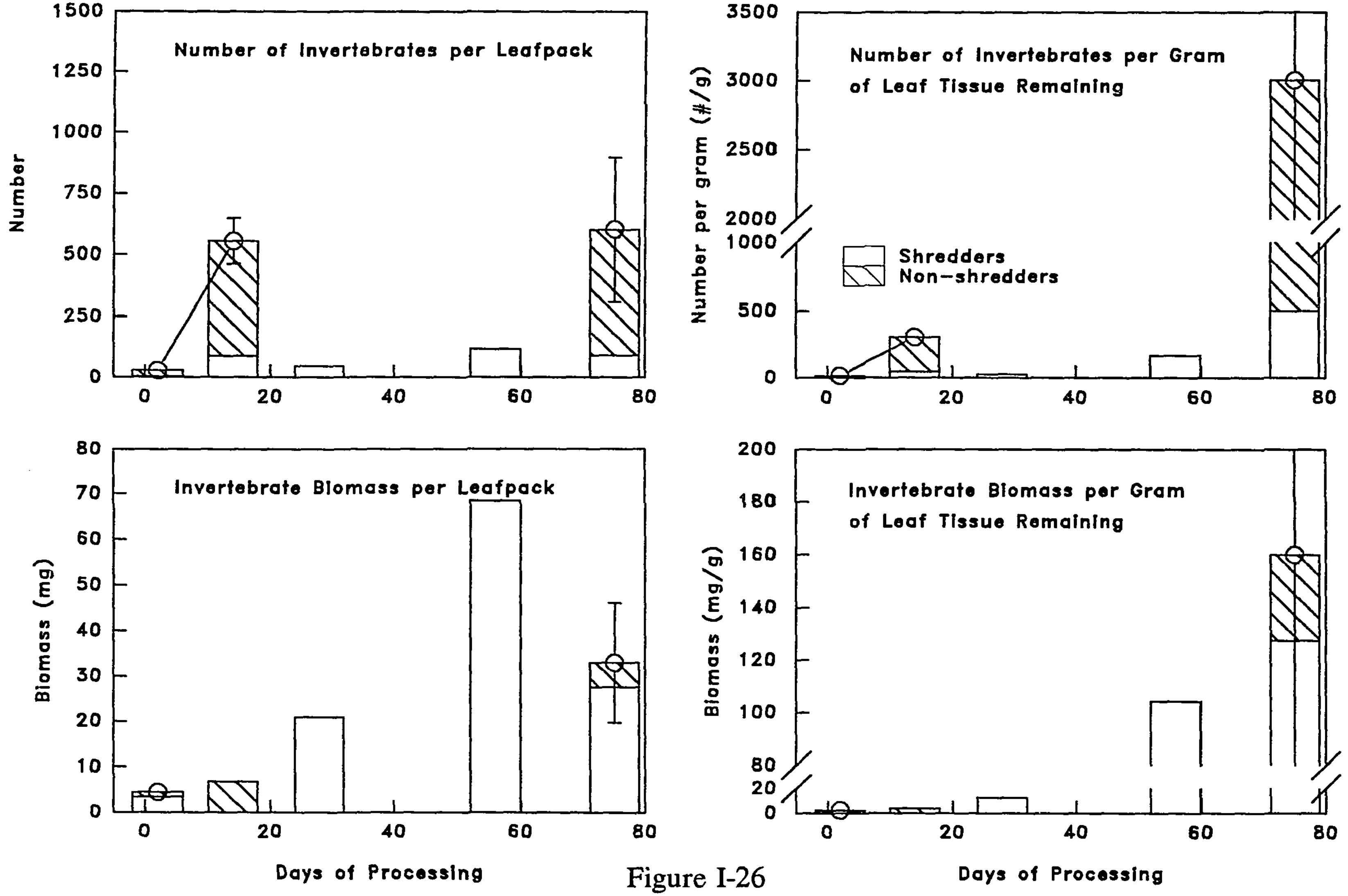


Figure I-26

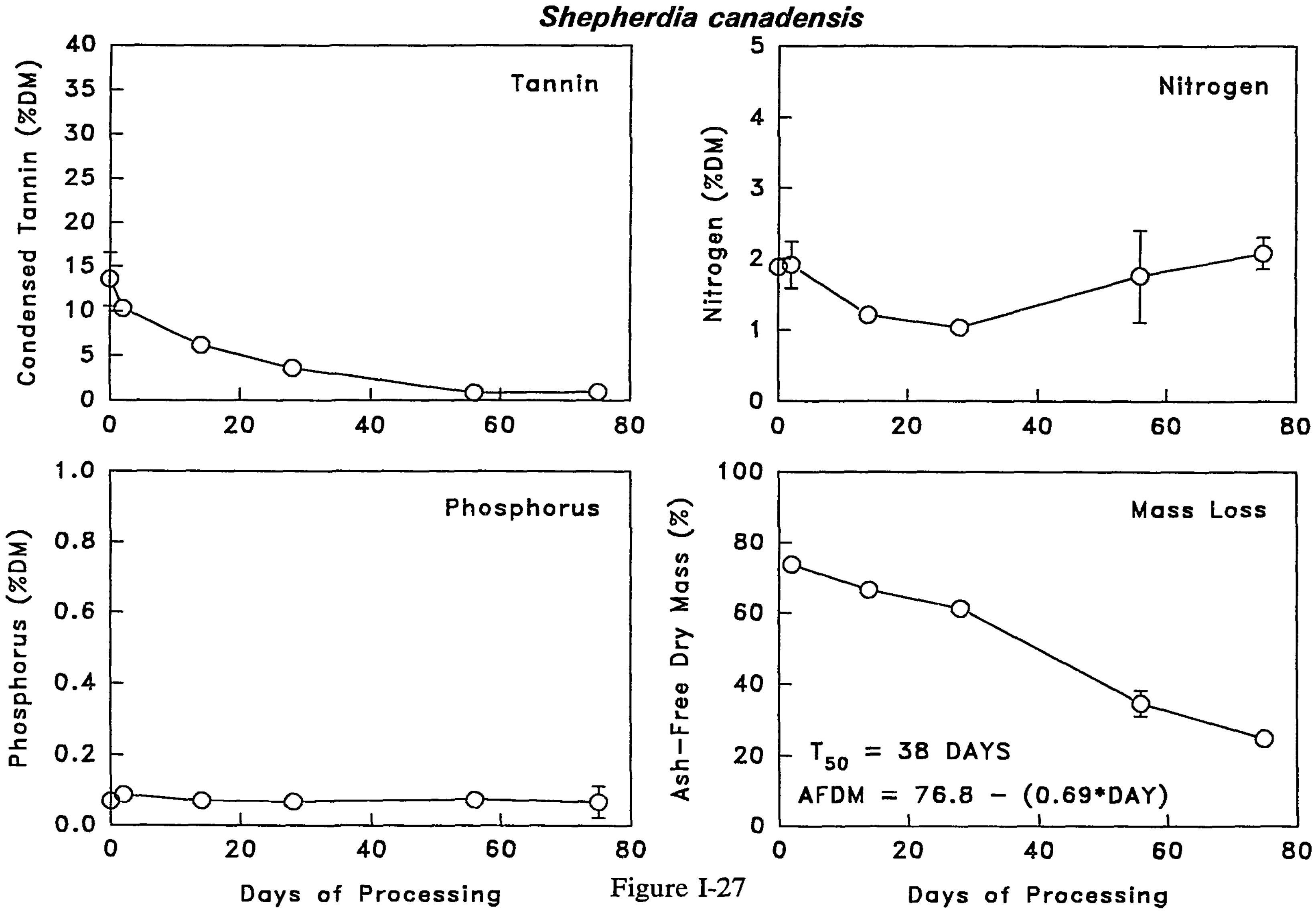

Shepherdia canadensis
Tannin
Condensed Tannin (%DM)
0
5
10
15
20
25
30
35
40
0
20
40
60
80
Nitrogen
Nitrogen (%DM)
0
1
2
3
4
5
0
20
40
60
80
Phosphorus
Phosphorus (%DM)
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
Days of Processing
Mass Loss
Ash-Free Dry Mass (%)
0
20
40
60
80
100
T_{50} = 38 DAYS
AFDM = 76.8 – (0.69*DAY)
0
20
40
60
80
Days of Processing

Figure I-27

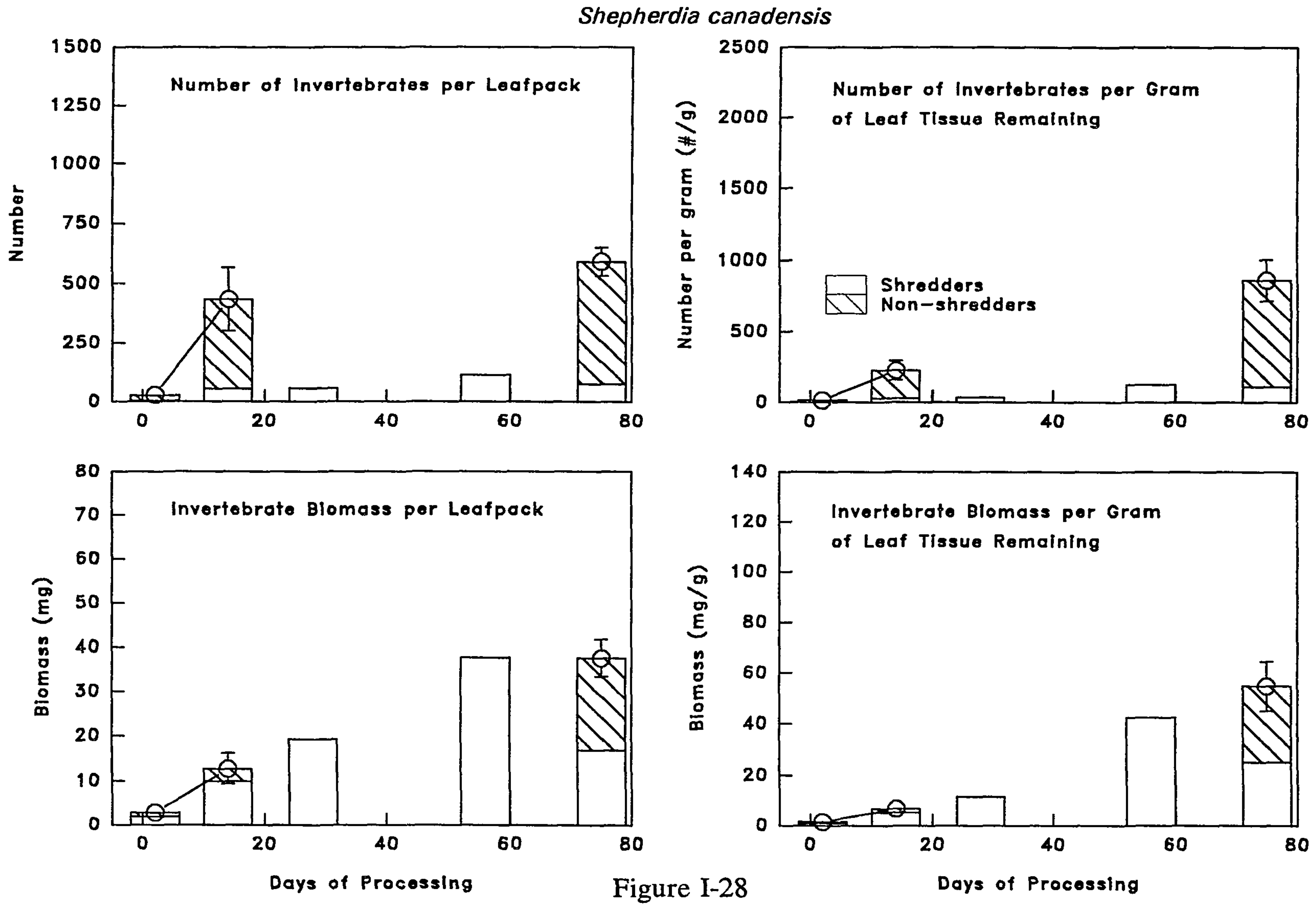

Shepherdia canadensis
Number of Invertebrates per Leafpack
Number
0
250
500
750
1000
1250
1500
Number of Invertebrates per Gram of Leaf Tissue Remaining
Number per gram (#/g)
0
500
1000
1500
2000
2500
Shredders
Non-shredders
Invertebrate Biomass per Leafpack
Biomass (mg)
0
10
20
30
40
50
60
70
80
Invertebrate Biomass per Gram of Leaf Tissue Remaining
Biomass (mg/g)
0
20
40
60
80
100
120
140
0
20
40
60
80
Days of Processing

Figure I-28

Alnus crispa (autumn)

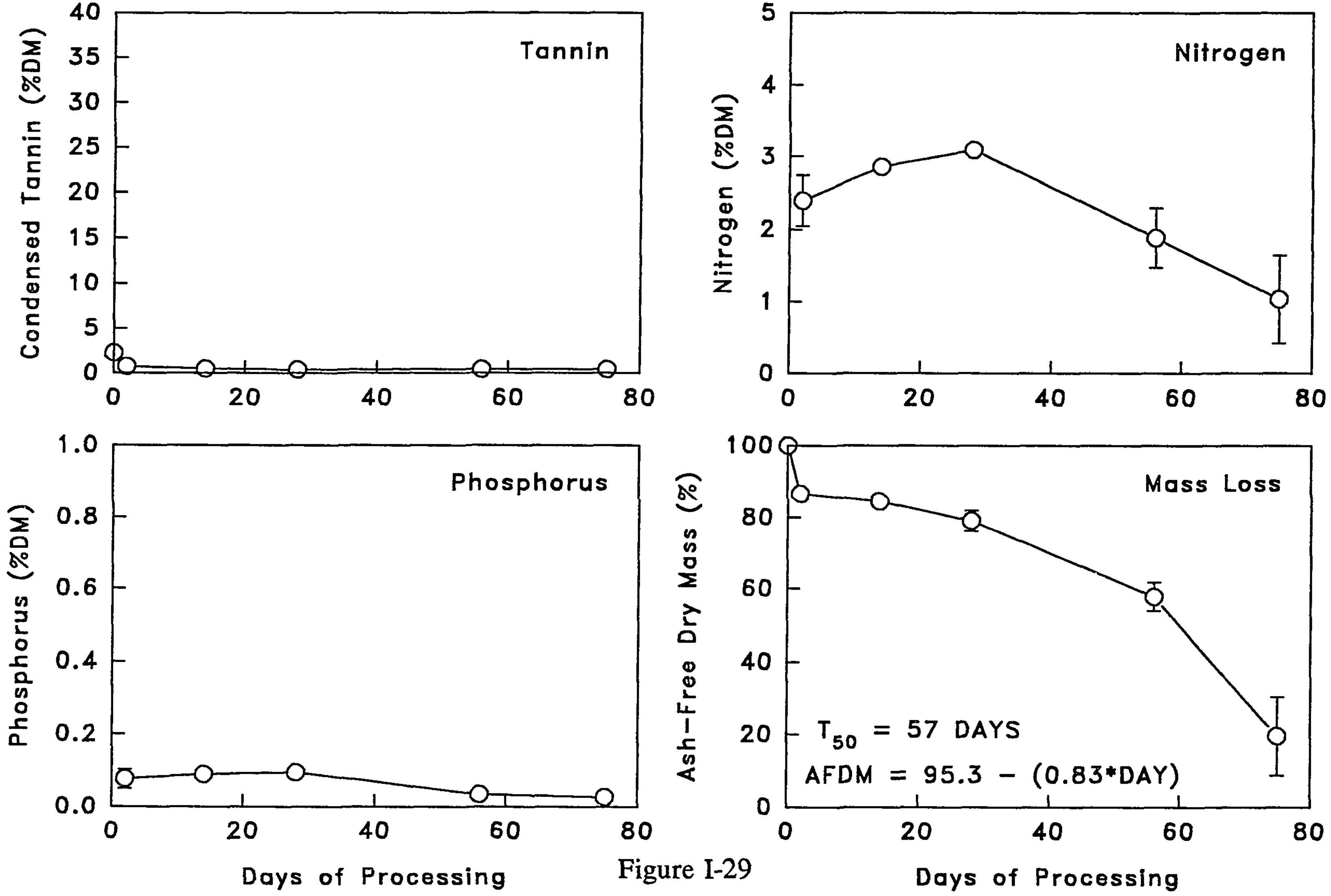


Figure I-29

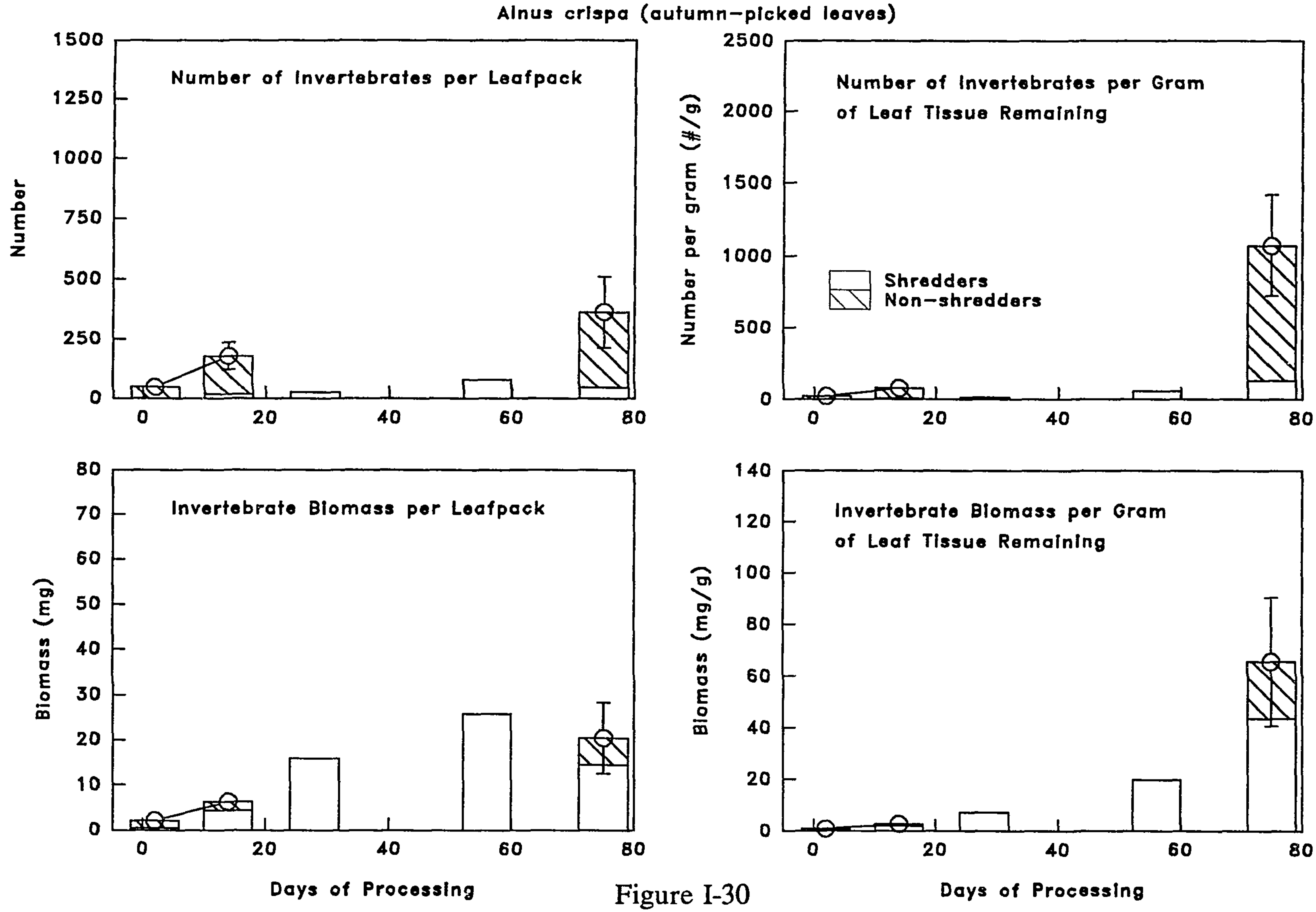

Alnus crispa (autumn-picked leaves)
Number of Invertebrates per Leafpack
Number
1500
1250
1000
750
500
250
0
0
20
40
60
80
Number of Invertebrates per Gram of Leaf Tissue Remaining
Number per gram (#/g)
2500
2000
1500
1000
500
0
Shredders
Non-shredders
Invertebrate Biomass per Leafpack
Biomass (mg)
80
70
60
50
40
30
20
10
0
Invertebrate Biomass per Gram of Leaf Tissue Remaining
Biomass (mg/g)
140
120
100
80
60
40
20
0
Days of Processing
Days of Processing

Figure I-30

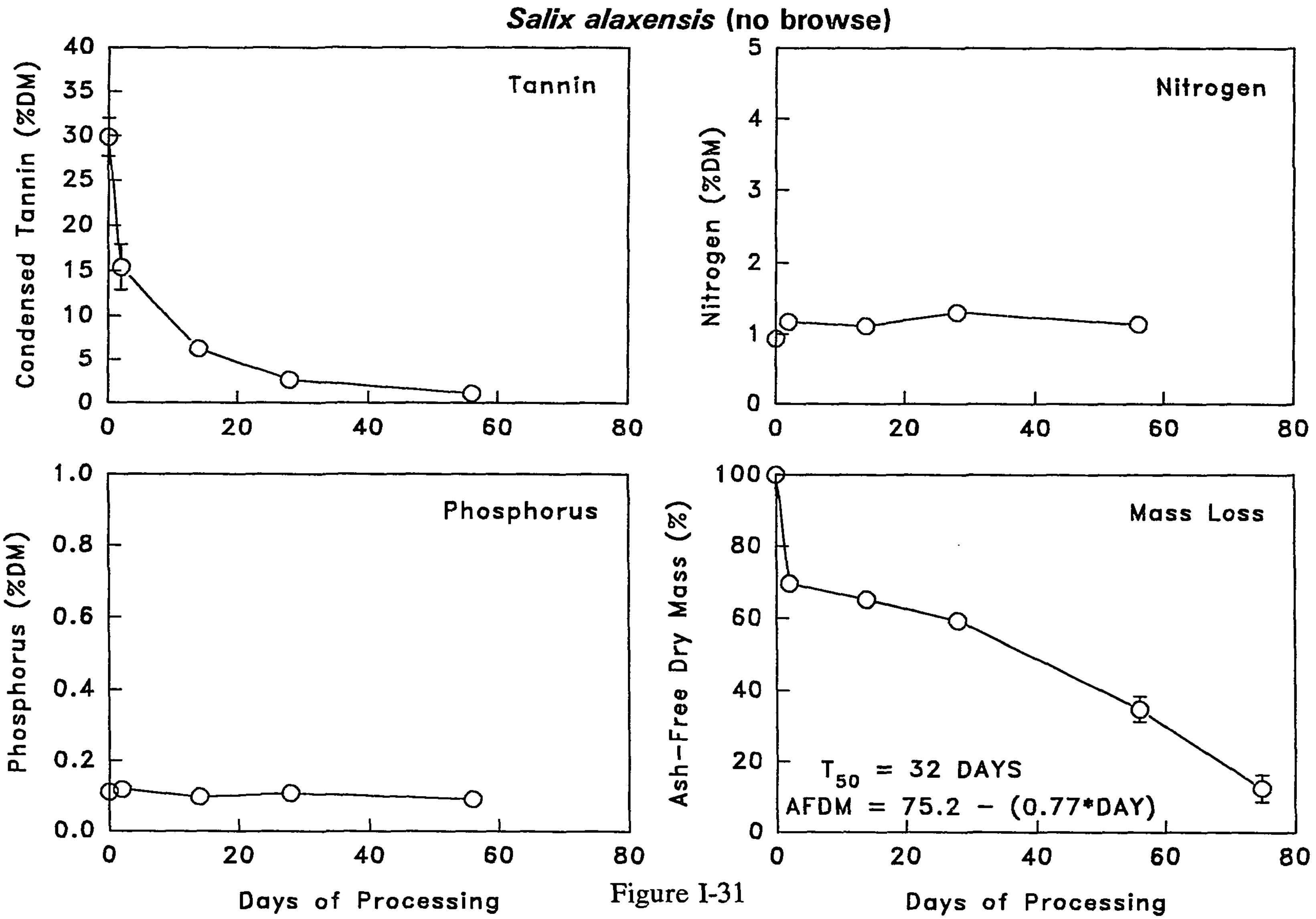

Salix alaxensis (no browse)
Tannin
Condensed Tannin (%DM)
0
5
10
15
20
25
30
35
40
Nitrogen
Nitrogen (%DM)
0
1
2
3
4
5
Phosphorus
Phosphorus (%DM)
0.0
0.2
0.4
0.6
0.8
1.0
Mass Loss
Ash-Free Dry Mass (%)
0
20
40
60
80
100
T50 = 32 DAYS
AFDM = 75.2 - (0.77*DAY)
0
20
40
60
80
Days of Processing
Days of Processing

Figure I-31

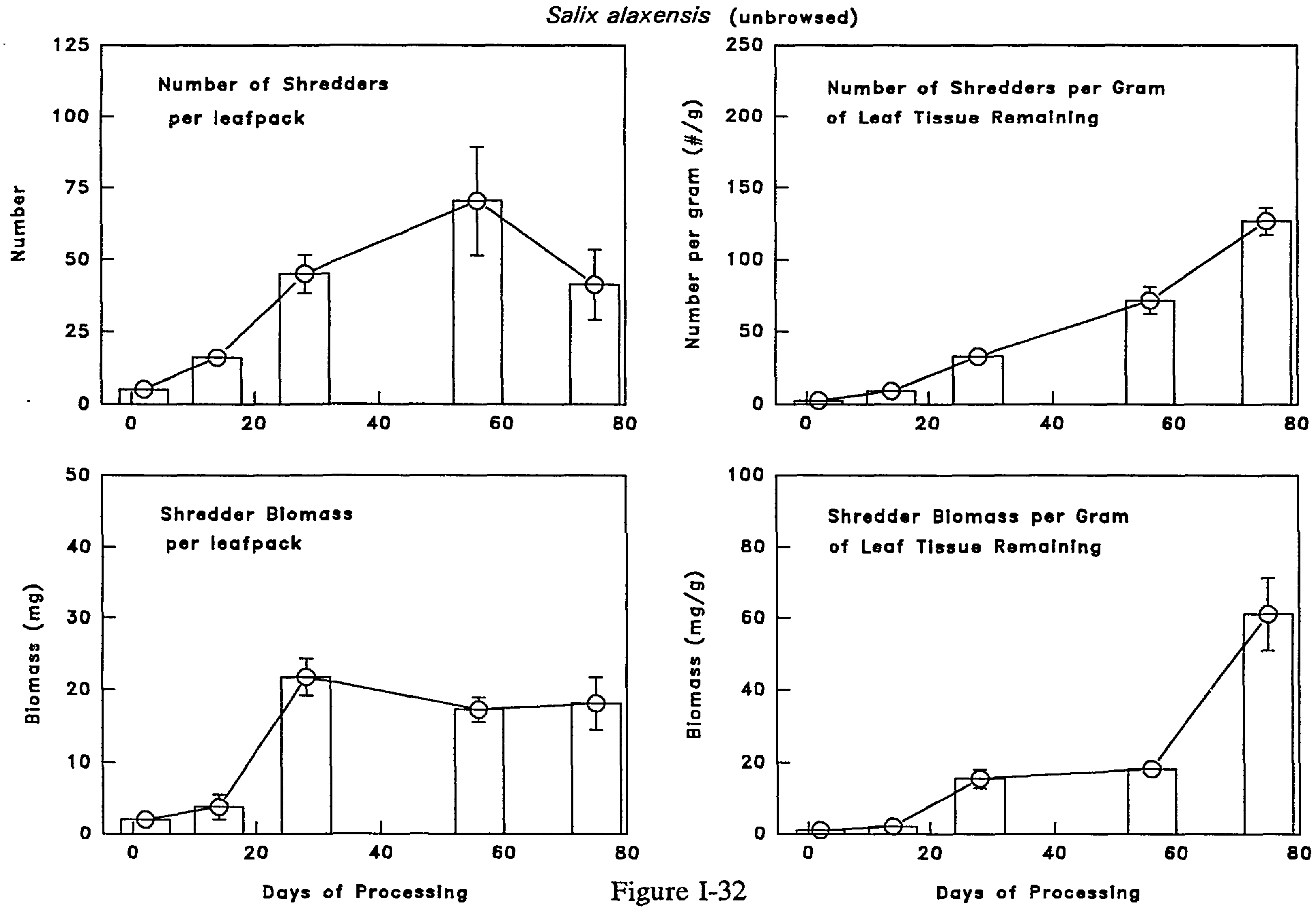

Salix alaxensis (unbrowsed)
Number of Shredders per leafpack
Number
0
25
50
75
100
125
Number of Shredders per Gram of Leaf Tissue Remaining
Number per gram (#/g)
0
50
100
150
200
250
Shredder Biomass per leafpack
Biomass (mg)
0
10
20
30
40
50
Shredder Biomass per Gram of Leaf Tissue Remaining
Biomass (mg/g)
0
20
40
60
80
100
0
20
40
60
80
Days of Processing
Days of Processing

Figure I-32

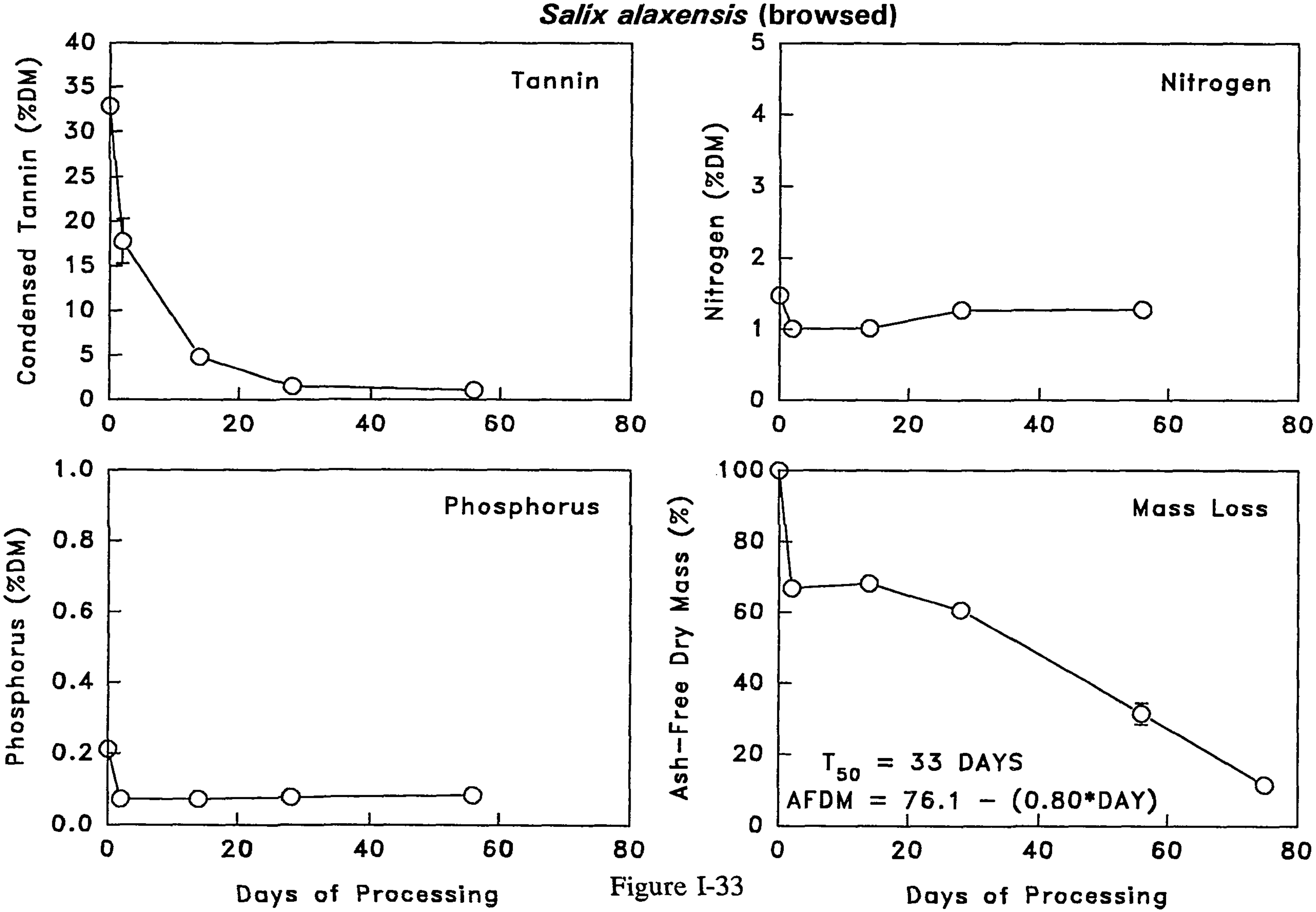

Salix alaxensis (browsed)
Tannin
Condensed Tannin (%DM)
0
5
10
15
20
25
30
35
40
Nitrogen
Nitrogen (%DM)
0
1
2
3
4
5
Phosphorus
Phosphorus (%DM)
0.0
0.2
0.4
0.6
0.8
1.0
Mass Loss
Ash–Free Dry Mass (%)
0
20
40
60
80
100
T_{50} = 33 DAYS
AFDM = 76.1 – (0.80*DAY)
0
20
40
60
80
Days of Processing
Days of Processing

Figure I-33

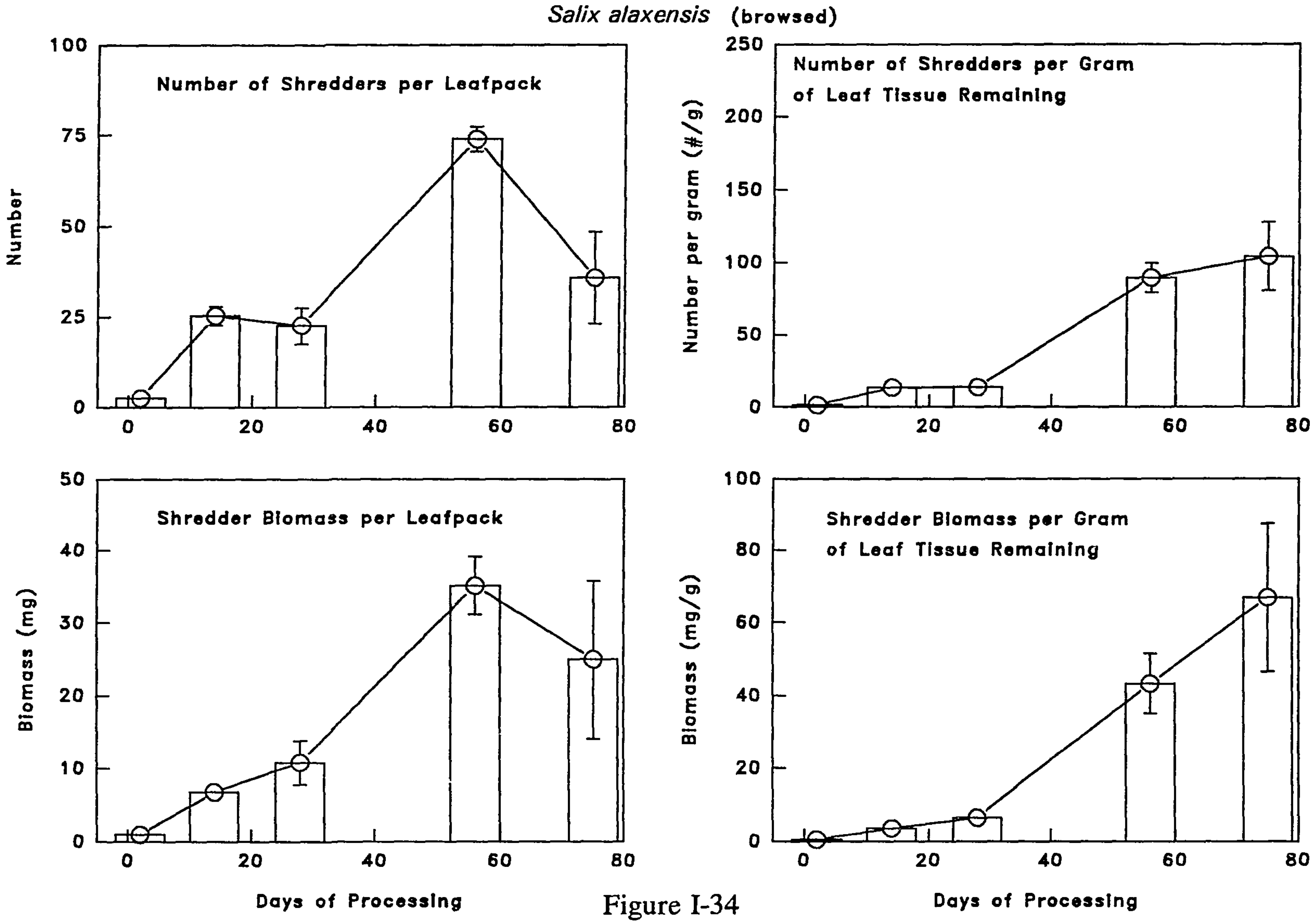

Salix alaxensis (browsed)
Number of Shredders per Leafpack
Number
0
25
50
75
100
Number of Shredders per Gram of Leaf Tissue Remaining
Number per gram (#/g)
0
50
100
150
200
250
Shredder Biomass per Leafpack
Biomass (mg)
0
10
20
30
40
50
Shredder Biomass per Gram of Leaf Tissue Remaining
Biomass (mg/g)
0
20
40
60
80
100
0
20
40
60
80
Days of Processing
Days of Processing

Figure I-34

Betula papyrifera **(no browse)**

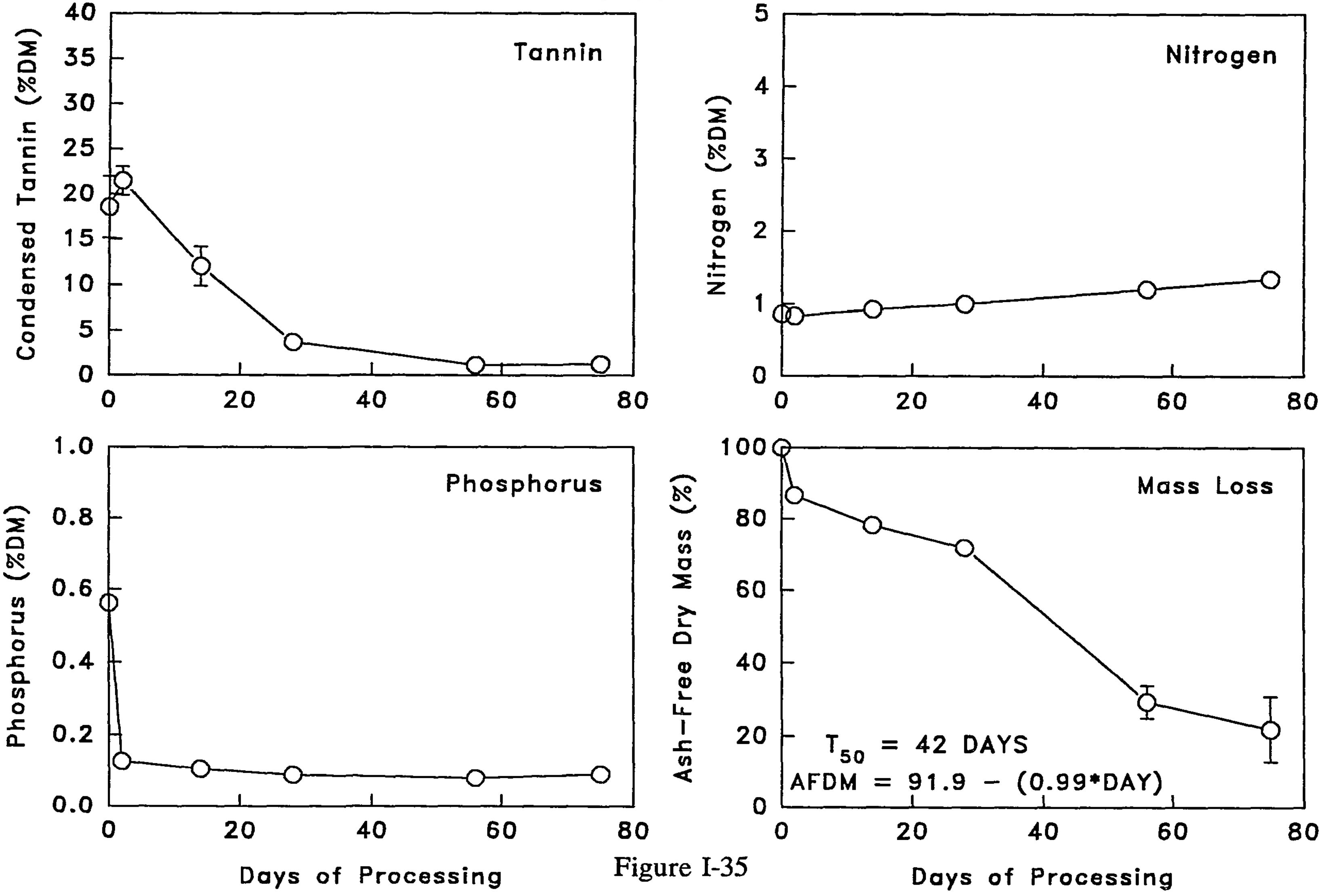


Figure I-35

Betula papyrifera (unbrowsed)

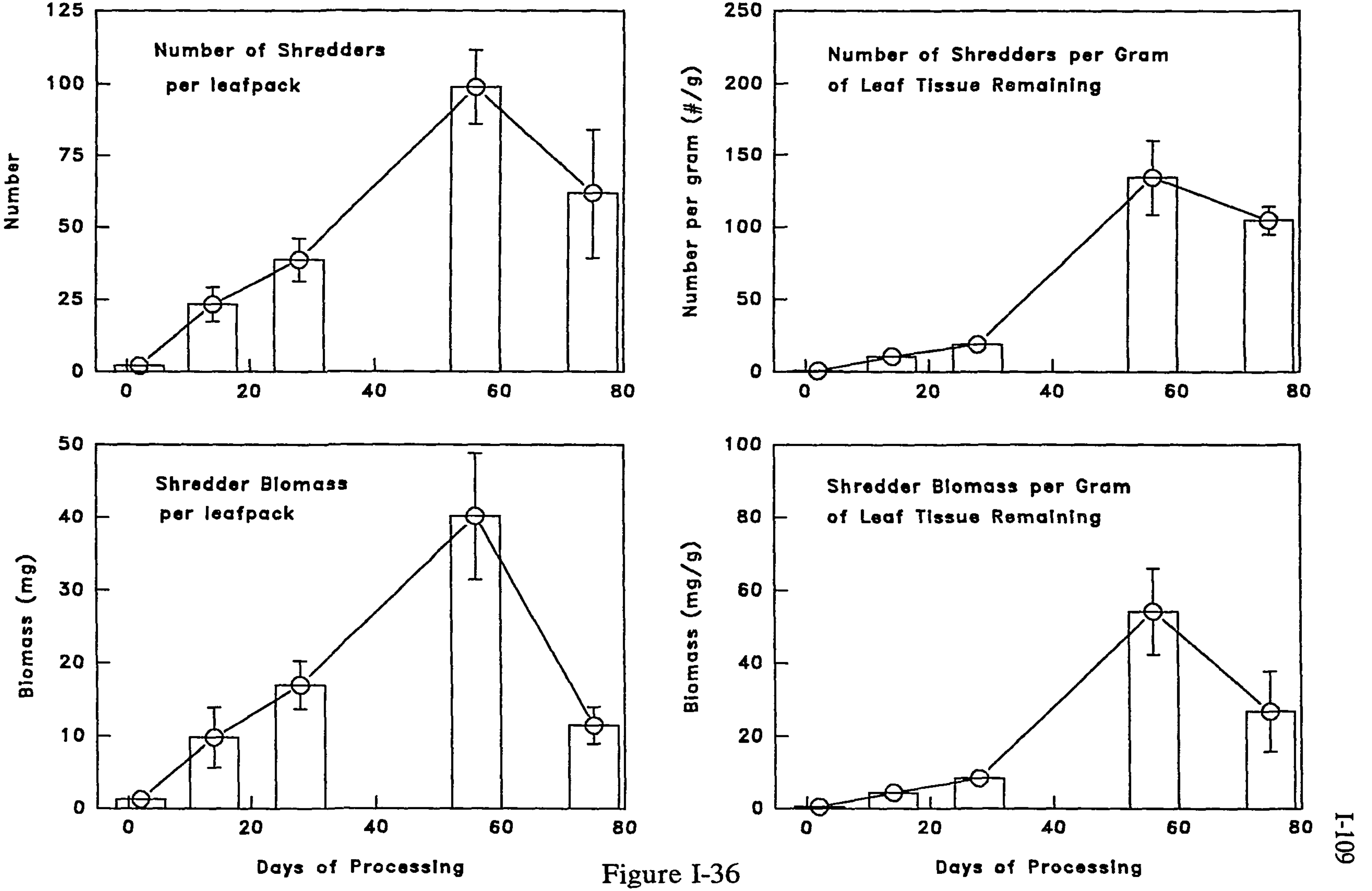


Figure I-36

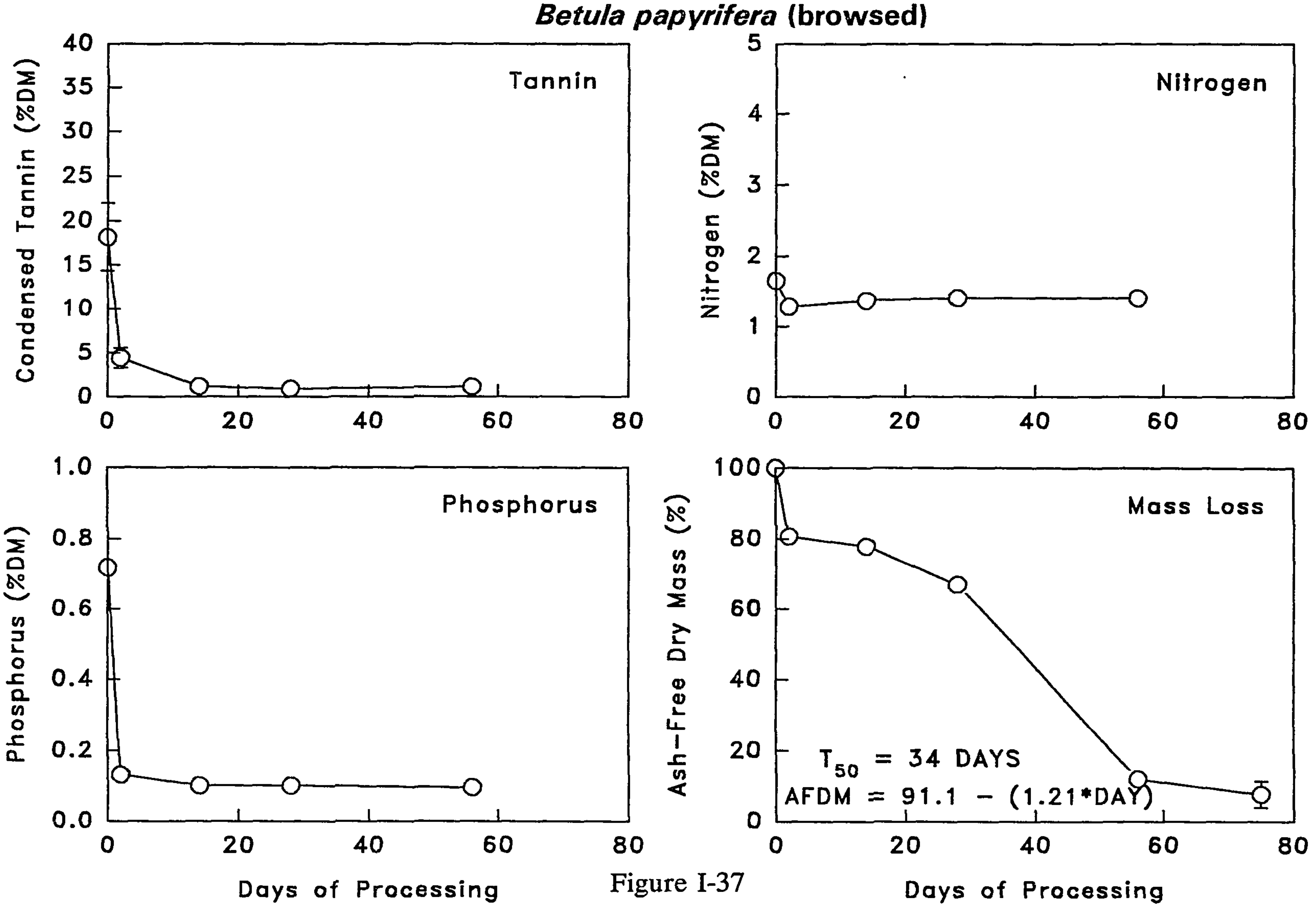

Betula papyrifera (browsed)
Tannin
Condensed Tannin (%DM)
40
35
30
25
20
15
10
5
0
0
20
40
60
80
Nitrogen
Nitrogen (%DM)
5
4
3
2
1
0
0
20
40
60
80
Phosphorus
Phosphorus (%DM)
1.0
0.8
0.6
0.4
0.2
0.0
0
20
40
60
80
Days of Processing
Mass Loss
Ash-Free Dry Mass (%)
100
80
60
40
20
0
T_{50} = 34 DAYS
AFDM = 91.1 - (1.21*DAY)
0
20
40
60
80
Days of Processing

Figure I-37

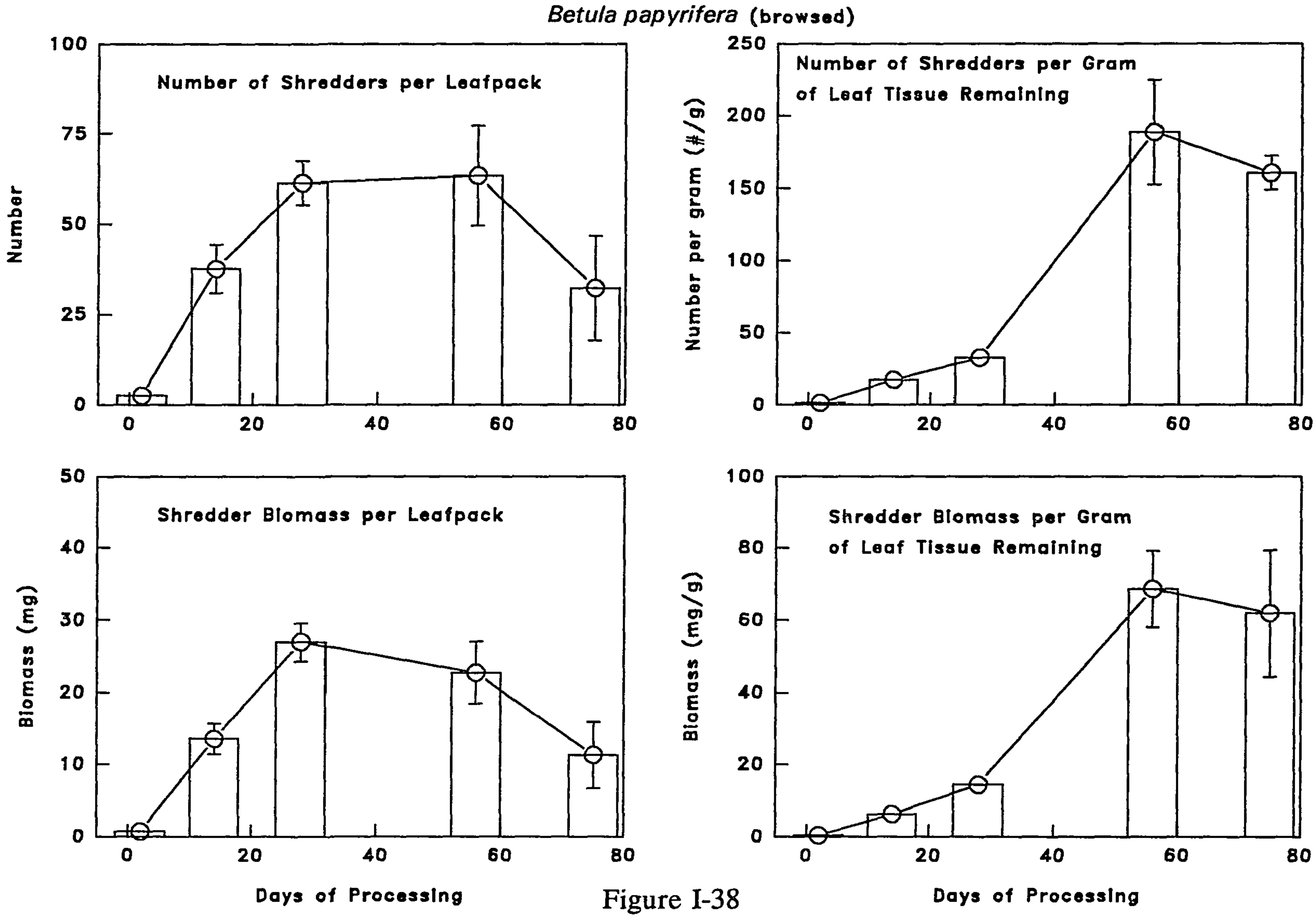

Betula papyrifera (browsed)
Number of Shredders per Leafpack
Number
100
75
50
25
0
0
20
40
60
80
Number of Shredders per Gram of Leaf Tissue Remaining
Number per gram (#/g)
250
200
150
100
50
0
0
20
40
60
80
Shredder Biomass per Leafpack
Biomass (mg)
50
40
30
20
10
0
0
20
40
60
80
Days of Processing
Shredder Biomass per Gram of Leaf Tissue Remaining
Biomass (mg/g)
100
80
60
40
20
0
0
20
40
60
80
Days of Processing

Figure I-38

EFFECTS OF FOLIAR NUTRIENTS AND SECONDARY COMPOUNDS ON LEAF LITTER DECOMPOSITION RATES IN STREAMS

R. Jean Stout[1]

John G. Irons III[2]

Cathy Pringle[3]

Mark W. Oswood[4]

John P. Bryant[4]

S.R. Reice[5]

W.H. McDowell[6]

---

[1] Department of Entomology, Michigan State University, East Lansing, MI, 48824, USA

[2] Institute of Northern Forestry, USDA Forest Service, 308 Tanana Drive, Fairbanks, AK 99775, USA.

[3] Institute of Ecology and Department of Zoology, University of Georgia, Athens, GA, 30602, USA.

[4] Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK, 99774-0180, USA.

[5] Department of Biology, CB 3280 Coker Hall, University of North Carolina, Chapel Hill, NC, 27599-3280, USA

[6] Forest Resources, James Hall, University of New Hampshire, Durham, NH, 03824, USA

ABSTRACT

The rate at which autumn-shed leaves that fall into streams decompose is partially determined by the chemistry of those leaves. Nitrogen has long been known to have a positive influence on decomposition rates in streams; we present evidence that plant secondary metabolites, thought to be plant defenses against terrestrial herbivores and pathogens, can negatively influence decomposition rates. In a reciprocal leaf litter transplant experiment, we studied the effect of nitrogen and condensed tannin concentrations in leaf litter (derived from trees in Costa Rica and the USA: North Carolina, New York, Michigan, and Alaska) on processing rates in streams in Costa Rica, Michigan, and Alaska. Decomposition rates were highest in Costa Rica and similar in Michigan and Alaska. Our data suggest that, at least for the ten species we used, tannin concentration may play a larger role in determining decomposition rates in streams than does nitrogen. We propose that, in addition to nutrient chemistry, stream ecologists studying leaf litter decomposition should take into consideration the plant secondary chemistry when investigating decomposition rates of leaves from different tree species or leaves from experimental manipulations of trees.

INTRODUCTION

Food webs of forested streams depend in large part on leaf litter input from the surrounding riparian vegetation (Minshall 1967, 1978). The processing of leaves in streams generally follows a three-stage progression of mass loss. First, compounds such as sugars and other soluble carbohydrates, amino acids, soluble tannins, and inorganic ions are leached from the leaves over a period of 24 to 48 hours. Second, leaves are colonized by a suite of decomposing microbes such as aquatic hyphomycetes and bacteria over a period of a few weeks (Suberkropp and Klug 1976, 1980, Maltby 1992). Third (with some overlap with the second stage), aquatic invertebrates colonize the leaves and consume the leaf detritus-microbe combination as their food source. This final stage continues until most of the less recalcitrant leaf material is gone. Aquatic invertebrates provide the trophic link between terrestrial riparian plant communities and higher trophic levels of aquatic food webs, such as fish.

There is a continuum of stream leaf processing (decomposition) rates among plant taxa. Early work on the decomposition of leaf litter in streams suggested a correlation between nitrogen concentration in the leaves and the rate at which leaves are processed (e.g. Kaushik and Hynes 1971, Anderson and Sedell 1979, reviewed by Webster and Benfield 1986). Leaves which have higher nitrogen concentrations tend to be processed more quickly than leaves that are low in nitrogen, presumably because total nitrogen concentration is proportional to protein and amino acid concentration. The increased processing rates found for species with higher nitrogen concentration could be a result of several factors. Increased rates of microbial colonization on leaves with high nitrogen content might enhance degradation by way of microbial exoenzymes which digest plant structural carbohydrates such as cellulose. High concentrations of endogenous nutrients might increase invertebrate feeding because such leaves are a more palatable food source to shredders. Finally, invertebrates might increase feeding rates due to higher microbial populations on leaves with high nutrient content. It is likely that all these factors play a role in the processing of leaf litter in streams.

Although nutrient content of leaves undoubtedly plays a role in the choice of food sources (species of leaf litter) and in the nutrition of stream shredders, other factors such as the presence of inhibitory compounds such as secondary metabolites (Webster and Benfield 1986) may influence the decomposition process. The initial conditioning phases (leaching and microbial colonization) can be qualitatively and quantitatively different when plant secondary metabolites are present in leaf tissue (Stout 1989, Irons et al. 1991). Because aquatic invertebrates prefer microbially-conditioned leaves (Triska 1970, Kaushik and Hynes 1971, Bärlocher 1980), not only could the initial processing of leaves be hindered, but large leaf losses attributable to invertebrate consumption could be reduced. In fact, secondary metabolites may be so effective as inhibitors of fungal and bacterial invasion that they consistently slow down decompositional processes, irrespective of foliar nitrogen concentration, following leaf senescence and death (Stout 1989).

Defensive compounds (i.e. secondary metabolites) have been pivotal foci for plant-animal interaction studies in terrestrial communities (Feeny 1970, Rosenthal and Janzen 1979, Zucker 1983, Harborne 1988, Rosenthal and Berenbaum 1991, 1992), but have received little attention by stream ecologists (Stout 1989). Secondary metabolites that are either sequestered back into plant tissue prior to leaf abscission or are easily leached in water are not expected to play a role in the processing of leaf litter in streams. There are, however, a number of plant secondary compounds that can continue to alter biotic activity after leaves and twigs die and fall on forest floors and into streams. A suite of protective agents that remain in leaf tissue after senescence are the condensed tannins (proanthocyanidins), which may play critical roles in the processing of leaf tissue in streams (Stout 1989). Condensed tannins can inhibit fungal and bacterial colonization or live or dead plant material (Benoit et al. 1968, Harrison 1971, Grant 1976, Zucker 1983), although not all tannins inhibit fungi. Tannins also have negative effects on behavior, growth and fecundity of insects (Werner 1979, Bryant et al. 1987, Feeny 1992, Städler 1992), and behavior and nutrition of vertebrate herbivores (Robbins et al. 1987, 1991, Bryant et al. 1991, 1992, Hanley et al. 1992).

From six research sites (three sites used for breakdown analyses and three sites used only for leaf litter collection) extending from 65°N to 10°N latitude, we each contributed leaves from two species of plants, one thought to be high and one low in foliar condensed tannin concentration, based on the literature or experimental data (see Stout 1989). We hypothesized that leaves high in condensed tannins would be processed more slowly in streams than leaves low or lacking in condensed tannins, irrespective of the original locale for the leaves. As the sites extended from Alaska to Costa Rica, water temperatures were taken to compute cumulative degree-day differences among sites. This paper describes mass losses from leaves of 10 species in an Alaskan, a Michigan, and a Costa Rican stream. At each stream site, two species were native and the remaining exotic. Although the original design included streams in New York, North Carolina, and Puerto Rico, methodological problems at the first two locations and no leaves being sent to Alaska from Puerto Rico, forced exclusion of those sites from data analysis. Leaves from New York and North Carolina were shipped to all investigators and they were used in Alaska, Michigan and Costa Rica. The Puerto Rican leaves were used in Michigan and in Costa Rica, and results for those two species, *Dacryodes excelsa* (Burseraceae) and *Sapium laurensce* (Euphorbiaceae) are available upon request (R.J. Stout).

In this study, we tested several alternative (but not mutually exclusive) hypotheses about processing rates of leaf litter in streams. These hypotheses include the effects of foliar concentrations of nitrogen and condensed tannin, stream temperature (i.e. latitude), and location of origin of the leaves (i.e., are stream decomposers more adapted to leaves of local trees than exotics?). We chose a reciprocal transplant method to tease apart these hypotheses. Here we report the effects of foliar concentrations of nitrogen and condensed tannin on mass loss rates in three streams.

METHODS AND MATERIALS

STUDY SITES

Study sites at each location (Figure II-1A) were chosen to be relatively similar in character. Study reaches were located in riffles, where water velocities were approximately 0.3 m/sec and water depths were approximately 30 to 50 cm. By choosing sites with similar character, we hoped to control for many of the physical stream variables that might influence decomposition rates, and so make the thermal regime and the invertebrate community the major variables that differed among sites.

Costa Rica

El Salto Creek, a second order stream, is located at La Selva Biological Field Station (owned and operated by The Organization for Tropical Studies) in Costa Rica near the town of Puerto Viejo at 10°N latitude and 84°W longitude (Figure II-1B). El Salto Creek is described in detail elsewhere (Pringle and Triska 1991, Pringle et al. 1986). The study site is located at approximately 45 m above sea level and it is approximately 2 km from the stream origin. The legume, *Pithecellobium longifolium*, is found only along stream courses at La Selva, but *Trema micrantha* is found in disturbed areas, including along stream courses. Canopy cover at the study site includes the legumes, *Pterocarpus officinalis* and *Pentaclethra macroloba*, the Central American rubber tree, *Castilla elastica*, and many species of understory palms. Water temperature varied little in this stream (minimum of 24.5° and maximum of 25.5°C). Accumulated degree-days were calculated by summing daily means, beginning August 3.

Michigan

The Ford River, a third order stream, is in the upper peninsula of Michigan. It lies at 46°N latitude and 88°W longitude (Figure II-1C). The experimental site in approximately 25 km from the source of the river. Riparian vegetation includes speckled alder (*Alnus rugosa*) and balm of gilead (*Populus gileadensis*), with occasional northern white cedar (*Thuja occidentalis*). There is approximately 10 percent canopy cover over the stream at the site. Water temperatures were continuously recorded with Omnidata datapods (Model DP 211), with field calibration twice weekly. In November, a Ryan thermograph, Model J, replaced the datapods. Accumulated water temperatures above 0°C were expressed as cumulative degree-days by summing daily means, beginning August 20.

Alaska

Monument Creek, a second order stream in the Chena River drainage, approximately 115 km from Fairbanks (Figure II-1D), was the Alaskan (U.S.A.) site.

Monument Creek has a catchment area of approximately 74 km^2, rises at about 850 m above sea level, and the study site is about 14 km downstream from the source at an elevation of 380 m at 65°N latitude and 146°W longitude. Riparian vegetation includes willow (*Salix* spp.), alder (*Alnus crispa*), balsam poplar (*Populus balsamifera*), with occasional white spruce (*Picea glauca*) and black spruce (*P. mariana*). The riparian canopy covers the stream only about 10-15% at the study site (although about 100 m upstream there is complete canopy closure). Streamwater and air temperatures were recorded continuously at Monument Creek on an Omnidata Easylogger. Details of the placement (streambed gravel temperatures were recorded also) and calibration of the thermocouples were reported in Irons et al. (1989) and Irons and Oswood (1992). Accumulated degree-days above 0°C were calculated by summing the daily means for each day of the 75 day study period.

SOURCE OF LEAVES

Leaves were obtained from a variety of locations, including tropical (Costa Rica), subtropical (North Carolina), temperate (New York, Michigan), and subarctic (Alaska). Two species from each location were used: one species thought to be high in condensed tannin and one species thought to be low in condensed tannin (hereafter referred to as "high tannin" and "low tannin" species). These categories were based on prior knowledge of the investigators and on data from the literature: these species are listed in Table 1. Leaves were dried at <50°C, then frozen at -25°C for 48 hr to minimize the potential for microbial contaminants prior to shipping. Although microbes in interior Alaska routinely face temperatures colder than this, all sites followed this protocol.

A coarse-meshed leaf litter bag technique was used to investigate litter processing rates. Envelopes of 2 cm mesh plastic bird-netting were constructed, each containing six pockets to which leaf packs were randomly assigned. All leaves were oven dried at 50°C, then weighed into approximately 3 g leaf packs (range of approximately ±0.1 g, depending on the species), hydrated to minimize breakage, and put into their assigned pocket in the envelopes. Envelopes were stored in large plastic bags in a 1°C refrigerator until they were put into the stream.

Envelopes were placed in each study stream in late summer or autumn of 1988: 3 August in Costa Rica, 20 August in Michigan, and 5 October in Alaska. Five replicates were removed from the stream on each collection date: after 2, 7, 14, 28, 56, and 75 days in Alaska; 2, 14, 21, 28, 54, 84, and 112 days in Michigan; and 2, 14, 28, 40, 56 and 86 days in Costa Rica. In order to accommodate widely varying processing rates, not all species were collected on each date; e.g., in Alaska, *Acer* and *Trema* were collected on day 7 but not on day 75, while the other species were not collected on day 7 but were collected on day 75. Exceptions include the last two dates in Alaska, when one (day 56) and five (day 75) of fifteen envelopes were frozen into the ice; and in Michigan, nine leafpacks of *Trema* were pulled on day 17, as they were rapidly losing mass, and two replicates each of *Q. rubra* and

Pithecellobium, and three replicates of *Fagus* were missing on the last collection date. Upon removal from the stream, individual pockets were cut apart, leaf bags placed in individual plastic bags, and the bags placed into a cooler for transport back to the laboratory. In the laboratory, invertebrates were rinsed from leaves and preserved in 80% ethanol; analyses of macroinvertebrate dynamics will be reported elsewhere. Leaf packs were then oven dried at 50°C to constant weight, and weighed to the nearest 0.01 g dry mass (DM). Percent of original dry mass remaining was used in decomposition rate calculations.

Rates of mass loss were calculated based both on a linear model and on a negative exponential model (e.g. Petersen and Cummins 1974). The linear model is based on the assumption that a constant proportion of the original mass is lost over a given time period, and the equation is $M_t/M_i = M_0/M_i, - m*t$ where M_i is the initial mass (approximately 3 g in this study), M_t is the mass remaining at time t, the slope m is the rate constant, and the intercept, M_0/M_i, represents the proportion of the original mass which would remain at time 0 if the mass lost to leaching were removed instantaneously. We chose to calculate an intercept, rather than forcing the curve through 1.0 (i.e. 100% mass remaining), because mass loss due to leaching is a fundamentally different process from microbial and invertebrate processing, and has very different rate constants (e.g. Petersen and Cummins 1974, Cowan et al. 1983, Webster and Benfield 1986). The exponential model, which is the model most generally used in litter decomposition studies, is based on the assumption that a constant proportion of the mass remaining, rather than the original mass, is lost during a given time period. This model is based on the equation $M_t/M_i = (M_0/M_i)e^{-kt}$, where k is the rate constant and the other parameters are the same as in the linear equation. Again, we calculated an intercept (M_0/M_i) to represent mass lost due to leaching. Values of zero were used for replicates with no remaining mass on the last day in which any mass was left in any of the five replicates (e.g. if only one leafpack had any remaining mass, the other four were considered to be 0.0, rather than missing), and all replicates of the next date were considered to be zero. Any subsequent dates were considered to be missing values. Calculations were performed in SYSTAT's (Wilkinson 1990) general linear module using proportion of dry mass remaining (M_t/M_i) for linear regression and natural log-transformed data $(\ln((M_t/M_i)+1)$ for negative exponential curves. We tested the hypotheses that tannin and nitrogen concentrations differed among sites and species using two-way analysis of variance (ANOVA), and developed a model of the effects of tannin and nitrogen concentrations on leaf litter decomposition using multivariate regression analysis. Statistical calculations were carried out in SYSTAT (Wilkinson 1990).

FOLIAR CHEMISTRY ANALYSES

Two of the five replicates collected on day 2 from Alaska and Michigan (i.e. following leaching, but before substantial colonization by microbes, here termed post-leached leaves) were used for foliar chemistry determinations. The Michigan leafpacks were sent to Alaska, and all chemical analyses were done in the Fairbanks laboratory. Concentration of condensed tannin was estimated using the butanol-HCl reaction for proanthocyanidins described by Martin and Martin (1982) and modified by Bryant et al. (1985) with quebracho tannin as a standard. Tannin concentration was determined colorimetrically on a Perkin-Elmer spectrophotometer at an absorbance wavelength of 550 nm. The calibration equation used to convert absorbance to Quebracho equivalents was determined empirically to be quadratic and was:

$$[TANNIN] = 429.607 \times (A_{550}) - 61.588 \times (A_{550})^2 \qquad r^2 = 0.999$$

where A_{550} is the absorbance at 550 nm and TANNIN is the amount of tannin in the sample in units of μg/0.3 ml (F ratio = 5513.383). The data were then converted to concentration of tannin in the remaining leaf material (percent dry mass). Because condensed tannins found in different plant species (including Quebracho a tropical shrub with high tannin concentration in its bark that is often used as a tannin standard) have different reactivities with this method (see below), the quebracho equivalent reported here should be used as a relative index, rather than as the true tannin concentration.

Total Kjeldahl nitrogen concentrations for two day 2 (post-leached) replicates each from Michigan and Alaska, were determined on a Technicon Autoanalyzer by a sulfuric/selenious acid digestion and colorimetric analysis with indophenol-salicylate reaction with ferricyanide blue as a catalyst for nitrogen.

RESULTS

MASS LOSS OF LEAF PACKS

Leaf packs of all species lost mass through time, although there were large differences among species and among sites in the rates at which the leaves decomposed. Figure II-2 shows mass loss curves for the species initially chosen to be high in tannins. In all cases, leaves decomposed most rapidly in Costa Rica, and with the exception of *Salix alaxensis* and perhaps *Fagus grandifolium*, slowest in Alaska. In species in the low tannin group, mass loss was generally more rapid than in high tannin species (Figure II-3). Again, mass loss was fastest in Costa Rica; however, mass loss was faster in Alaska than in Michigan for *Alnus rugosa* and *A. crispa*, faster in Michigan than Alaska for *Trema* and *Acer*, and similar for *Cornus* (Figure II-3). Rate constants based on the linear model, along with F ratios, are given in Table 2, and rate constants based on the negative exponential model are given in Table 3.

In all but one case, both models were statistically significant at $P < 0.001$; *Fagus grandifolium* in Alaska had probabilities of $P = 0.002$ (linear model) and $P = 0.004$ (exponential model). In many cases, a linear regression model fit the data better than a negative exponential model. For example, *Cornus florida*, *Fagus grandifolia*, and *Alnus crispa* in both Michigan and Alaska all appeared to have processing curves that were more linear than exponential. Indeed, some species (e.g. *Alnus rugosa*, *A. crispa*, and *Salix alaxensis* in Alaska) exhibited curves that were concave downward, suggesting that a quadratic equation would provide a better mathematical fit than either a linear or a negative exponential equation. While a quadratic equation may fit the data better mathematically, it is difficult to explain biologically, and because quadratic equations only provided a better fit in about four species, they are not discussed further. When comparing fit of data to linear versus negative exponential models, in eight of ten species in both Michigan and Alaska, linear regression was more highly significant (based on F ratios), while in Costa Rica, a negative exponential equation was more significant in all but one species (comparison of *F* ratios in Table 2 and Table 3). However, because many of the Costa Rican equations were based on only two or three collection dates (including the first date on which no mass remained), these equations must be interpreted with caution.

FOLIAR CHEMISTRY

All comparisons of mass loss rates and foliar chemistry were done on leaves from Michigan and Alaska collected following two days (post-leached) in the stream. While it is obvious that processing rates were more rapid in warmer water (i.e. in Costa Rica) than in cooler water (i.e. in Michigan and Alaska) (Figures II-2 and II-3), we felt that temperature-related differences in short-term mass loss from leaching would be minimal (that is, leachable materials would be quantitatively lost from leaf litter over 48 hours, regardless of water temperature). Most studies (e.g. Petersen and Cummins 1974, Cowan et al. 1983) have shown that virtually all leaching occurs within the first 48 hours, and we assumed that the chemistry of leaves leached for 48 hours would likely be representative of the condition faced by colonizing microbes and invertebrates.

Tannin

Concentrations of condensed tannin in post-leached leaves of these ten species differed (Figure II-4). Concentrations ranged from 0.0% (*Trema*) to 11.3% (*Pithecellobium* in Alaska), expressed as Quebracho tannin equivalents. In a two-way analysis of variance (Table 4) with species and location as main effects, the overriding difference in tannin concentrations was among species ($P < 0.0001$), while the location of the study and the interaction between species and location were much less significant ($P = 0.0150$ and $P = 0.0313$, respectively). In post hoc comparisons of the means, *Pithecellobium*, *Quercus falcata*, and *Fagus* contained significantly more tannin than did any of the low-tannin species (using Bonferroni's adjustment). *Q. rubra* (mean = 4.9%) was not different from *Fagus* (5.9%) or from two of the low-tannin species, *Acer* (2.9%) or *Alnus rugosa* (2.5%), due to the large between-site variance found in *Q. rubra*. The five low-tannin species and *Salix* were not significantly different from each other.

We interpret the significant location and location-by-species interaction effects to mean that while species differed in tannin content (not surprising since the species used were originally selected on that basis), the stream in which the leaves were placed also affected tannin concentration after leaching. Leaves placed in the Alaskan stream (Monument Creek) had higher concentrations of tannin than did those placed in the Michigan stream (Ford River): leaching of tannin was reduced in Monument Creek. The significant interaction between location and species suggests that this pattern depended on which species were being compared, and indeed, visual inspection of Figure II-4 suggests that all species in the *a priori* low-tannin group (with the exception of *Trema*, which had no measurable condensed tannin) had lower tannin concentrations in Michigan than in Alaska, while two species in the high-tannin group (*Fagus* and *Salix*) were lower in Michigan, one species was higher in Michigan (*Q. rubra*), and two species were not different (*Q. falcata* and *Pithecellobium*). This pattern suggests that different tree species have qualitatively different tannins, and that they show a range of solubilities at differing water temperatures. The only species which had a higher concentration in Michigan than in Alaska (*Q. rubra*) was also the only species which apparently lost a greater mass of tannin than of dry mass, suggesting that the tannin found in this species is somehow qualitatively different, and that using Quebracho bark as a standard introduced an artifact.

Nitrogen

Concentrations of total Kjeldahl nitrogen in leaf tissues (based on dry mass) of leaves collected on Day 2 varied among species (Figure II-4). *Trema micrantha* had the highest nitrogen concentration on Day 2 (4.6%), *Quercus falcata* had the lowest (0.7%), and other species were intermediate. In a two-way analysis of variance with species and location of study (Michigan or Alaska) as the independent variables, species was highly significant, location was slightly significant, and the interaction was non-significant (Table 4), suggesting that, like tannin concentration but to a lesser extent, nitrogen concentration after two days of leaching depends upon leaching temperature. On average, leaves from the Alaskan stream were slightly higher in nitrogen than leaves from the Michigan stream. There were three groups of species which were significantly different in nitrogen concentration (using Bonferroni's adjustment for multiple comparisons): the lowest group included *Quercus falcata*, *Cornus florida*, and *Salix alaxensis*, the highest group included only *Trema micrantha*, and the intermediate group included all other species.

EFFECT OF FOLIAR CHEMISTRY ON MASS LOSS

Because condensed tannin and nitrogen concentrations often co-vary within (Irons et al. 1988, 1991) and between (Bryant et al. 1983) tree species, the response of mass loss must be assessed with both variables simultaneously. Figure II-5 shows mass loss rate (m) as a function of both tannin and nitrogen concentrations. We used the linear decomposition coefficient m because we only had foliar chemistry data from Michigan and Alaskan (see methods), and because linear regression equations fit the data at these two sites better than negative exponential equations. At low tannin concentrations, increasing nitrogen concentration has an apparent positive effect on loss rate, while at higher tannin concentrations, mass loss rates are uniformly slow and nitrogen has little effect. Multivariate regression analysis showed that decomposition rates are significantly correlated with both nitrogen (positively) and tannin (negatively) concentrations: overall significance of the model is $P = 0.002$ (F ratio = 9.373, df = 2,17). The correlation between tannin and nitrogen in this data set is low (-0.188). The standardized regression coefficients suggested that tannin concentration (-0.581) has approximately twice the effect on mass loss rates as has nitrogen concentration (0.337).

DISCUSSION

HIGH TANNIN VERSUS LOW TANNIN GROUPS

In choosing the two species from each collection location, we attempted to select one species that contained high condensed tannin concentrations and one species that had low tannin concentration. Most species chosen fit these *a priori* notions of tannin concentration, with two exceptions. *Salix alaxensis* was chosen to be the Alaskan species with high tannin concentration, but the Day 2 concentrations were 2.6% in Alaska and 0.04% in Michigan. These leaves were collected in winter (March), from shrubs which still retained foliage. In retrospect, we feel that they are not representative of the species, as autumn-collected leaves had 28.6% tannin prior to leaching and 9.2% tannin following 48 hours in Monument Creek (Irons, unpublished data). These winter leaves undoubtedly experienced leaching due to fall and winter precipitation, and perhaps were also affected by desiccation, freezing, and sublimation. See Gessner & Schwoerbel (1989), Bärlocher (1991, 1992) Gessner (1991), and Chergui & Pattée (1992) for discussion on the effects of drying on leaching and decomposition of leaf litter in streams.

Quercus rubra was also chosen to be a species high in tannin. Although the tannin concentration in leaves following 48 hours of leaching was only 4.1%, unleached leaves had a condensed tannin concentration of 8.7%. Apparently, the tannin in this species is readily leached in cold water (perhaps due to reduced polymerization or cell-wall binding), and tannin concentrations of unleached leaves do not predict well the concentrations in leached leaves. Other species initially high in tannin (e.g. *Q. falcata* and *Pithecellobium*) did not show as much tannin loss due to leaching as *Q. rubra*. Thus, tannin concentration often differed substantially on a species-specific basis between unleached senescent leaves and leaves leached for two days. Choosing species as high- or low-tannin species for stream decomposition studies from the literature may be risky if choices are based on unleached values from the literature.

FOLIAR CHEMISTRY

A review of condensed tannin concentrations in leaves of North and Central American tree species, and a theoretical model of the potential influence of tannin on leaf litter decomposition in streams was presented by Stout (1989). Tannin concentrations in the ten species in this study were within the range of concentrations reported, with the two tropical species being the extremes at either end: *Trema* had no measurable tannin while *Pithecellobium* had 10.2% following leaching. Some tropical trees have condensed tannin concentrations as high as 40% (Janzen and Waterman 1984) while some subarctic and arctic species may contain over 30% prior to leaching (Irons and Bryant, unpublished data). Use of different methods for tannin analysis (see Tempel (1982) and Hagerman & Butler (1991) for discussion of methods of tannin analysis), use of tannin from other species (e.g Quebracho) as standards for calculation of conversion equations (Irons, unpubl. data), and season of leaf collection (see Chapin and Kedrowski (1983) and Chapin & Shaver (1988)) all may affect the results obtained for condensed tannin concentrations in leaves. Nonetheless, because all leaves used in this study were collected after translocation of nutrients and tannin out of the leaves, were leached the same amount of time before analysis, and were analyzed by the same technique, comparisons within this study can be made, although the "Quebracho problem" remains.

Nitrogen concentrations in leaves of the ten species used in this study ranged from 0.7% (*Quercus falcata* in Alaska) to 4.8% (*Trema* in Alaska), and, like tannin concentrations, were within the range of concentrations reported in the literature. Coley (1983) reported nitrogen concentrations in leaves of young and mature trees for 22 pioneer species and 24 persistent species from the Central American tropics in Panama: values ranged from 1.7% to 5.1%, with the highest values found in young trees. Grigal et al. (1976) reported foliar nitrogen concentrations in five species of north-temperate zone trees and shrubs to be between about 1% and 3%, depending on the species and the season. Nitrogen concentrations in leaves of two subarctic (taiga) woody species in Alaska were 2.48% in *Alnus crispa* and 1.99% in *Betula papyrifera* (Chapin and Kedrowski 1983), while arctic (tundra) deciduous shrubs ranged from about 1.7% to about 3.3% in June, declining to less than 1% in August as nutrients are translocated out of the leaves before senescence (Chapin and Shaver 1988).

Withdrawal of nutrients from leaves prior to leaf-fall is common in deciduous woody plants (Grigal et al. 1976, Chapin and Kedrowski 1983, Chapin and Shaver 1988), and may potentially affect conclusions of decomposition studies if the concentration values are obtained from the literature (usually summer measurements). Estimates of foliar nitrogen concentration should be obtained from the leaves being used, generally autumn-shed leaves. However, unusual events (e.g hurricanes or violent thunderstorms) may add green, summer leaves to streams ecosystems. Several studies have shown that green summer leaves have higher nitrogen concentrations than autumn-senescened leaves (McArthur et al. 1986, Leff and McArthur 1990, Risley and Crossley 1993), and that green leaves falling into streams in summer decompose more rapidly than autumn-shed leaves (Stout et al. 1985, Horton and Brown 1991). However, two of the above studies showed no difference in decomposition rates despite higher nutrient concentrations: the authors speculated that inhibitory compounds offset the nutrient gains (McArthur et al. 1986, Leff and McArthur 1990).

Although other studies (e.g. Irons et al. 1988, 1991) have shown that nitrogen and tannin are often negatively correlated (especially under experimental perturbations of nutrient availability within a species), in this study we had species that were high in both tannin and nitrogen concentration (e.g. *Pithecellobium*) and species that were low in both (e.g.*Cornus*). Indeed, while *Pithecellobium* was highest in tannin concentration, it was second only to *Trema* in nitrogen concentration. This allowed us to decouple the positive effects of nitrogen and the negative effects of tannin, and test the relative importance of these two ubiquitous components of leaves of deciduous trees and shrubs in determining decomposition rates in streams.

EFFECT OF FOLIAR CHEMISTRY ON MASS LOSS RATES

Leaves high in condensed tannin concentration and low in nitrogen concentration were processed more slowly than leaves low in tannins and high in nitrogen in each of the three streams studied, irrespective of the origin of the leaves. Tannin concentration, however was more highly correlated with mass loss rates than was nitrogen concentration. Leaves of *P. longifolium* from Costa Rica (high tannin, high N), *Q. falcata* from North Carolina (high tannin, low N), *F. grandifolia* from New York (high tannin, intermediate N), and *Q. rubra* from Michigan (high tannin, intermediate N) were generally processed more slowly at each of the three sites than were the remaining six species of leaves lacking or low in condensed tannins.

Stream ecologists have long known that nitrogen affects leaf litter processing rates in streams (Kaushik and Hynes 1968, 1971, review by Webster and Benfield 1986). Alder is a nitrogen-fixing shrub, has high nitrogen concentrations in leaves, and generally is among the fastest decomposers (e.g. Hart and Howmiller 1975, Sedell et al. 1975, Chauvet 1987). Nitrogen is an essential nutrient for plant growth, and presumably higher foliar nitrogen concentration is reflected in a higher concentration of essential amino acids and proteins in leaf litter.

In terrestrial ecosystems, the effects of secondary compounds such as condensed tannin on invertebrate and vertebrate herbivory (see Rosenthal and Berenbaum 1991, 1992 for recent reviews) have been well documented. These secondary compounds likely evolved as a chemical defense to levels of herbivory that were detrimental to the fitness of individual plants (Harborne 1988). There are several theories as to the mechanisms of induction of a defensive response: short-term inducible defense (Haukioja and Niemela 1976, Haukioja 1980, 1990), long-term inducible defense (Haukioja 1980), the carbon/nutrient balance theory (Bryant et al. 1983), and the growth/differentiation theory (Herms and Mattson in press). Regardless of the mechanism inducing their production, secondary compounds have a detrimental effect on herbivores lacking mechanisms for neutralizing the defense.

The nutrient (e.g. nitrogen) and secondary compound (e.g. condensed tannin) concentrations in leaves are not constant either among individual trees or within an individual tree among seasons in any deciduous tree species studied to date. Many environmental factors can alter these concentrations, including vertebrate and insect herbivory, fertilization by humans or by forest fire, and moisture, light, or nutrient stress. In general, environmental conditions that cause an excess of nutrients over labile carbohydrate, such as fertilization, nutrient release by forest fire, or winter browsing by vertebrates, results in an increase in leaf quality (e.g increased nitrogen and decreased tannin concentrations), because carbohydrate is put into growth rather than carbon-based defense. Conversely, conditions that cause an excess of labile carbohydrate over nutrient concentrations, such as defoliation by insects or nutrient stress, results in a lowering of leaf quality. This theory has been described as the carbon/nutrient balance theory (Bryant et al. 1983).

When autumn-shed leaves fall into streams, they bring with them not only the heritable characteristics of the tree species, but also the history of all the various environmental factors which can modify foliar chemistry. Irons et al. (1988) showed that fertilization with either nitrogen, phosphorus, or both can alter the nitrogen and tannin concentrations of four Alaskan tree species, and that nitrogen has a positive and tannin a negative effect on palatability to and consumption by a stream shredder caddisfly. In another study, Irons et al. (1991) demonstrated that birch leaves from trees previously browsed by moose differed in initial nitrogen concentration and in the leaching characteristics of condensed tannin. Although initial tannin concentrations were similar, after two days of leaching tannin concentration in leaves from unbrowsed trees was four times higher than in leaves from browsed trees. Leaves from the browsed trees decomposed faster than leaves from the unbrowsed trees. Thus, the environmental history of the tree likely plays a role in determining the rate of processing of its leaves in streams.

Foliar chemistry might affect mass loss rates in streams during any of the three phases of processing. Different compounds have different solubilities in water (often temperature dependant), thus having different leaching dynamics. Many secondary compounds are detrimental to microbes (Zucker 1983), and greater concentrations of condensed tannin might inhibit microbial colonization and growth. Finally, invertebrates choose leaves that have high nitrogen and low tannin concentrations over leaves with the opposite characteristics. Previous studies demonstrated foliar chemistry effects on the leaching (Irons et al. 1991) and invertebrate feeding (Irons et al. 1988) stages, and this study and Irons et al. (1991) demonstrated the foliar chemistry effects on processing rates. In order to construct a more complete model of the interaction of nutrients and secondary metabolites on processing rates of leaves in streams, we need to incorporate microbial community dynamics in future studies.

In summary, foliar chemistry plays an important role in controlling rates of leaf litter decomposition in streams. In addition to the widely known positive effect of nitrogen, we have shown that condensed tannin has a negative effect on rates of leaf mass loss. Secondary metabolites, evolved as chemical defenses against herbivores, are ubiquitous and varied in the plant kingdom. Many of these defensive compounds have low solubilities in water, and cannot be disregarded as substances inhibitory to stream decomposers. The positive effects of nutrients and feeding attractants, and the negative effects of inhibitory compounds, and their effects on leaching, microbial dynamics, and invertebrate feeding must all be included in a complete model of the controls of leaf litter decomposition in streams. At the landscape scale, we must also include the spatial and temporal variability of plant chemistry (litter quality), as well as variation in plant litter production (litter quantity) when developing ecosystem models. Nutrient and secondary metabolite concentrations naturally vary seasonally, and environmental perturbations can alter nutrient and tannin concentrations four-fold in both time and space. Thus, in the metaphor of microbes being the equivalent of nutritious "peanut butter" on a "cracker" made of leaves (Cummins 1977), we suggest that there are many types of "crackers" found in the environment, with varying levels of nutritiousness and palatability, and that this variation exerts another level of control on rates of leaf litter decomposition in streams.

ACKNOWLEDGEMENTS

First and foremost, we thank the National Science Foundation who brought the participants of this project together by sponsoring a workshop held at Flathead Lake, Montana, in 1987: "Factors controlling community structure and function in tropical versus temperate streams (Stanford and Covich 1988).

Funding for RJS was provided by the U.S. Department of the Navy, Contract #N000039-81-C-0357, as part of a project on potential effects of extremely low frequency (ELF) electromagnetic fields in stream ecosystems. Help in the field was generously provided by Amy Babinchek and Bill Cooper. Thanks go to Michael

Rondinelli for his critical reading of the manuscript and to Clyde Asbury for providing leaves from Puerto Rico.

Funding to JGI, MWO, and JPB for this project was provided by the National Science Foundation Taiga Forest Long Term Ecological Research grant BSR-8702629, with additional assistance from the Institute of Arctic Biology and the Institute of Northern Forestry. Field help in Alaska was provided by J. Johnson, D. Kennedy, S. Peek, and M. Wagener. S. Kennedy sewed the litter bag, K. Frisby performed the tannin analysis, and Lori Moilinan performed the nitrogen analysis. We thank the Chena Hot Springs Resort for access to Monument Creek.

CMP acknowledges support from the National Science Foundation, Grant BSR-87-17736 which supported field work and BSR-91-07772 which partially supported data synthesis. Field help in Costa Rica was provided by R. Vargas-Ramirez, R. Tiffer-Sotomayor, and G. Browder. We thank the Organization for Tropical Studies for providing logistical support.

LITERATURE CITED

Anderson, N. H., and J. R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Annual Review of Entomology 24:351-377.

Bärlocher, F. 1980. Leaf-eating invertebrates as competitors of aquatic hyphomycetes. Oecologia 47:303-306.

---. 1991. Fungal colonization of fresh and dried leaves in the River Teign (Devon, England). Nova Hedwigia **52**:349-357.

---. 1992. Effects of drying and freezing autumn leaves on leaching and colonization by aquatic hyphomycetes. Freshwater Biology **28**:1-7.

Benoit, R. E., R. L. Starkey, and J. Basaraba. 1968. Effect of purified tannin on decomposition of some organic compounds and plant materials. Soil Science **105**:153-158.

Bryant, J. P., F. S. Chapin III, and D. R. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos **40**:357-368.

Bryant, J. P., G. D. Wieland, T. Clausen, and P. Kuropat. 1985. Interactions of snowshoe hares and feltleaf willow (*Salix alaxensis*) in Alaska. Ecology **66**:1564-1573.

Bryant, J. P., T. P. Clausen, P. B. Reichardt, M. C. McCarthy, and R. A. Werner. 1987. Effect of nitrogen fertilization upon the secondary chemistry and nutritional value of quaking aspen (*Populus tremuloides* Michx.) leaves for the large aspen tortrix (*Choristoneura conflictana* (Walker)). Oecologia **73**:513-517.

Bryant, J. P., F. D. Provenza, J. Pastor, P. B. Reichardt, T. P. Clausen, and J. T. DuToit. 1991. Interactions between woody plants and mammals mediated by secondary metabolites. Annual Review of Ecology and Systematics **22**:431-436.

Bryant, J. P., P. B. Reichardt, T. P. Clausen, F. D. Provenza, and P. J. Kuropat. 1992. Woody plant-mammal interactions. Pages 343-370 *in* G. A. Rosenthal and M. A. Berenbaum, editors. Herbivores: their interactions with secondary plant metabolites, Second Edition. Volume II: Ecological and evolutionary processes. Academic Press, New York.

Chapin, F. S., III, and R. A. Kedrowski. 1983. Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. Ecology **64**:376-391.

Chapin, F. S., III, and G. R. Shaver. 1988. Differences in carbon and nutrient fractions among arctic growth forms. Oecologia **77**:506-514.

Chauvet, E. 1987. Changes in the chemical composition of alder, poplar, and willow leaves during decomposition in a river. Hydrobiologia **148**:35-44.

Chergui, H., and E. Pattée. 1992. Processing of fresh and dry *Salix* leaves in a

Moroccan river system. Acta Oecologia **13**:291-298.

Coley, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecological Monographs **53**:209-233.

Cowan, C. A., M. W. Oswood, C. A. Buttimore, and P. W. Flanagan. 1983. Processing and macroinvertebrate colonization of detritus in and Alaskan subarctic stream. Holarctic Ecology **6**:340-348.

Cummins, K. W. 1977. From headwater streams to rivers. American Biology Teacher **39**:305-312.

Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology **51**:565-581.

---. 1992. The evolution of chemical ecology: contributions form the study of herbivorous insects. Pages 1-44 *in* G. A. Rosenthal and M. A. Berenbaum, editors. Herbivores: their interactions with secondary plant metabolites, Second Edition. Volume II: Ecological and evolutionary processes. Academic Press, New York.

Gessner, M. O. 1991. Differences in processing dynamics of fresh and dried leaf litter in a stream ecosystem. Freshwater Biology **26**:387-398.

Gessner, M. O., and J. Schwoerbel. 1989. Leaching kinetics of fresh leaf litter with implications for the current concept of leaf processing in streams. Archive fur Hydrobiologia **115**:81-90.

Grant, W. D. 1976. Microbial degradation of condensed tannins. Science **193**:1137-1139.

Grigal, D. F., L. F. Ohman, and R. B. Brander. 1976. Seasonal dynamics of tall shrubs in northeastern Minnesota: Biomass and nutrient element changes. Forest Science **22**:195-208.

Hagerman, A. E., and L. G. Butler. 1991. Tannins and lignins. Pages 355-388 *in* G. A. Rosenthal and M. A. Berenbaum, editors. Herbivores: their interactions with secondary plant metabolites, Second Edition. Volume I: The chemical participants. Academic Press, New York.

Hanley, T. A., C. T. Robbins, A. E. Hagerman, and C. McArthur. 1992. Predicting digestible protein and digestible dry matter in tannin-containing forages consumed by ruminants. Ecology **73**:537-541.

Harborne, J. B. 1988. Phytochemical ecology. Academic Press, New York. (check date)

Harrison, A. F. 1971. The inhibitory effect of oak leaf litter tannins on the growth of fungi in relation to litter decomposition. Soil Biology and Biochemistry **3**:167-172.

Hart, S. D., and R. P. Howmiller. 1975. Studies on the decomposition of allochthonous detritus in two southern California streams. Verh. Int. Verein. Limnol. **19**:1665-1674.

Haukioja, E. 1980. On the role of plant defenses in the fluctuations of herbivore populations. Oikos **35**:202-213.

---. 1990. Induction of defenses in trees. Annual Review of Entomology **36**:25-42.

Haukioja, E., and P. Niemela. 1976. Does birch defend itself actively against herbivores? Report from the Kevo Subarctic Research Station **13**:44-47.

Herms, D. A., and W. J. Mattson. in press. The dilemma of plants: to grow or defend. Q. Rev. Biol.

Horton, R. T., and A. V. Brown. 1991. Processing of green American elm leaves in first, third, and fifth order reaches of an Ozark stream. Journal of Freshwater Ecology **6**:115-119.

Irons, J. G., III, and M. W. Oswood. 1992. Seasonal temperature patterns in an arctic and two subarctic Alaskan (USA) headwater streams. Hydrobiologia **237**:147-157.

Irons, J. G., III, M. W. Oswood, and J. P. Bryant. 1988. Consumption of leaf detritus by a stream shredder: influence of tree species and nutrient status. Hydrobiologia **160**:53-61.

Irons, J. G., III, S. R. Ray, L. K. Miller, and M. W. Oswood. 1989. Spatial and seasonal patterns of streambed water temperatures in an Alaskan subarctic stream. Pages 381-390 *in* W. W. Woessner and D. F. Potts, editors. Symposium proceedings on headwaters hydrology. June 1989, Missoula, MT. Am. Water Res. Assoc., Bethesda, MD.

Irons, J. G., III, J. P. Bryant, and M. W. Oswood. 1991. Effects of moose browsing on decomposition rates of birch leaf litter in a subarctic stream. Canadian Journal of Fisheries and Aquatic Sciences **48**:442-444.

Janzen, D. H., and P. G. Waterman. 1984. A seasonal census of phenolics, fibre, and alkaloids in foliage of forest trees in Costa Rica: some factors influencing their distribution and relation to host selection by Sphingidae and Saturniidae. Botanical Journal of the Linnean Society **21**:229-242.

Kaushik, N. K., and H. B. N. Hynes. 1968. Experimental study on the role of autumn-shed leaves in aquatic environments. Journal of Ecology **56**:229-243.

---. 1971. The fate of the dead leaves that fall into streams. Archive fur Hydrobiologia **68**:465-515.

Leff, L. G., and J. V. McArthur. 1990. Effect of nutrient content on leaf decomposition in a coastal plain stream: a comparison of green and senescent leaves. Journal of Freshwater Ecology **5**:269-278.

Maltby, L. 1992. Heterotrophic microbes. Pages 165-194 *in* P. Calow and G. E. Petts, editors. The rivers handbook: hydrological and ecological principles. Blackwell Scientific Publications, London.

Martin, J. S., and M. M. Martin. 1982. Tannin assays in ecological studies: Lack of correlation between phenolics, proanthocyanidins and protein-precipitating constituents in mature foliage of six oak species. Oecologia **54**:205-211.

McArthur, J. V., L. G. Leff, D. A. Kovacic, and J. Jaroscak. 1986. Green leaf decomposition in coastal plain streams. Journal of Freshwater Ecology **3**:553-558.

Minshall, G. W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. Ecology **48**:139-149.

---. 1978. Autotrophy in stream ecosystems. BioScience **28**:767-771.

Petersen, R. C., and K. W. Cummins. 1974. Leaf processing in a woodland stream. Freshwater Biology **4**:343-368.

Pringle, C.M., P. Paaby-Hansen, P.D. Vaux, and C.R. Goldman. 1986. *In situ* nutrient assays of periphyton growth in a lowland Costa Rican stream. Hydrobiologia **134**:207-213

Pringle, C.M. and F.J. Triska. 1991. Effects of geothermal waters on nutrient dynamics of a lowland Costa Rican stream. Ecology **72**:951-965.

Risley, L. S., and D. A. Crossley Jr. 1993. Contribution of herbivore-caused greenfall to litterfall nitrogen flux in several southern Appalachian forested watersheds. American Midland Naturalist **129**:67-74.

Robbins, C. T., S. Mole, A. E. Hagerman, and T. A. Hanley. 1987. Role of tannins in defending plants against ruminants: reduction in dry matter digestion? Ecology **68**:1606-1615.

Robbins, C. T., A. E. Hagerman, P. J. Austin, C. McArthur, and T. A. Hanley. 1991. Variation in mammalian physiological responses to a condensed tannin and its ecological implications. Journal of Mammalogy **72**:480-486.

Rosenthal, G. A., and M. R. Berenbaum, editors. 1991. Herbivores: their interactions with secondary plant metabolites, Second Edition. Volume I: The chemical participants. Academic Press, New York.

---, editors. 1992. Herbivores: their interactions with secondary plant metabolites, Second Edition. Volume II: Ecological and evolutionary processes. Academic Press, New York.

Rosenthal, G. A., and D. H. Janzen, editors. 1979. Herbivores: their interactions with secondary plant metabolites. Academic Press, New York.

Sedell, J. R., F. J. Triska, and N. S. Triska. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams: I. Weight loss and associated invertebrates. Verh. Int. Verein. Limnol. **19**:1617-1627.

Städler, E. 1992. Behavioral responses of insects to plant secondary compounds. Pages 45-88 *in* G. A. Rosenthal and M. A. Berenbaum, editors. Herbivores: their interactions with secondary plant metabolites, Second Edition. Volume II: Ecological and evolutionary processes. Academic Press, New York.

Stanford, J. and A. Covich. 1988. Factors controlling community structure and function in tropical versus temperate streams. Journal of the North American Benthological Society **7**:261-262.

Stout, R. J. 1989. Effects of condensed tannins on leaf processing in mid-latitude and tropical streams: a theoretical approach. Canadian Journal of Fisheries and Aquatic Sciences **46**:1097-1106.

Stout, R. J., W. H. Taft, and R. W. Merritt. 1985. Patterns of macroinvertebrate colonization on fresh and senescent alder leaves in two Michigan streams. Freshwater Biology **15**:573-580.

Suberkropp, K., and M. J. Klug. 1976. Fungi and bacteria associated with leaves during processing in a woodland stream. Ecology **57**:707-719.

---. 1980. The maceration of deciduous leaf litter by aquatic hyphomycetes. Canadian Journal of Botany **58**:1025-1031.

Tempel, A. S. 1982. Tannin-measuring techniques: a review. Journal of Chemical Ecology **8**:1289-1298.

Triska, F. J. 1970. Seasonal distribution of aquatic hyphomycetes in relation to the disappearance of leaf litter from a woodland stream. Ph.D. Thesis. University of Pittsburgh, Pittsburgh, Pennsylvania.

Webster, J. R., and E. F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics **17**:567-594.

Werner, R. A. 1979. Influence of host foliage on development, survival, fecundity, and oviposition of the spear-marked black moth, *Rheumaptera hastata* (Lepidoptera: Geometridae). Canadian Entomologist **111**:317-322.

Wilkinson, L. 1990. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, IL.

Zucker, W. V. 1983. Tannins: does structure determine function? An ecological perspective. American Naturalist 121:335-365.

Table II-1. Species and location of origin of leaves used in this study.

SPECIES	COLLECTION LOCATION	INVESTIGATOR
Pithecellobium longifolium	Costa Rica	C.M. Pringle
Trema micrantha	Costa Rica	C.M. Pringle
Cornus florida	North Carolina	S.R. Reice
Quercus falcata	North Carolina	S.R. Reice
Acer saccharum	New York	W.H. McDowell
Fagus grandifolia	New York	W.H. McDowell
Alnus rugosa	Michigan	R.J. Stout
Quercus rubra	Michigan	R.J. Stout
Alnus crispa	Alaska	M.W. Oswood and J.G. Irons
Salix alaxensis	Alaska	M.W. Oswood and J.G. Irons

Table II-2. Coefficients and F ratios of leaf litter mass loss (percent DM remaining) through time on a per day basis for ten species of leaves placed in streams in Alaska (Monument Creek), Michigan (Ford River), and Costa Rica (El Salto Creek) in autumn of 1988. The coefficients are the slope (m) and intercept (b), calculated as y = mx + b via linear regression. All regression equations were significant at the $p < 0.001$ level except *Fagus* from Alaska ($p = 0.002$). Abbreviations: ORIG = source of leaf litter, CR = Costa Rica, SC = South Carolina, NY = New York, MI = Michigan, AK = Alaska, H = High Tannin Group, L = Low Tannin Group.

			Coefficients of Decay								
			Alaska			Michigan			Costa Rica		
SPECIES	ORIG	H/L	m	b	F	m	b	F	m	b	F
Pithecellobium	CR	H	-0.00116	0.954	21.0	-0.00281	0.961	78.5	-0.00938	0.894	281.9
Quercus falcata	SC	H	-0.00183	0.990	21.4	-0.00532	1.038	86.8	-0.01851	0.928	145.6
Fagus grandifolia	NY	H	-0.00314	0.928	12.6	-0.00418	0.930	37.5	-0.03601	0.966	204.2
Quercus rubra	MI	H	-0.00413	0.980	502.9	-0.00599	0.902	136.6	-0.01534	0.711	53.7
Salix alaxensis	AK	H	-0.00966	0.901	157.6	-0.00605	0.802	102.0	-0.01333	0.627	86.5
Trema micrantha	CR	L	-0.01088	0.708	189.1	-0.02000	0.584	73.7	-0.04456	0.624	1183.8
Cornus florida	SC	L	-0.00567	0.775	58.5	-0.00710	0.818	208.9	-0.06289	0.886	7460.8
Acer saccharum	NY	L	-0.00844	0.915	96.4	-0.00648	0.678	99.5	-0.03197	0.802	66.1
Alnus rugosa	MI	L	-0.01275	0.923	195.1	-0.00422	0.847	58.8	-0.02987	0.724	40.5
Alnus crispa	AK	L	-0.01210	0.866	373.0	-0.00799	0.810	196.4	-0.02723	0.651	36.6

Table II-3. Comparison of coefficients and F ratios of leaf litter mass loss (proportion of DM remaining) through time on a per day basis for ten species of leaves placed in streams in Alaska (Monument Creek), Michigan (Ford River), and Costa Rica (El Salto Creek) in autumn of 1988. The coefficients are the decay constant (k) and initial mass (M_0) from $M_t = M_0e^{kt}$, calculated via linear regression on log-transformed data [ln(DM+1)], and M_0 was calculated by transforming the logarithm back to percent dry mass [exp(ln(DM+1))-1]. All regression equations were significant at the $p < 0.001$ level except *Fagus* from Alaska ($p = 0.004$). Abbreviations are the same as in Table 2.

			Coefficients of Decay								
			Alaska			Michigan			Costa Rica		
SPECIES	ORIG	H/L	k	M_0	F	k	M_0	F	k	M_0	F
Pithecellobium	CR	H	-0.00061	0.954	20.5	-0.00155	0.964	74.7	-0.00639	0.921	348.2
Quercus falcata	SC	H	-0.00096	0.989	22.5	-0.00330	1.066	72.2	-0.01295	0.956	171.3
Fagus grandifolia	NY	H	-0.00189	0.934	10.9	-0.00262	0.944	31.1	-0.02546	1.012	315.6
Quercus rubra	MI	H	-0.00226	0.983	469.1	-0.00386	0.919	102.5	-0.01125	0.697	56.4
Salix alaxensis	AK	H	-0.00662	0.937	135.8	-0.00417	0.824	69.0	-0.01022	0.631	106.1
Trema micrantha	CR	L	-0.00805	0.730	182.9	-0.01542	0.599	88.0	-0.03568	0.647	1749.2
Cornus florida	SC	L	-0.00424	0.790	80.1	-0.00486	0.842	156.5	-0.04667	0.933	7245.9
Acer saccharum	NY	L	-0.00527	0.929	94.0	-0.00456	0.685	116.0	-0.02321	0.808	84.0
Alnus rugosa	MI	L	-0.00924	0.978	188.9	-0.00266	0.857	47.7	-0.02200	0.711	42.3
Alnus crispa	AK	L	-0.00989	0.914	327.3	-0.00567	0.840	158.5	-0.02048	0.636	38.1

Table II-4. Analysis of Variance for proanthocyanidin condensed tannin and total Kjeldahl nitrogen concentrations in ten species of leaves placed in Ford River, MI and Monument Creek, AK, in autumn and winter of 1988. Leaves were removed from the streams after two days of processing. Each location had two replicates for each species.

Condensed Tannin Concentration: $R^2 = 0.956$

Source	SS	DF	MS	F	P
Species	0.0455	9	0.0051	45.309	0.000
Location	0.0008	1	0.0008	7.079	0.015
Spp*Loc	0.0027	9	0.0003	2.690	0.0313
Error	0.0001	20	0.0000		

Nitrogen Concentration: $R^2 = 0.988$

Source	SS	DF	MS	F	P
Species	0.0049	9	0.0005	173.669	0.0000
Location	0.0000	1	0.0000	4.356	0.0499
Spp*Loc	0.0000	9	0.0000	1.509	0.2117
Error	0.0001	20	0.0000		

FIGURE CAPTIONS

Figure II-1. Location maps of the three study sites used in this study. A) Locator map of North and Central America showing El Salto Creek (Costa Rica), Ford River (Michigan), and Monument Creek (Alaska). B) Regional map of El Salto Creek. C) Regional map of Ford River. D) Regional map of Monument Creek.

Figure II-2. Mass loss curves for leaf packs of five species chosen to be high in foliar condensed tannin concentration (low quality) as estimated in streams in Costa Rica (El Salto Creek), Michigan (Ford River), and Alaska (Monument Creek). Error bars are one standard error of the mean (n=5 in most cases). Unapparent error bars are hidden by symbols.

Figure II-3. Mass loss curves for leaf packs of five species chosen to be low in foliar condensed tannin concentration (high quality) as estimated in streams in Costa Rica (El Salto Creek), Michigan (Ford River), and Alaska (Monument Creek). Error bars are one standard error of the mean (n=5 in most cases). Unapparent error bars are hidden by symbols.

Figure II-4. Tannin and nitrogen concentrations in leaf litter of ten species following two days of processing in Monument Creek (first bar) and Ford River, Michigan (second bar). Error bars are one standard error of the mean (n=2). Abbreviations:

TM = *Trema micrantha*, CF = *Cornus florida*, AS = *Acer saccharum*, AR = *Alnus rugosa*, AC = *Alnus crispa*, PL = *Pithecellobium longifolium*, QF = *Quercus falcata*, FG = *Fagus grandifolia*, QR = *Quercus rubra*, SA = *Salix alaxensis*. Note that lack of bars for *Trema* tannin indicates a lack of measurable tannin, not missing samples.

Figure II-5. Slope (m) of linear decomposition regression equations for leaf litter of ten species of trees in Monument Creek, AK, and Ford River, MI (see Table 2), compared with the tannin and nitrogen concentrations of each species (see Figure II-4) in each of the study streams.

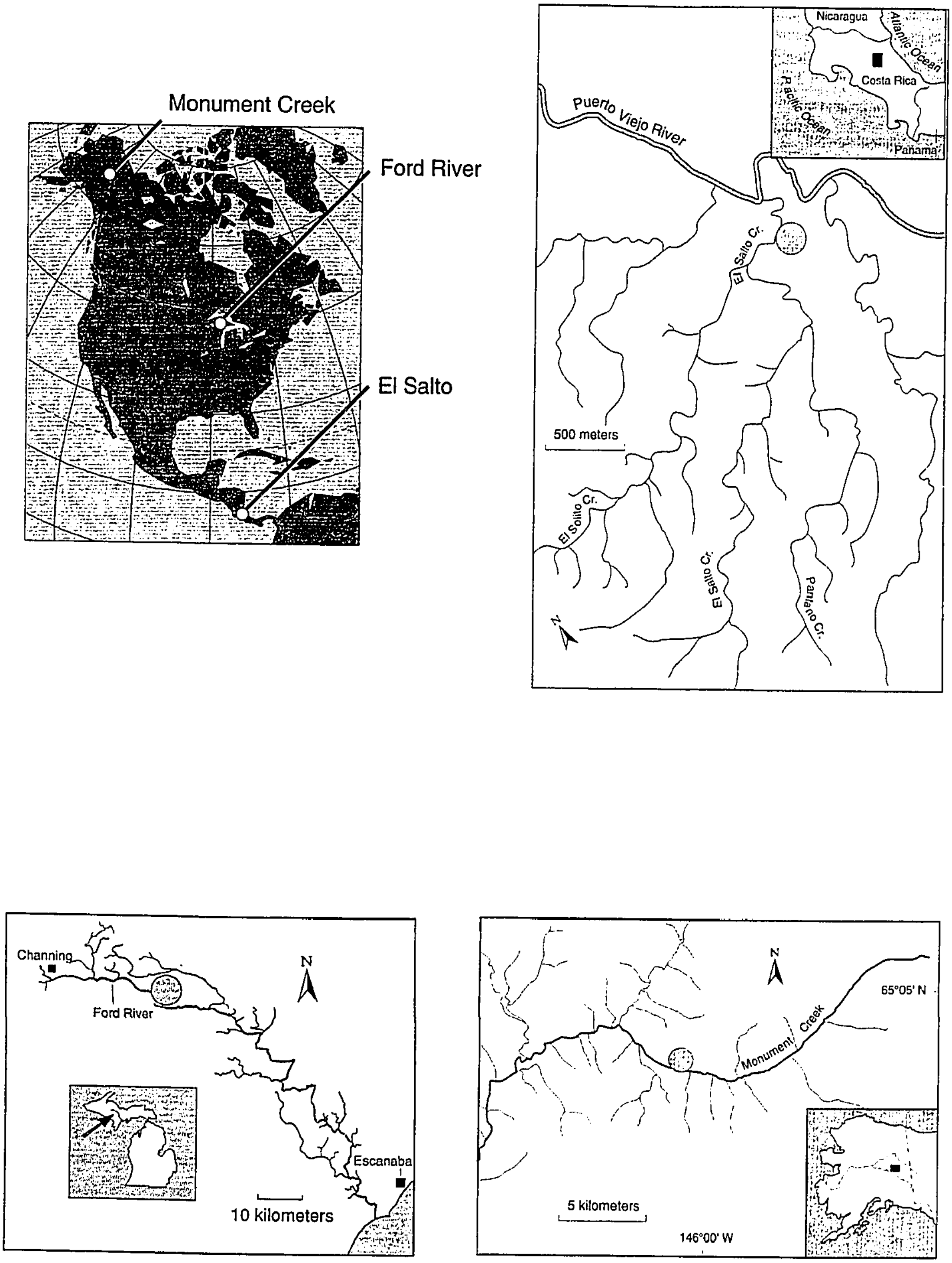

Monument Creek
Ford River
El Salto
Nicaragua
Atlantic Ocean
Costa Rica
Pacific Ocean
Panama
Puerto Viejo River
El Salto Cr.
500 meters
El Salito Cr.
El Salto Cr.
Pantano Cr.
N
Channing
Ford River
N
Escanaba
10 kilometers
N
Monument Creek
65°05' N
5 kilometers
146°00' W

Figure II-1

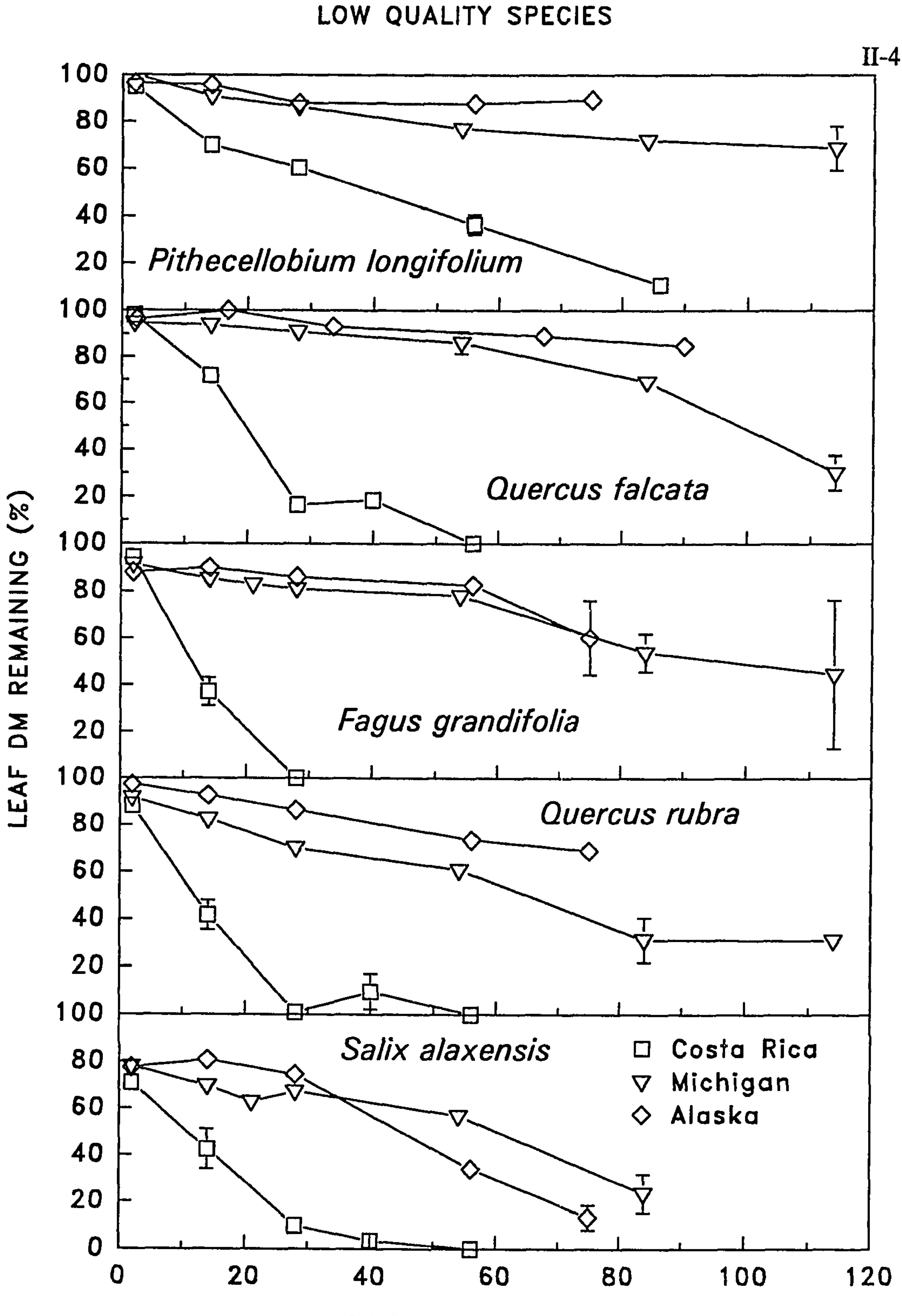

LOW QUALITY SPECIES
LEAF DM REMAINING (%)
100
80
60
40
20
0
Pithecellobium longifolium
Quercus falcata
Fagus grandifolia
Quercus rubra
Salix alaxensis
□ Costa Rica
▽ Michigan
◇ Alaska
0
20
40
60
80
100
120
DAYS OF PROCESSING

Figure II-2

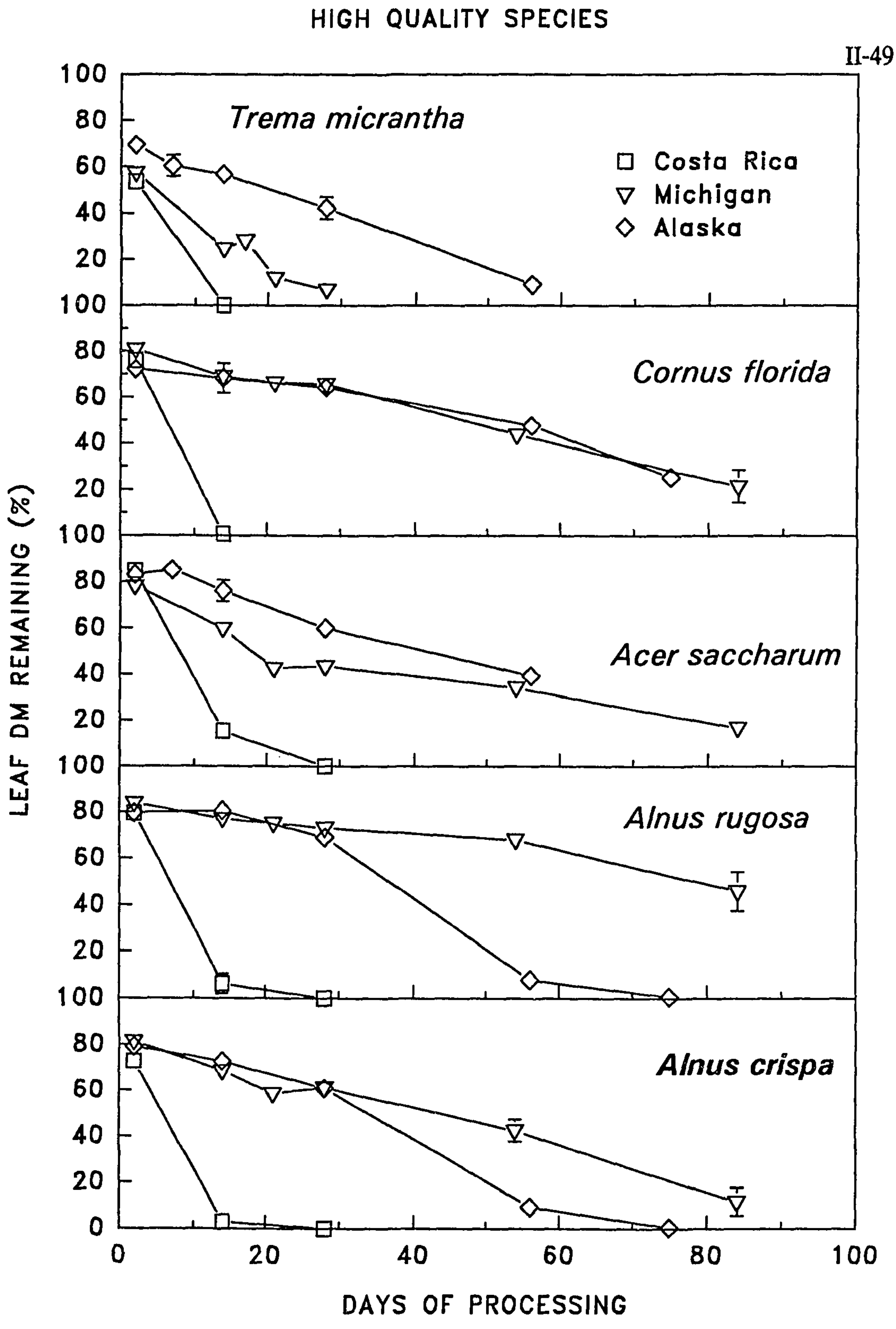

HIGH QUALITY SPECIES
Trema micrantha
Costa Rica
Michigan
Alaska
Cornus florida
Acer saccharum
Alnus rugosa
Alnus crispa
LEAF DM REMAINING (%)
100
80
60
40
20
0
20
40
60
80
100
DAYS OF PROCESSING

Figure II-3

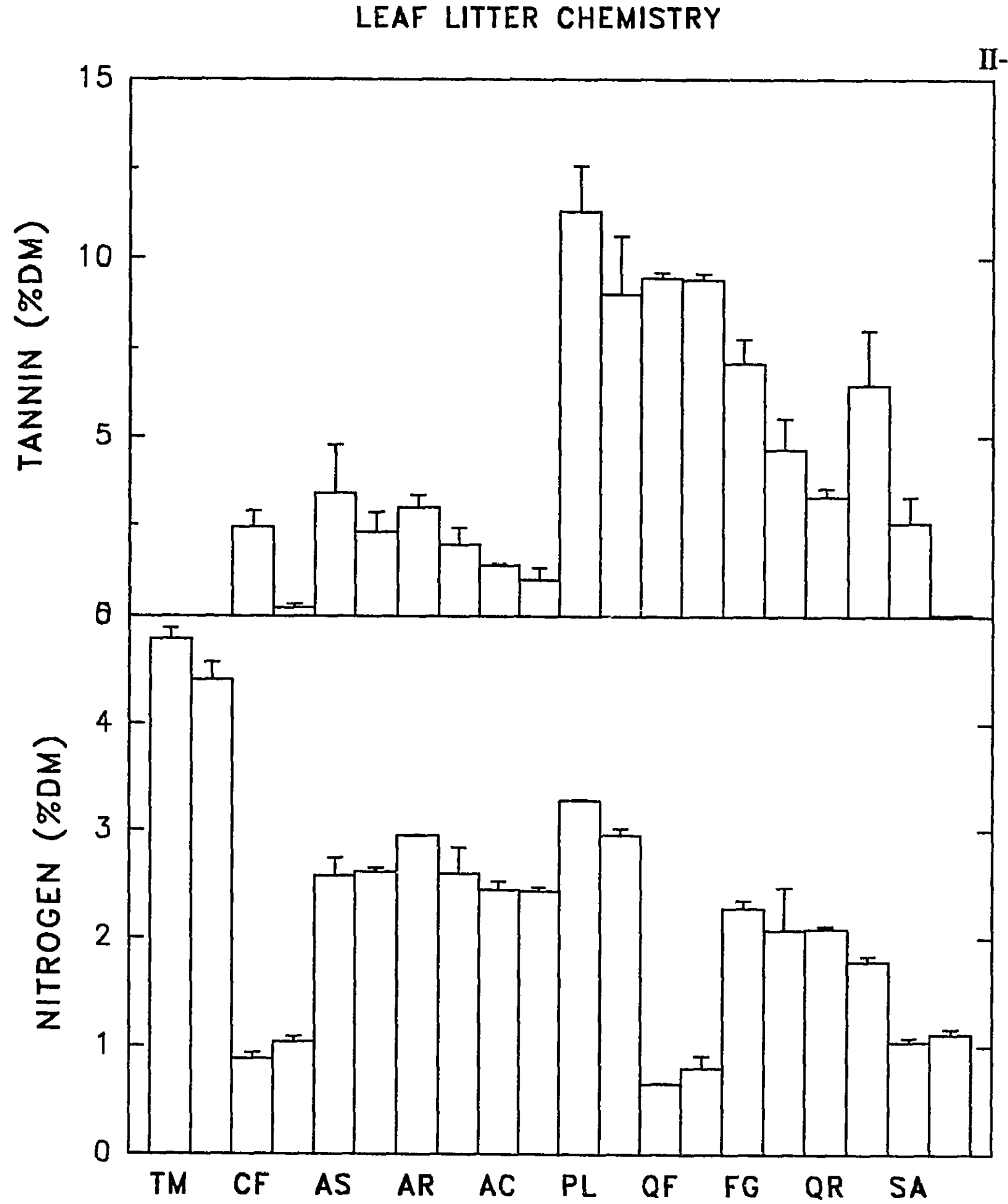

LEAF LITTER CHEMISTRY
TANNIN (%DM)
15
10
5
0
NITROGEN (%DM)
4
3
2
1
0
TM
CF
AS
AR
AC
PL
QF
FG
QR
SA

Figure II-4

$M = 0.007 + 0.137(NITR) - 0.076(TANN)$

$R^2 = 0.468,\ P = 0.002$

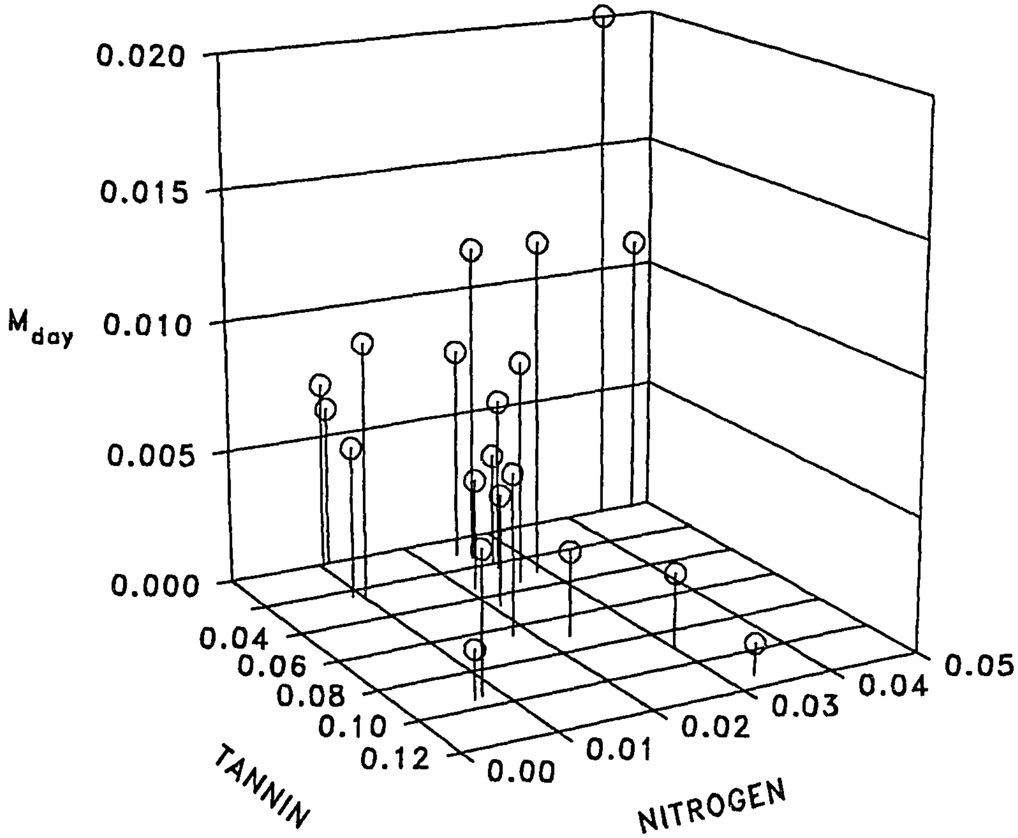


Figure II-5

PHENOLOGY OF BREAKDOWN OF LEAF LITTER FROM NATIVE AND EXOTIC TREES: LEAF CHEMISTRY AND MACROINVERTEBRATE SHREDDER DYNAMICS IN AN ALASKAN BOREAL FOREST STREAM

John G. Irons III[1,2]

Mark W. Oswood[1]

John P. Bryant[1]

R. Jean Stout[3]

Cathy Pringle[4]

To be submitted to the Journal of the North American Benthological Society

---

[1] Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775-0180, USA.

[2] Current address: Institute of Northern Forestry, USDA Forest Service, 308 Tanana Drive, Fairbanks, AK, 99775-5500, USA.

[3] Department of Entomology, Michigan State University, East Lansing, MI, 48824, USA.

[4] Institute of Ecology and Department of Zoology, University of Georgia, Athens, GA, 30602, USA.

INTRODUCTION

The processing of leaf litter from the riparian zone provides a major food source for the microbial and invertebrate detritivores in forest streams (Webster and Benfield 1986). There is an orderly sequence of abiotic and biotic processes that result in mass loss of leaf litter in streams. First, as soon as the leaves fall into the stream, abiotic leaching of soluble cell contents causes a loss of about 5-30% of the initial dry mass of the leaves (Petersen and Cummins 1974). Following leaching, decomposer microbes (aquatic hyphomycetes and bacteria) colonize the leaves and begin to break them down, a process known as conditioning. As the microbes degrade the leaf litter, structural compounds like cellulose and lignin are broken into their constituent parts, and the litter becomes softer, more nutritious, and more easily digested by macroinvertebrates. These invertebrates, known as shredders (Cummins 1973), ingest the leaf-microbe complex, gaining their nutrition from leaf tissue, microbial biomass, and exoenzymes of microbial origin that are present on the leaf surface. Shredder feces and feeding activities produce small particles of organic matter that are then eaten by invertebrate collectors, filter-feeders and gatherers, consuming fine particulate organic matter in transport and in the benthos, respectively (Cummins 1973). In forested regions, the detrital pathway from riparian leaves through shredders and collectors is the major energy flow in stream ecosystems (Petersen and Cummins 1974, Petersen et al. 1989).

The chemical makeup of leaves undergoes many changes during the conditioning and breakdown process (e.g. Suberkropp et al. 1976). One of the most studied characteristics of leaf litter is nitrogen concentration. Most studies have found that nitrogen concentration increases with time during litter breakdown, and have attributed the increase to microbial immobilization (e.g. Kaushik and Hynes 1971, Suberkropp et al. 1976, Melillo et al. 1984, Bärlocher 1985). In other studies, however, the results have been more equivocal (e.g. Chauvet 1987, 1988, Chergui and Pattee 1990, Stewart 1992). Other leaf constituents that have been monitored through time are soluble sugars, lipids, phosphorus, polyphenolics, cellulose, and lignin, and ratios such as carbon:nitrogen (e.g. Suberkropp et al. 1976, Melillo et al. 1984, Chauvet 1987, 1988, Bunn 1988).

Macroinvertebrate colonization and feeding rates are influenced by many factors. Different species of fungi have different palatability to shredders (Suberkropp et al. 1983, Arsuffi and Suberkropp 1984, 1985). Leaves from different tree species are differentially attractive to shredders (e.g. Kaushik and Hynes 1971, Petersen and Cummins 1974, Anderson and Sedell 1979, Short et al. 1980, Webster and Benfield 1986) and shredder consumption and growth are correlated with the nutritional quality of the leaves of different species (e.g. Golladay et al. 1983, Smock and MacGregor 1988). Within a tree species, leaves from trees encountering different environmental conditions (e.g. fertilization and herbivory) can have different foliar chemistry, influencing palatability of leaf litter to shredders (Irons et al. 1988) and breakdown rate (Irons et al. 1991). Thus, leaf litter breakdown is a complex process: initial leaf chemistry influences microbial colonization and growth, initial leaf chemistry and the microbial community both affect shredder colonization and feeding, and microbial degradation and shredder feeding both affect breakdown rates.

In conjunction with a larger study involving several study sites along a latitudinal gradient from Costa Rica to Alaska, we investigated the phenology of leaf litter processing using litter from ten tree species with a wide range of food quality. At all sites, mass loss and macroinvertebrate abundance were monitored during leafpack decomposition, and nitrogen and condensed tannin were measured on a subset of leafpacks exposed to two days of leaching. In addition, in Alaska only, we monitored changes in foliar chemistry throughout the study in order to ascertain whether changes in concentrations of secondary compounds (i.e. condensed tannin) or nutrients (i.e. nitrogen) influenced macroinvertebrate colonization dynamics or processing rates. In this paper we discuss the detailed phenology of leaf litter from ten species of trees, two native and eight exotic, during the process of breakdown in an Alaskan subarctic boreal forest stream.

STUDY SITE

Monument Creek is a second-order tributary of the Chena River approximately 115 km from Fairbanks with a catchment area of approximately 74 km^2. The headwaters of Monument Creek are about 850 m above sea level, and the study site is about 14 km downstream from the headwaters at an elevation of 380 at 65°N latitude and 146°W longitude. Riparian vegetation includes willow (*Salix* spp.), alder (*Alnus crispa*), balsam poplar (*Populus balsamifera*), with occasional white spruce (*Picea glauca*) and black spruce (*P. mariana*).

Average discharge in Monument Creek was estimated at 1.45 $m^3 \bullet s^{-1}$ (range 0.34 - 3.65 $m^3 \bullet s^{-1}$) in 1979/1980 (Cowan et al. 1983) and 1.2 $m^3 \bullet s^{-1}$ (range 0.2 - 1.91 $m^3 \bullet s^{-1}$) in 1982/1983 (Anderson 1984), based on infrequent discharge measurements (the stream is not gauged). Mean annual inorganic nitrogen concentration was 0.85 ± 0.27 $mg \bullet L^{-1}$ (± standard deviation), and total phosphorus concentration was 59 ± 5 $\mu g \bullet L^{-1}$ in 1982/1983 (Anderson 1984). Specific conductance in 1982/1983 averaged 86 ± 50 $\mu mhos \bullet cm^{-1}$ (Anderson 1984). Air temperature was below freezing during the entire study period, reaching a minimum daily mean of -34.0°C on 6 December 1988. The study began just as water temperature was reaching zero degrees Celcius: it was 1.4°C on 5 October, 0.25°C on 22 October and remained about 0.2°C throughout the remainder of the study. This stream accumulated 912 degree-days in 1988, and 21.9 degree-days during the 75 day study period. See Irons et al. (1989) and Irons and Oswood (1992) for a detailed discussion of the thermal regime of Monument Creek.

METHODS

TREE SPECIES AND SOURCE OF LEAVES

Leaves were obtained from a variety of regions in North and Central America, including tropical (Costa Rica: *Pithecellobium longifolium* (H. & B.) Standley (Leguminosae) and *Trema micrantha* (L.) Blume (Ulmaceae)), subtropical (North Carolina: *Quercus falcata* Michx. (Fagaceae) and *Cornus florida* L. (Cornaceae)), temperate (New York: *Fagus grandifolia* Ehrh. (Fagaceae) and *Acer saccharum* Marshall (Aceraceae); Michigan: *Quercus rubra* L. (Fagaceae) and *Alnus rugosa* (Du Roi) Spreng. (Betulacea)), and subarctic (Alaska: *Salix alaxensis* (Anderss.) Cov. (Salicaceae) and *Alnus crispa* (Ait.) Pursh (Betulacaea)). Of two species selected from each region, one species was chosen to be high leaf litter quality as food for stream shredders and one species chosen to be low in food quality. These categories were based on tannin and nitrogen concentrations in leaves, and were designed to give as wide a range of litter quality as possible. At most sites, leaves were collected at abscision, dried at 50°C, leaves from each location were sent to all other locations. Investigators at each of the above locations performed the same experiment in streams of similar depth, velocity, and water quality (see chapter I and chapter II for more detailed descriptions). Only the Alaskan results are reported here.

PREPARATION OF LITTER BAGS AND LEAF PACKS

We used a coarse-meshed (2 cm) leaf litter bag technique to investigate leaf litter processing rates in Monument Creek. All leaves were oven dried at 50°C, then weighed into approximately 3 g leafpacks. Twenty five sets of envelopes (six litter bags per envelope) were fastened to the stream substrate randomly with hardwood dowels driven into the stream bottom in an area of moderate depth (30 to 50 cm) and velocity (approximately 0.3 m/s). The trailing edges of the envelopes were weighted down with small rocks to prevent them from being lifted by the current. Five replicates were removed from the stream on each of five dates (with the exception of the last two dates, when some envelopes were frozen in the ice). Collection dates were days 2, 14, 28, 56, and 75 for all but two species. Because *Trema* and *Acer* were known to disappear very rapidly at other locations (R.J. Stout, C.R. Pringle, pers. observ.), these two species were collected on days 2, 7, 14, 28, and 56.

In the laboratory after collection, packs were placed in enamel pans, and invertebrates and adhering material was rinsed from leaves. Leafpacks were dried at 50°C to constant weight, and invertebrates preserved in 80% ethanol for subsequent sorting, identifying, enumeration, and biomass determination. Following drying, leafpacks were weighed to the nearest 0.01 g. Leafpacks were then ground in a Wiley mill (mesh = 850μm) and 200 mg removed for chemical analysis (if more than 400 mg remained), while the remainder was combusted at 500°C for ash-free dry mass (AFDM) calculation. If less than 400 mg was left, then the entire sample was used for AFDM determination.

FOLIAR CHEMISTRY ANALYSES

Subsamples (74-76 g) of each replicate were analyzed for condensed tannin using the butanol-HCl reaction for proanthocyanidins described by Martin and Martin (1982) and modified by Bryant et al. (1987), with quebracho tannin as a standard. Tannin concentration was determined colorimetrically on a Perkin-Elmer spectrophotometer at an absorbance wavelength of 550 nm, and is reported as percent leaf dry mass in quebracho equivalents. Total Kjeldahl nitrogen and phosphorus concentrations for two replicates collected on day 2 were determined on a Technicon Autoanalyzer by a sulfuric/selenious acid digestion and colorimetric analysis with ferricyanide blue reaction for nitrogen and molybdate blue for phosphorus. These data were used as initial post-leaching values in latitudinal comparisons, as similar samples from Michigan were also analyzed by this technique at the same time (chapter II). Subsequently, the rest of the leaf packs (those with enough remaining mass) were analyzed for total Kjeldahl nitrogen and phosphorus concentrations using a copper sulfate-hydrogen peroxide-sulfuric acid digestion, followed by similar colorimetric analyses on a Lachet Autoanalyzer.

MACROINVERTEBRATE ANALYSES

Most macroinvertebrates were sorted from detritus, identified to genus (species when possible), and enumerated using a Wild dissecting microscope. Chironomidae were sorted to family, although specimens representing the twelve most abundant morphologically distinct taxa were identified to genus. Taxa were placed into functional feeding groups using published data from Cowan et al. (1983), Howe

(1981), and Irons (1988), and taxa not included in these works were assigned to functional groups using Merritt and Cummins (1984). Individuals of the representative chironomids were cleared in polyvinyl alcohol (BioQuip Co.), and gut contents were determined; although *Brillia* was a shredder in Monument Creek, it was a small proportion of the chironomid fauna and all chironomids were classified as non-shredders. Biomass of shredders and non-shredders were expressed as mg AFDM. Both total number and biomass of invertebrates were expressed on a per leafpack and a per gram of leaf tissue remaining basis.

RESULTS

TANNIN

Condensed tannin concentration in leaves declined through time in all species (Figures III-1, III-3). We fit the data to three mathematical models of concentration change through time (linear, exponential, and quadratic): the exponential model was the best fit overall. In five species, the best fit was a negative exponential curve, in two species it was linear, in one species it was quadratic, and in two species, tannin concentration did not change with time (based on comparison of F ratios). Two-way Analysis of Variance (ANOVA) showed that time, not surprisingly, was a significant main effect, that species was even more important, and that the interaction between the two was not significant (Table 1). In this analysis, the variables time and tree species accounted for 98% of the variance in tannin concentration. Because of missing cells in the data matrix (not enough leaf material left for pre-leached analyses, and not enough mass left after decomposition for analyses in some species), only days 2, 14, and 28 were analyzed in this ANOVA.

NITROGEN

Phenology of nitrogen concentration was substantially different from that of tannin concentration. Although there was substantial change through time in almost every species, it was not consistent among species. Linear and exponential regressions were statistically significant in only two of ten species, while quadratic regressions were significant for four of ten species. There was substantial variation in the direction of change in nitrogen concentration as well: three species gained nitrogen, six species lost nitrogen, and one showed no significant change (based on the sign of a linear slope). Four of five species in the low quality group had significant increases in N concentration between Day 2 and Day 14 (Figure III-1), while only two of five species in the high quality group had such a pattern (Figure III-3). In a two-way ANOVA on leaf species and time, time was not a significant main effect, but species was. The interaction between time and species was also significant: how nitrogen concentration changed through time depended upon the tree species.

MASS LOSS

Mass Loss due to Leaching

Leaching is the first process by which leaf litter loses mass in streams. Mass loss due to leaching varied among tree species (Figure III-5A, Table III-1). *Post hoc* comparisons of means showed four groups of species that differed in amount of leaching: *T. micrantha*, *C. florida*, and *A. saccharum* had the highest leachability, followed by *A. rugosa*, *A. crispa*, and *S. alaxensis*. The third group consisted of only *F. grandifolia*, and the fourth and least leachable group consisted of *Q. rubra*, *Q. falcata*, and *P. longifolium* (Figure III-5A). With the exception of *S. alaxensis*, the first two groups were composed of the *a priori* high quality litter category, while the final two groups were composed of the low quality category. The amount of inorganic material left as ash following combustion of unleached leaves was correlated with the amount of mass leached in 48 hours (Figure III-5B). While we did not conduct any analyses on the leachate, we suspect much of it must be intracellular inorganic ions that do not burn at 500°C and are readily leachable.

Overall Decomposition Rates

Leaf litter mass declined through time in all species studied (Figures III-1, III-3). Regression analyses on mass loss (linear regression, linear regression on log-transformed data, and quadratic regression) suggested that decomposition rates of leaf litter in subarctic streams is best approximated by a linear model, rather than by negative exponential or quadratic models (Stout et al. 1993). In all species, the linear regression equation had a slope different from zero at a significance level of P =

0.002 or less, and the linear model always had a higher F ratio than did the negative exponential model (Stout et al. 1993). In general, breakdown curves followed our initial hypothesis: that species chosen to have low leaf litter food quality based on higher tannin levels had slower rates of litter processing in streams. *Salix alaxensis* is the exception. This willow was initially high in tannin; however, tannin was leached rapidly from the leaves by streamwater.

Two-way analysis of variance showed that, for mass loss overall, both the time and species main effects were significant, as well as the interaction between the two (Table 1). The significance of the main effect of time means that leaf litter did indeed lose mass over time, a conclusion already reached by regression analysis. The significant species effect means that different species decomposed different amounts, and the interaction term means that the rate at which decomposition occurred depended on the species of leaves. *Post hoc* comparisons (using Bonferonni's adjustment) showed that there were four significantly different groups of species. Fastest was *T. micrantha*, followed by a large group consisting of (in descending order of mass loss) *A. crispa*, *A. saccharum*, *A. rugosa*, *C. florida*, and *S. alaxensis*. The third group consisted of *F. grandifolia* and *Q. rubra* and the fourth group consisted of *P. longifolium* and *Q. falcata*.

MACROINVERTEBRATES

Most of the invertebrates that colonized leafpacks in Monument Creek were collector-gatherers, dominated by several genera of chironomids (e.g. *Brillia* sp., *Corynoneura* sp. *Cricotopus tremulus* gp., *Diamesia* spp. [at least four species], *Pagastia* sp., *Pseudodiamesa* sp., *Rheocricotopus* sp., *Tanytarsus* sp., *Thienemanniella xena*, *Tuetenia bavarica* gp.), but with a substantial number of baetid mayflies (*Baetis* sp.) as well. Early in the processing season, many early-instar filter-feeding blackfly larvae (*Simulium* sp. and *Prosimulium* sp.) used leafpacks, presumably as habitat. All of these non-shredders were either very small throughout their larval life history, or were present as small early-instar larvae during this study. The shredders were dominated in number by a nemourid stonefly (*Zapada* sp., probably *Z. cinctipes*: Cowan 1983), while biomass was dominated by both *Zapada* and several limnephilid caddisflies (*Ecclisomyia conspersa*, *Onocosmoecus unicolor*, and *Chyranda centralis*; Irons 1988). Predators were represented by the caddisfly *Rhyacophila*, the stoneflies *Plumiperla* (Chloroperlidae) and *Arcynopteryx* (Perlodidae) and the empidid fly *Chelifera* sp. See Appendix for a complete taxa list with numbers and biomass.

While macroinvertebrate numbers were dominated by non-shredders (mean of 86% over all tree species), biomass was dominated by shredders (mean of 63% over all species). The percent of total macroinvertebrate numbers that were shredders did not differ as a function of time of processing (Figure III-6A) or amount of leaf mass remaining (Figure III-7A) (linear regression, $P > 0.10$). However, the percent of total invertebrate biomass that was made up of shredders showed a quadratic distribution (as a function of processing time) for the high quality species but not for the low quality species, with the peak for high quality species at about 40 days (Figure III-6B). We believe that this is due to the fact that the estimated time until 50% of leaf mass was left was greater than 100 days (i.e. greater than the length of the study) in most low quality species. This relationship shows up more clearly when comparing percent biomass as shredders with the percent leaf mass remaining. Here, both low and high quality species showed a quadratic distribution, with the peaks at about 37 and 50% mass gone respectively (Figure III-7B). Thus, in this study, the proportion of total number of invertebrates that were shredders remained constant at about 15% throughout the study, while the proportion of invertebrate biomass that was shredders increased from about 50% to a maximum of about 80% at the time when 50% of the post-leaching leaf mass was gone, regardless of substrate quality.

Patterns of leaf pack colonization by macroinvertebrates were similar to those seen in other biomes (e.g. temperate deciduous forest, Cummins et al. 1989), with overall maximum number and biomass of invertebrates being present at the time when approximately 50% of the leaf material was left. The distribution of shredder numbers and biomass with respect to the amount of leaf mass remaining in the leafpack is described best mathematically by quadratic equations (Figure III-8). Because the high and low leaf litter quality groups leached different amounts, we analyzed the two groups separately. Quadratic regressions of numbers and biomass within each group were significant at the $P < 0.0005$ level, whether based on individual leafpacks or on means for each collection date. The estimated peak number and biomass of shredders were slightly higher in the high quality group, and occurred at about 38% mass remaining rather than at about 50% remaining for the low quality group. The offset of this peak is due to the amount of mass lost to leaching (estimated by the quadratic equations at about 22% for the high quality group and about 5% for the low quality group), and both groups show peak estimate shredder biomass at about 50% post-leaching leaf mass remaining.

Most individual species conformed to this pattern. For example, both *Alnus* species had the highest number and biomass of shredder between day 28 and day 56, and estimated time until 50% of the leaf mass was remaining was 32 and 31 days. Quadratic regression equations showed that fitted curves for shredder numbers against mass remaining were statistically significant (except on *Pithecellobium* leafpacks) and concave downward (except on *Acer* leafpacks). Shredder numbers were still increasing in *Acer* leafpacks at the end of the study, and shredder abundance was consistently low in *Pithecellobium*.

Equations for shredder biomass were less consistent with the overall pattern than were equations for numerical abundance. All species had significant equations at the $P = 0.05$ level, but the equations for four species (*Acer*, *Pithecellobium*, *Q. rubra*, and *Fagus*) were concave upward, indicating that biomass of shredders was still increasing at the end of the study. The latter three species were all in the low quality group, and this result is consistent with that found in Figure III-6, in which the shredder biomass on the low quality group was continuing to increase at the end of the study, when biomass of the high quality group was declining.

Shredder numbers and biomass showed a unimodal (i.e. quadratic) distribution when compared with decomposition rates (Figure III-9). Shredder numbers and biomass are low on slowly decomposing species (e.g. *P. longifolium*, *Q. falcata*), highest on species with intermediate decomposition rates, and lower on the fastest decomposing species (but not as low as on the slow species). Note that the quadratic equations shown in the figure are based on overall means for the species (error bars for mean values are shown to provide a feel for the variation around these means). This pattern is likely due to lack of litter left near the end of processing in fast decomposing species: the litter was processed so fast that the overall mean shredder abundance is low.

Colonization of leaf litter by shredders is likely influenced by the chemistry of the leaves. We compared mean shredder abundance (over the entire study period) to condensed tannin and nitrogen concentrations in the leaf litter on day 2. Univariate regressions showed that shredder biomass was highly correlated with tannin concentration but not with nitrogen concentration, and that shredder number was nearly correlated with tannin concentration but not with nitrogen (Table 2). In multiple regression analyses, mean shredder number and biomass were significantly correlated with tannin and nitrogen concentrations together (Figures III-10, III-11); however, the improvement over the model of just tannin concentration was slight, as the F ratio increased from 24.5 to 26.9 and the R^2 increased from 0.72 to 0.85 (Table III-2). We performed the same analyses using mean tannin and nitrogen concentrations over the entire study period: they followed the same pattern but were slightly less significant statistically, and are not shown in figures or tables.

We also analyzed several models of controlling variables of mass loss in leaf litter. Of the four predictor variables analyzed, tannin concentration on day 2 and mean shredder biomass significantly predicted mass loss rates of leafpacks of these ten species of trees, while nitrogen concentration and shredder numbers were not significant (Table III-3). Tannin concentration explained the largest amount of the variance, and had the highest F ratio. Unfortunately, tannin concentration and shredder biomass were highly correlated ($R = -0.88$). Adding biomass to the univariate tannin model resulted in a higher R^2, but reduced the F ratio (due to a loss of degrees of freedom), which we interpret to mean that the model has less explanatory power. Thus, the most parsimonious model for controlling variables on processing rates of leafpacks made from these ten species of trees is that decomposition rates were controlled by tannin concentration.

DISCUSSION

Leaf litter that falls into streams breaks down via a number of degradative processes. Leaching begins as soon as the leaves are immersed, and significant mass loss can occur via this process. Following (and perhaps during) leaching, microbial decomposers and macroinvertebrate shredders colonize the leaves and use the carbon and nutrients of the leaf tissue for their own growth. These leaves, however, come from trees that have had a history of defending themselves against herbivory (both insect and mammalian) and fungal invasion, both in evolutionary time as species and in ecological time as individuals (Janzen 1979). The legacy of these anti-herbivore defenses follows the leaves into the stream, and although the tree no longer needs the defense once the leaves are shed, the defense remains. Many plant defenses are water soluble and are lost quickly from litter in streams (e.g. hydrolyzable tannins, latex), while others have low solubility in cold water and are leached only slowly (e.g. condensed tannin). Thus, stream organisms that depend on leaf litter face a suite of attractants (e.g. nutrients, digestible carbon compounds) and inhibitors (e.g. plant defensive compounds) in their food.

TANNIN

Condensed tannin concentrations in leafpacks differed among the ten tree species used in this study, and concentrations declined through time in all ten species. Our results support the contention that loss of condensed tannin from leaves is a physical process that starts at different concentrations for different species, but the rate of loss is exponential and similar among species (i.e. the interaction term in the two-way ANOVA was not significant). This implies that species that start with a high concentration of tannin continue to have relatively higher concentrations than low tannin species through the litter breakdown process. Other leaf processing studies have shown that tannin concentrations decline through time, both in soils (often measured as polyphenols) (e.g. Nykvist 1963, Anderson 1973) and in streams (e.g. Bunn 1988, Irons et al. 1991). In another part of this study, we showed that condensed tannin concentration after leaching (i.e. on day 2) is a good predictor of decomposition rates (Stout et al. 1993). Irons et al. (1988) showed that a limnephilid shredder preferred leaf litter that was high in nitrogen and low in tannin concentration, and Cameron and LaPoint (1978) showed that tannin inhibits feeding by invertebrates. A shredding gastropod experienced higher mortality on fresh willow leaves than on dried leaves: dried leaves lost more mass to leaching, perhaps an inhibitory compound was part of the leachate (Chergui and Pattée 1992). Decomposition rates are slower for species that have higher concentrations of tannin (Irons et al. 1991, Stout et al. 1993) or for treatments that produce leaves with lower tannin concentration (Bunn 1988). In this study, we showed that tannin concentration is negatively correlated with shredder abundance as well as with decomposition rates.

Many secondary compounds made by plants are antibiotic (i.e. inhibitory to microbes). Zucker (1983) speculated that tannins evolved as protection from fungal pathogens rather than as protection from herbivores. Microbes (e.g. aquatic hyphomycetes) colonize leaves of different species at different rates in streams (e.g. Buttimore et al. 1984, Chamier 1987) and have different growth and respiration rates on leaves of different tree species (e.g. Buttimore et al. 1984, Findlay and Arsuffi

1989), suggesting that compounds present in the leaves of some species may be either inhibitory or stimulatory. Drying and freezing of leaves increases the leaching rates, and breakdown of dried leaves is faster than breakdown of fresh leaves for the early part of processing (Gessner and Schwoerbel 1989, Gessner 1991, Chergui and Pattée 1992), while in the later part of processing, mass loss rates become similar. Extracts from pine needles (Bärlocher and Oertli 1978), fresh (but not dried) alder leaves (Bärlocher 1990), and fresh (but not dried or frozen) maple, birch, and elm leaves (Bärlocher 1992) inhibit microbial colonization and growth. Thus, colonization and degradation rates of leaf litter by microbes in streams may be partially mediated by the secondary chemistry of the leaves. Whether the slower decomposition of leaves with large amounts of tannin is a result of less macroinvertebrate feeding, of less microbial degradation, or an interaction between the two remains to be determined.

NITROGEN

Nitrogen concentration in leafpacks used in this study changed during decomposition on a species-specific basis: nitrogen concentration increased in some species and decreased in others, and the shape of the curve also depended on the species. There was a positive slope only in three species, none of which was significantly different from zero. Six species showed an increase between day 2 and day 14, but then declined. Four of the six species that showed an increase in nitrogen between day 2 and day 14 were in the high tannin group. Such a result is not likely to be due to a purely physical process such as leaching, but is consistent with concentration changes being mediated by biological processes (e.g. microbial colonization). If microbial species have different colonization rates, and different affinities for leaves of different tree species, then the varying amount (depending on tree species) of microbially sequestered nitrogen could account for the differing patterns of nitrogen concentration change. Unfortunately, no measures of the microbial community were obtained.

Most sttudies have found that, following the short period of leaching, nitrogen concentration in leaf litter rises as microbes colonize the leaves and add microbial nitrogen (both in cells and as exoenzymes) by sequestering nitrogen from stream water (e.g. Kaushik and Hynes 1971, Hart and Howmiller 1975, Suberkropp et al. 1976, Blackburn and Petr 1979, Melillo et al. 1984, Mulholland et al. 1987, Bunn 1988, Stewart 1992). Melillo et al. (1984) discussed the phenology of nitrogen concentration in submerged leaves, and provided a method of estimating the maximum amount of nitrogen that the microbial community on leaf litter can sequester. Their method involves plotting the amount of mass remaining against the nitrogen concentration in that remaining material. For this technique to work, the data must fit the often-observed pattern of a steady increase in nitrogen as mass is lost. Unfortunately, none of the ten species used in this study showed a consistent increase in nitrogen, and we could not use this technique.

Other investigators have found that little of the increase in nitrogen concentration in leafpacks can be attributed to nitrogen in microbial cells (Bärlocher 1985). Iversen (1973) found that less than 10% of the nitrogen gained by decaying beech leaves was due to microbial cells, and speculated that much of the non-microbial nitrogen was due to microbial secretions such as exoenzymes that degrade leaf material outside the microbial cells. Especially in species with high concentrations of polyphenols (e.g. oak), much of the increase in litter nitrogen may be due to insoluble nitrogen-lignin and nitrogen-tannin complexes that are nutritionally unavailable to both microbes and shredders (Suberkropp et al. 1976).

The microbial community on leafpacks in Monument Creek grows vigorously even at temperatures very close to 0°C (Buttimore et al. 1984); however, activity (measured as oxygen consumption) at a given temperature (e.g. 5°C) in Monument Creek was lower than in a temperate stream in Michigan (Petersen, R. C. and Cummins 1974). The amount of mass loss attributable to microbial degradation of alder, birch and willow leafpacks was estimated at 7-10% of total mass loss in Monument Creek (Buttimore et al. 1984). Nitrogen concentration in Monument Creek is low (annual mean of 0.85 $mg \cdot L^{-1}$, Anderson 1984), and perhaps the microbial community, although vigorous even at low temperatures, cannot sequester enough inorganic nitrogen from the stream water to result in a consistent increase in nitrogen concentration through time (e.g. Melillo et al. 1984).

We suggest that the lack of concordance between the nitrogen phenology of leafpacks in Monument Creek and those in temperate streams may be a result of reduced microbial activity due to low temperatures and low nitrogen concentration in stream water. Further, nitrogen concentration in decomposing leafpacks is a result of 1) leaching of soluble nitrogen-containing compounds, 2) increasing concentration in microbial biomass and associated exoenzymes, and 3) the creation of insoluble, unavailable complexes with tannin and lignin. The differing patterns of N concentration among species also may be due in part to the interaction of tannin inhibition of microbial colonization and complexation with protein (e.g. microbial exoenzymes).

Heal et al. (1981) argued that low quality leaf litter has a number of characteristics that make it so; e.g., high concentrations of lignin and inhibitory compounds such as polyphenols like tannins, and low concentrations of nutrients and soluble organic compounds. These positive and negative characteristics interact, and separating cause and effect are difficult (Heal et al. 1981). Regardless of the mechanism causing the nitrogen phenology of leafpacks in Monument Creek, we feel that the microbial community plays a relatively minor but important role in the breakdown of leaf litter in subarctic streams (Buttimore et al. 1984, chapter IV). Thus, the initial leaf chemistry (i.e. concentrations and solubility of nutrients and secondary compounds) sets the stage for the biotic processes of leaf litter breakdown, namely microbial and invertebrate colonization and growth.

MACROINVERTEBRATES

Macroinvertebrate shredders (Cummins 1973) consume leaf litter in streams, generally after conditioning by microbes (Anderson and Sedell 1979), and can be an important component of the decomposition process (Webster and Benfield 1986). In a previous study in Monument Creek, macroinvertebrates were considered to be more important in breakdown of leaf litter of three tree species than were microbes (Cowan et al. 1983, Buttimore et al. 1984). Studies have found a wide range of relative importance of microbes versus shredders. For instance, Mathews and Kowalczewski (1969) and Benfield et al. (1977) found that macroinvertebrates had little impact on mass loss rates of leaf litter; however, both studies were conducted in rivers with few shredders. In a study of the effect of pH on decomposition rates, Mulholland et al. (1987) found that shredder numbers or biomass did not explain the reduction in decomposition rate in streams of low pH, and attributed the reduction to the effect of acid on microbes. Other studies found that macroinvertebrates are important in controlling litter breakdown rates. For example, Hart and Howmiller (1975) suggested that the difference in breakdown rates among species and among streams is best explained by macroinvertebrate density. Iversen (1975) found that there was a good (negative) correlation between number of macroinvertebrates in 6 mm mesh litter bags and the time required to process 50% of the leaf mass. Bartodziej and Perry (1990) found that shredders were important in breaking down boxelder leaves, but not watercress leaves. When large shredders were excluded from leafpacks in a Utah and an eastern Washington stream, breakdown rates were lower: although shredder numbers were similar, apparently shredder biomass was higher in the control leafpacks (biomass was not measured directly) (Barnes et al. 1986). Similarly, when predators of shredders were excluded from leafpacks, shredder density increased, as did breakdown rate (Oberndorfer et al. 1984).

The amount of conditioning of leaf litter that is required before macroinvertebrates colonize it and start feeding is also variable. McArthur and Barnes (1988) found that nearly 100 macroinvertebrates were present per two five-gram leafpacks of box elder after only two days in a Utah stream, and that shredders made up about 85% of them. Short et al. (1980) found substantial colonization within seven days; however, most of these were collector-gatherers. Other studies have found much longer periods before substantial colonization (e.g. Bunn 1988). In this study, there was also substantial colonization in the first two days: an average of almost 30 per 3 g leafpack, virtually the same as found by McArthur and Barnes (1988) on a per gram of leaf material basis. Shredders made up about 15% (by numbers) or about 50% (by biomass) of the invertebrate community on day 2. Shredder abundance peaked when about 50% of the post-leaching mass was left; shredders reached their highest proportion of the total community (by biomass) at this time as well.

Cummins et al. (1989) developed an elegant model linking riparian vegetation and shredding macroinvertebrates. They suggested that the maximum biomass of shredders would be achieved at the time when half of the leaf mass was gone, and that species in the fast processing category would likely have a peak shredder biomass of about 60-80 mg/g leaf tissue, while those in the slow processing category would likely have a biomass of about 20-40 mg/g. In our study, shredder biomass on a per leafpack basis was highest at about 50% remaining (after correcting for leaching), but on a per gram of remaining leaf tissue basis, shredder biomass on leafpacks of all species continued to increase as mass was lost, reaching 2100 and 710 mg/g in the two alder species.

Studies have shown that leaf chemistry plays a role in controlling leaf litter breakdown rates. In addition to the studies showing that nitrogen and breakdown rates are positively correlated (see Introduction), a few studies have suggested that inhibitors may slow litter breakdown (Stout 1989). In an Australian species high in tannin, Bunn (1988) found that the concentration of polyphenols (measured as tannic acid equivalents) caused a reduction in microbes, and that shredders were not important until late in processing. Blackburn and Petr (1979) also found that *Eucalyptus* leaves had a long period of no mass loss, and that an exotic species (oak) had faster breakdown rate than the two native species (southern beech and eucalyptus). Tree species (alder, birch, willow, poplar) and fertilization history (N, P, N+P, unfertilized control) influenced the tannin and nitrogen concentrations of leaves and hence consumption rates by a stream shredder (Irons et al. 1988). Leaf litter from birch trees that had been browsed by moose had higher nitrogen, lower tannin (after leaching) and faster breakdown rates than litter from trees that had not experienced browsing (Irons et al. 1991). Thus, many studies have shown the positive correlation between nitrogen and breakdown rates, and several studies have shown the negative correlation between tannin and breakdown rates. In this study, because we had species that were high in both nitrogen and tannin, and species that were low in both, we were able to separate the two factors. We previously suggested that tannin is more important in controlling breakdown rates (Stout et al. 1993), and here we suggest that tannin concentration is more highly correlated with shredder abundance than is nitrogen concentration.

Clearly, initial chemistry of leaves plays a role in controlling the rate at which they break down in streams. In many previous studies, nitrogen was found to be highly correlated with breakdown rates. However, nitrogen concentration is often highly correlated (negatively) with tannin concentration in leaf litter (Irons et al. 1988). The species used in our study provided a range of nitrogen and tannin concentrations that were not highly correlated ($R=-0.33$). Using multiple regression to construct models of the influence of initial leaf litter chemistry on colonization by macroinvertebrate shredders and litter breakdown rates (Tables 2 and 3) leads us to conclude that the correlation between initial tannin concentration and shredder numbers and biomass is higher than is the correlation between initial nitrogen concentration.

The suite of physical and chemical characteristics of leaf litter that falls into streams influences the colonization and growth of microbes and macroinvertebrate shredders, and ultimately the rate at which the leaf litter breaks down. Toughness and high lignin and tannin concentrations are often negatively correlated with concentrations of nutrients and soluble organic compounds (Heal et al. 1981, Haslam 1989). Secondary compounds such as condensed tannins affect microbial (Zucker 1983) and shredder (Irons et al. 1988) preference for leaves, which in turn influence decomposition rates. In this study, we have shown that condensed tannin concentration explains the variance in shredder biomass roughly three times as well as does nitrogen concentration. However, it behooves us as ecologists to remember that correlation does not equal causation. In order to construct a complete model of leaf litter processing, we must elucidate the mechanism by which concentrations of nutrients and secondary compounds affect microbes and shredding macroinvertebrates.

ACKNOWLEDGMENTS

Funding for this project was provided by the National Science Foundation Taiga Forest Long Term Ecological Research grant BSR-8702629, with additional assistance from the Institute of Northern Forestry (Aquatic/Land Interaction Program) and the Institute of Arctic Biology. I thank the Chena Hot Springs Resort for access to the Monument Creek study site via their airstrip and the colleagues listed in Table 1 for providing leaf material. Field help was provided by J. Johnson, D. Kennedy, S. Peek, and M. Wagener. S. Kennedy sewed the litter bags, K. Frisby and R. Stafford performed the tannin analysis, and Lori Moilinan and Allen Doyle performed the nitrogen analysis. E. Gabrielson, S. Peek, and S. Tuccio helped with macroinvertebrate sorting and biomass determination. Early versions of this manuscript were improved with help from Drs. T. Clausen, P. Quang, E. Rexstad, and K. Van Cleve.

LITERATURE CITED

ANDERSON, J. M. 1973. The breakdown and decomposition of sweet chestnut (*Castanea sativa Mill.*) and beech (*Fagus sylvatica* L.) leaf litter in two deciduous woodland soils. II. Changes in the carbon, hydrogen, nitrogen and polyphenol content. Oecologia 12:275-288.

ANDERSON, N. H., AND J. R. SEDELL. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Annual Review of Entomology 24:351-377.

ANDERSON, P. R. 1984. Seasonal changes in attached algae in two Alaskan subarctic streams. M.Sc. Thesis. University of Alaska Fairbanks.

ARSUFFI, T. L., AND K. SUBERKROPP. 1984. Leaf processing capabilities of aquatic hyphomycetes: interspecific differences and influence on shredder feeding preferences. Oikos 42:144-154.

ARSUFFI, T. L., AND K. SUBERKROPP. 1985. Selective feeding by stream caddisfly (Trichoptera) detritivores on leaves with fungal-colonized patches. Oikos 45:50-58.

BÄRLOCHER, F. 1985. The role of fungi in the nutrition of stream invertebrates. Botanical Journal of the Linnean Society 91:83-94.

BÄRLOCHER, F. 1990. Factors that delay colonization of fresh alder leaves by aquatic hyphomycetes. Archive fur Hydrobiologia 119:249-255.

BÄRLOCHER, F. 1992. Effects of drying and freezing autumn leaves on leaching and colonization by aquatic hyphomycetes. Freshwater Biology 28:1-7.

BÄRLOCHER, F., AND J. J. OERTLI. 1978. Colonization of conifer needles by aquatic hyphomycetes. Canadian Journal of Botany 56:57-62.

BARNES, J. R., J. V. MCARTHUR, AND C. E. CUSHING. 1986. Effect of excluding shredders on leaf litter decomposing in two streams. Great Basin Naturalist 46:204-207.

BARTODZIEJ, W., AND J. A. PERRY. 1990. Litter processing in diffuse and conduit springs. Hydrobiologia 206:87-97.

BENFIELD, E. F., D. S. JONES, AND M. F. PATTERSON. 1977. Leaf pack processing in a pastureland stream. Oikos 29:99-103.

BLACKBURN, W. M., AND T. PETR. 1979. Forest litter decomposition and benthos in a mountain stream in Victoria, Australia. Archive fur Hydrobiologia 86:453-498.

BRYANT, J. P., T. P. CLAUSEN, P. B. REICHARDT, M. C. MCCARTHY, AND R. A. WERNER. 1987. Effect of nitrogen fertilization upon the secondary chemistry and nutritional value of quaking aspen (Populus tremuloides Michx.) leaves for the large aspen tortrix (Choristoneura conflictana (Walker)). Oecologia 73:513-517.

BUNN, S. E. 1988. Processing of leaf litter in two northern jarrah forest streams, Western Australia: II. The role of macroinvertebrates and the influence of soluble polyphenols and inorganic sediment. Hydrobiologia 162:211-223.

BUTTIMORE, C. A., P. W. FLANAGAN, C. A. COWAN, AND M. W. OSWOOD. 1984. Microbial activity during leaf decomposition in an Alaskan subarctic stream. Holarctic Ecology 7:104-110.

CAMERON, G. N., AND T. W. LAPOINT. 1978. Effects of tannins on the decomposition of Chinese tallow leaves by terrestrial and aquatic invertebrates. Oecologia 32:349-366.

CHAMIER, A.-C. 1987. Effect of pH on microbial degradation of leaf litter in seven streams of the English Lake District. Oecologia 71:491-500.

CHAUVET, E. 1987. Changes in the chemical composition of alder, poplar, and willow leaves during decomposition in a river. Hydrobiologia 148:35-44.

CHAUVET, E. 1988. Influence of the environment on willow leaf litter decomposition in the alluvial corridor of the Garrone River. Archive fur Hydrobiologia 112:371-386.

CHERGUI, H., AND E. PATTEE. 1990. The influence of season on the breakdown of submerged leaves. Archive fur Hydrobiologia 120:1-12.

CHERGUI, H., AND E. PATTÉE. 1992. Processing of fresh and dry *Salix* leaves in a Moroccan river system. Acta Oecologica 13:291-298.

COWAN, C. A. 1983. Phenology of detritus input, storage and processing in an Alaskan subarctic stream. M.Sc. Thesis. University of Alaska Fairbanks.

COWAN, C. A., M. W. OSWOOD, C. A. BUTTIMORE, AND P. W. FLANAGAN. 1983. Processing and macroinvertebrate colonization of detritus in and Alaskan subarctic stream. Holarctic Ecology 6:340-348.

CUMMINS, K. W. 1973. Trophic relations of aquatic insects. Annual Review of Entomology 18:183-206.

CUMMINS, K. W., M. A. WILZBACH, D. M. GATES, J. B. PERRY, AND W. B. TALIAFERRO. 1989. Shredders and riparian vegetation. BioScience 39:24-30.

FINDLAY, S. E. G., AND T. L. ARSUFFI. 1989. Microbial growth and detritus transformations during decomposition of leaf litter in a stream. Freshwater Biology 21:261-269.

GESSNER, M. O. 1991. Differences in processing dynamics of fresh and dried leaf litter in a stream ecosystem. Freshwater Biology 26:387-398.

GESSNER, M. O., AND J. SCHWOERBEL. 1989. Leaching kinetics of fresh leaf litter with implications for the current concept of leaf processing in streams. Archive fur Hydrobiologia 115:81-90.

GOLLADAY, S. W., J. R. WEBSTER, AND E. F. BENFIELD. 1983. Factors affecting food utilization by a leaf shredding aquatic insect: leaf species and conditioning time. Holarctic Ecology 6:157-162.

HART, S. D., AND R. P. HOWMILLER. 1975. Studies on the decomposition of allochthonous detritus in two southern California streams. Verh. Int. Verein. Limnol. 19:1665-1674.

HASLAM, E. 1989. Plant polyhenols: vegetable tannins revisited. Cambridge University Press, Cambridge.

HEAL, O. W., P. W. FLANAGAN, D. D. FRENCH, AND S. F. MACLEAN Jr. 1981. Decomposition and accumulation of organic matter. Pages 587-633 *in* L.C. Bliss, O.W. Heal and J.J. Moore (editors). Tundra ecosystems: A comparative analysis. Cambridge University Press, Cambridge, U.K.

HOWE, A. L. 1981. Life histories and community structures of Ephemeroptera and Plecoptera in two Alaskan subarctic streams. M.Sc. Thesis. University of Alaska

Fairbanks.

IRONS, J. G., III. 1988. Life history patterns and trophic ecology of Trichoptera in two Alaskan (U.S.A.) subarctic streams. Canadian Journal of Zoology 66:1258-1265.

IRONS, J. G., III, AND M. W. OSWOOD. 1992. Seasonal temperature patterns in an arctic and two subarctic Alaskan (USA) headwater streams. Hydrobiologia 237:147-157.

IRONS, J. G., III, M. W. OSWOOD, AND J. P. BRYANT. 1988. Consumption of leaf detritus by a stream shredder: influence of tree species and nutrient status. Hydrobiologia 160:53-61.

IRONS, J. G., III, S. R. RAY, L. K. MILLER, AND M. W. OSWOOD. 1989. Spatial and seasonal patterns of streambed water temperatures in an Alaskan subarctic stream. Pages 381-390 *in* W.W. Woessner and D.F. Potts (editors). Symposium proceedings on headwaters hydrology. June 1989, Missoula, MT. Am. Water Res. Assoc., Bethesda, MD.

IRONS, J. G., III, J. P. BRYANT, AND M. W. OSWOOD. 1991. Effects of moose browsing on decomposition rates of birch leaf litter in a subarctic stream.

Canadian Journal of Fisheries and Aquatic Sciences 48:442-444.

IVERSEN, T. 1973. Decomposition of autumn-shed beech leaves in a springbrook and its significance for the fauna. Archive fur Hydrobiologia 72:305-312.

IVERSEN, T. M. 1975. Disappearance of autumn-shed beech leaves placed in bags in small streams. Verh. Int. Verein. Limnol. 19:1687-1692.

JANZEN, D. H. 1979. New horizons in the biology of plant defenses. Pages 331-350 *in* G.A. Rosenthal and D.H. Janzen (editors). Herbivores: their interaction with secondary plant metabolites. Academic Press, New York.

KAUSHIK, N. K., AND H. B. N. HYNES. 1971. The fate of the dead leaves that fall into streams. Archive fur Hydrobiologia 68:465-515.

MARTIN, J. S., AND M. M. MARTIN. 1982. Tannin assays in ecological studies: Lack of correlation between phenolics, proanthocyanidins and protein-precipitating constituents in mature foliage of six oak species. Oecologia 54:205-211.

MATHEWS, C. P., AND A. KOWALCZEWSKI. 1969. The disappearance of leaf litter and its contribution to production in the River Thames. Journal of Ecology

57:543-555.

MCARTHUR, J. V., AND J. R. BARNES. 1988. Community dynamics of leaf litter breakdown in a Utah alpine stream. Journal of the North American Benthological Society 7:37-43.

MELILLO, J. M., R. J. NAIMAN, J. D. ABER, AND A. E. LINKENS. 1984. Factors controlling mass loss and nitrogen dynamics of plant litter decaying in northern streams. Bulletin of Marine Science 35:341-356.

MERRITT, R. W., AND K. W. CUMMINS. 1984. An introduction to the aquatic insects of North America, 2nd edition. Kendall/Hunt Publ. Co., Dubuque.

MULHOLLAND, P. J., A. V. PALUMBO, J. W. ELWOOD, AND A. D. ROSEMOND. 1987. Effects of acidification on leaf decomposition in streams. Journal of the North American Benthological Society 6:147-158.

NYKVIST, N. 1963. Leaching and decomposition of water-soluble organic substances from different types of leaf and needle litter. Stud. For. Suecica 3:1-29.

OBERNDORFER, R. Y., J. V. MCARTHUR, AND J. R. BARNES. 1984. The effect of invertebrate predators on leaf litter processing in an alpine stream. Ecology 65:1325-1331.

PETERSEN, R. C., AND K. W. CUMMINS. 1974. Leaf processing in a woodland stream. Freshwater Biology 4:343-368.

PETERSEN, R. C., Jr., K. W. CUMMINS, AND G. M. WARD. 1989. Microbial and animal processing of detritus in a woodland stream. Ecological Monographs 59:21-39.

SHORT, R. A., S. P. CANTON, AND J. V. WARD. 1980. Detrital processing and associated macroinvertebrates in a Colorado mountain stream. Ecology 61:727-732.

SMOCK, L. A., AND C. M. MACGREGOR. 1988. Impact of the American chestnut blight on aquatic shredding macroinvertebrates. Journal of the North American Benthological Society 7:212-221.

STEWART, B. A. 1992. The effect of invertebrates on leaf decomposition rates in two small woodland streams in southern Africa. Archive fur Hydrobiologia 124:19-33.

STOUT, R. J. 1989. Effects of condensed tannins on leaf processing in mid-latitude and tropical streams: a theoretical approach. Canadian Journal of Fisheries and Aquatic Sciences 46:1097-1106.

SUBERKROPP, K., G. L. GODSHALK, AND M. J. KLUG. 1976. Changes in the chemical composition of leaves during processing in a woodland stream. Ecology 57:720-727.

SUBERKROPP, K., T. L. ARSUFFI, AND J. P. ANDERSON. 1983. Comparison of degradative ability, enzyme activity, and palatability of aquatic hyphomycetes grown on leaf litter. Applied and Environmental Microbiology 46:237-244.

WEBSTER, J. R., AND E. F. BENFIELD. 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics 17:567-594.

ZUCKER, W. V. 1983. Tannins: does structure determine function? An ecological perspective. American Naturalist 121:335-365.

Table III-1. Analysis of Variance for condensed tannin and nitrogen concentrations, and leaf litter mass loss rates in ten species of leaves placed in Monument Creek in autumn and winter of 1988.

CONDENSED TANNIN

Source	SS	DF	MS	F	P
Species	1816.247	2	201.805	21.609	0.000
Day	75.636	9	37.818	115.308	0.000
Spp*Day	51.421	18	2.857	1.632	0.063
Error	206.516	118	1.750		

NITROGEN

Species	0.00627	9	0.00070	53.847	0.000
Day	0.00001	2	0.00000	0.228	0.797
Spp*Day	0.00387	18	0.00021	16.623	0.000
Error	0.00102	79	0.00001		

MASS LOSS: TWO WAY ANOVA

Source	SS	DF	MS	F	P
Species	43404.674	3	14468.225	1040.830	0.000
Day	48879.086	9	5431.010	390.702	0.000
Spp*Day	18369.990	27	680.370	48.945	0.000
Error	2126.801	153	13.901		

DAY 2: Mass Loss due to Leaching

Species	4139.006	9	459.890	172.515	0.000
Error	106.632	40	2.666		

Table III-2. Models of controls of leaf chemistry on shredder abundance in leaf packs.

Model	Regression Equation	R^2	F	P
Biomass = Constant + Tannin	$Y = 16.09 - 0.98*T$	0.723	24.5	0.001
Biomass = Constant + Nitrogen	$Y = 11.7 - 0.19*N$	0.000	0.02	0.879
Number = Constant + Tannin	$Y = 39.9 - 1.78*T$	0.217	3.5	0.098
Number = Constant + Nitrogen	$Y = 39.1 - 3.45*N$	0.007	1.1	0.333
Biomass = Constant + Tannin + Nitrogen	$Y = 19.90 - 1.22*T - 1.35*N$	0.853	26.9	0.001
Number = Constant + Tannin + Nitrogen	$Y = 56.60 - 2.40*T - 5.93*N$	0.501	5.5	0.036

Table III-3. Models of controls (tannin, nitrogen, and shredder abundance) over decomposition rates (M).

Model	Regression Equation	R^2	F	P
M = Constant + Tannin	Y = 1.24 - 0.10*T	0.736	26.1	0.001
M = Constant + Nitrogen	Y = 0.40 + 0.14*N	0.042	1.4	0.272
M = Constant + Shredder Biomass	Y = -0.06 + 0.07*B	0.371	6.3	0.036
M = Constant + Shredder Number	Y = 0.24 + 0.02*#	0.076	1.7	0.224
M = Constant + Tannin + Nitrogen	Y = 1.12 - 0.10*T + 0.04*N	0.711	12.1	0.005
M = Constant + Tann + Biomass	Y = 1.89 - 0.14*T - 0.04*B	0.745	14.2	0.003
M = Constant + Nitr + Biomass	Y = -0.45 + 0.16*N + 0.07*B	0.511	5.7	0.034
M = Constant + Tann + Number	Y = 1.36 - 0.11*T - 0.003*#	0.705	11.7	0.006
M = Constant + Nitr + Number	Y = -0.50 + 0.22*N + 0.02*#	0.352	3.4	0.091
M = Constant + Tann + Nitr + Biomass	Y = 2.18 - 0.16*T - 0.03*N - 0.05*B	0.708	8.3	0.015
M = Constant + Tann + Nitr + Number	Y = 1.14 - 0.10*T + 0.04*N - 0.00*#	0.663	6.9	0.023

FIGURE CAPTIONS

Figure III-1. Mass loss (A), condensed tannin concentration (B), and nitrogen concentration (C) on each collection date for the five species in the low quality leaf litter category. Error bars are one standard error of the mean (n=5), unapparent error bars are hidden by the symbol.

Figure III-2. Mean number (A) and biomass (B) of shredders on each collection date for the five species in the low quality leaf litter category. Error bars are one standard error of the mean (n=5), unapparent error bars are hidden by the symbol.

Figure III-3. Mass loss (A), condensed tannin concentration (B), and nitrogen concentration (C) on each collection date for the five species in the high quality leaf litter category. Error bars are one standard error of the mean (n=5), unapparent error bars are hidden by the symbol.

Figure III-4. Mean number (A) and biomass (B) of shredders on each collection date for the five species in the high quality leaf litter category. Error bars are one standard error of the mean (n=5), unapparent error bars are hidden by the symbol.

Figure III-5. (A) Percent of original mass (3 g) lost due to leaching for two days in Monument Creek. Lines above the bars connect means that are not significantly different (one way ANOVA, post hoc comparison of means using Bonferroni's correction). (B) Relationship between ash content of unleached leaves combusted at 500°C and mass lost to leaching. Note that there was insufficient material for ash content in unleached leaves of *Acer* and *Pithecellobium*. Error bars are one standard error of the mean (n=2 for A, n=5 for B). See text for full names corresponding to species abbreviations.

Figure III-6. Percent of the macroinvertebrate community that was composed of shredders as a function of time, by (A) numerical abundance and (B) biomass. Each point is the mean of five leafpacks on a given collection date.

Figure III-7. Percent of the macroinvertebrate community that was composed of shredders as a function of the amount of leaf mass remaining, by (A) numerical abundance and (B) biomass. Each point is the mean of five leafpacks on a given collection date.

Figure III-8. (A) Number of shredders per leafpack. (B) Average biomass of shredders per leafpack. (C) Average biomass of shredders per gram of leaf material remaining. Each point is the mean of five leafpacks on a given collection date.

Figure III-9. Average shredder number (A) and biomass (B) as a function of the breakdown coefficient for each tree species. Note that curves were calculated on means: the error bars are provided to the reader as a estimate of the dispersion around the mean.

Figure III-10. Average shredder biomass as a function of tannin and nitrogen concentrations following two days of leaching in Monument Creek.

Figure III-11. Average number of shredders as a function of tannin and nitrogen concentrations following two days of leaching in Monument Creek.

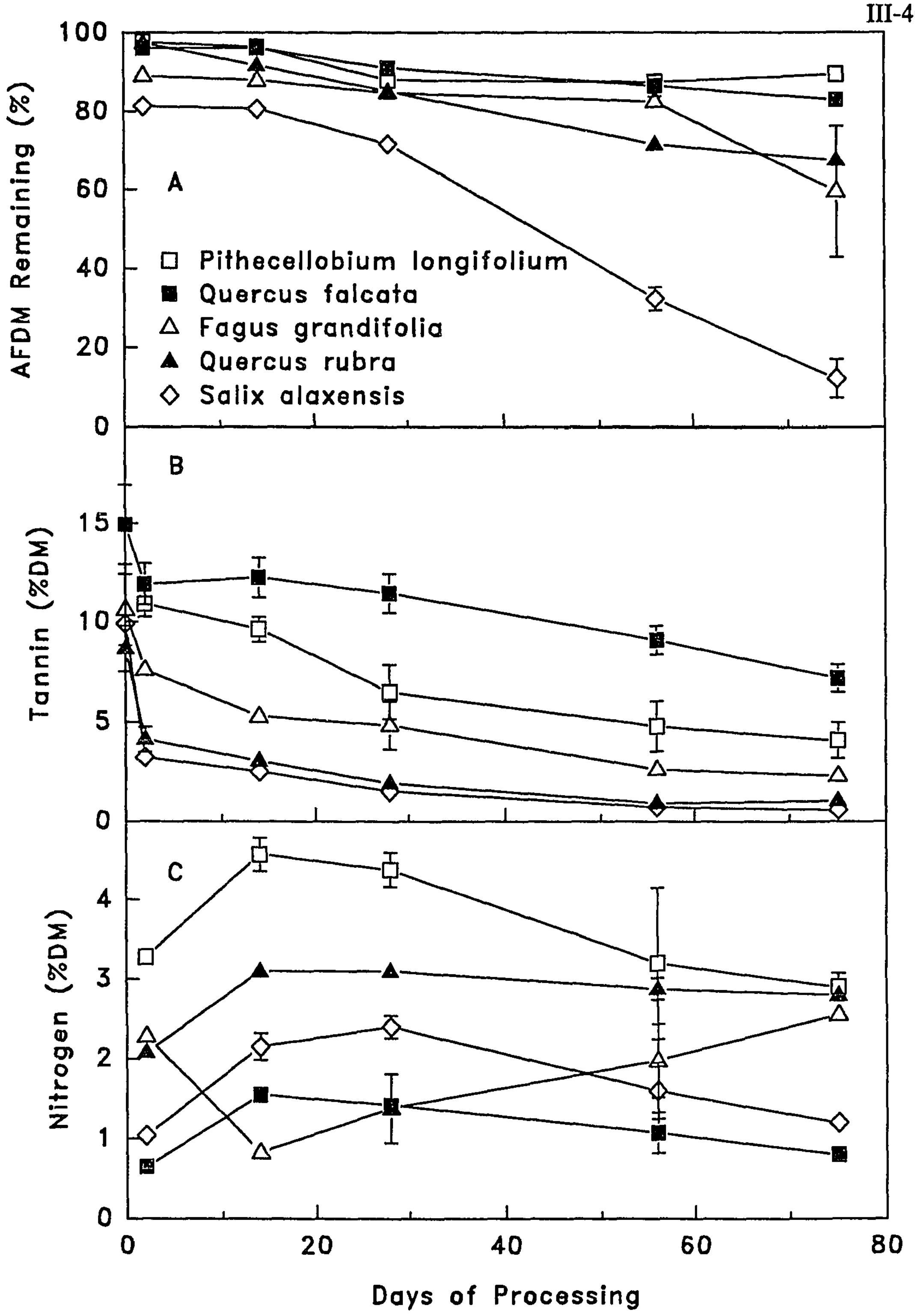

AFDM Remaining (%)
100
80
60
40
20
0
A
□ Pithecellobium longifolium
■ Quercus falcata
△ Fagus grandifolia
▲ Quercus rubra
◇ Salix alaxensis
B
Tannin (%DM)
15
10
5
0
C
Nitrogen (%DM)
4
3
2
1
0
0
20
40
60
80
Days of Processing

Figure III-1

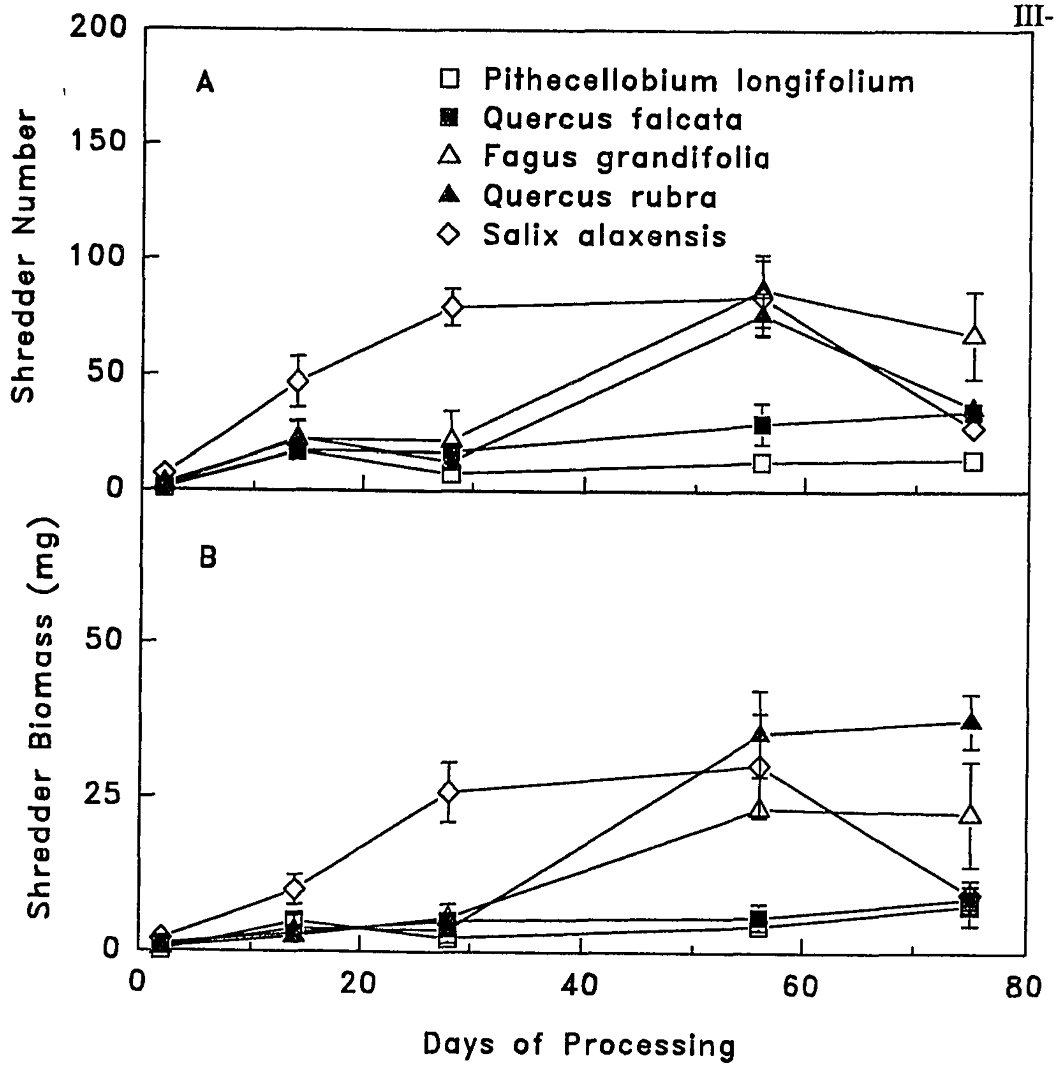

A
□ Pithecellobium longifolium
■ Quercus falcata
△ Fagus grandifolia
▲ Quercus rubra
◇ Salix alaxensis
Shredder Number
0
50
100
150
200
B
Shredder Biomass (mg)
0
25
50
0
20
40
60
80
Days of Processing

Figure III-2

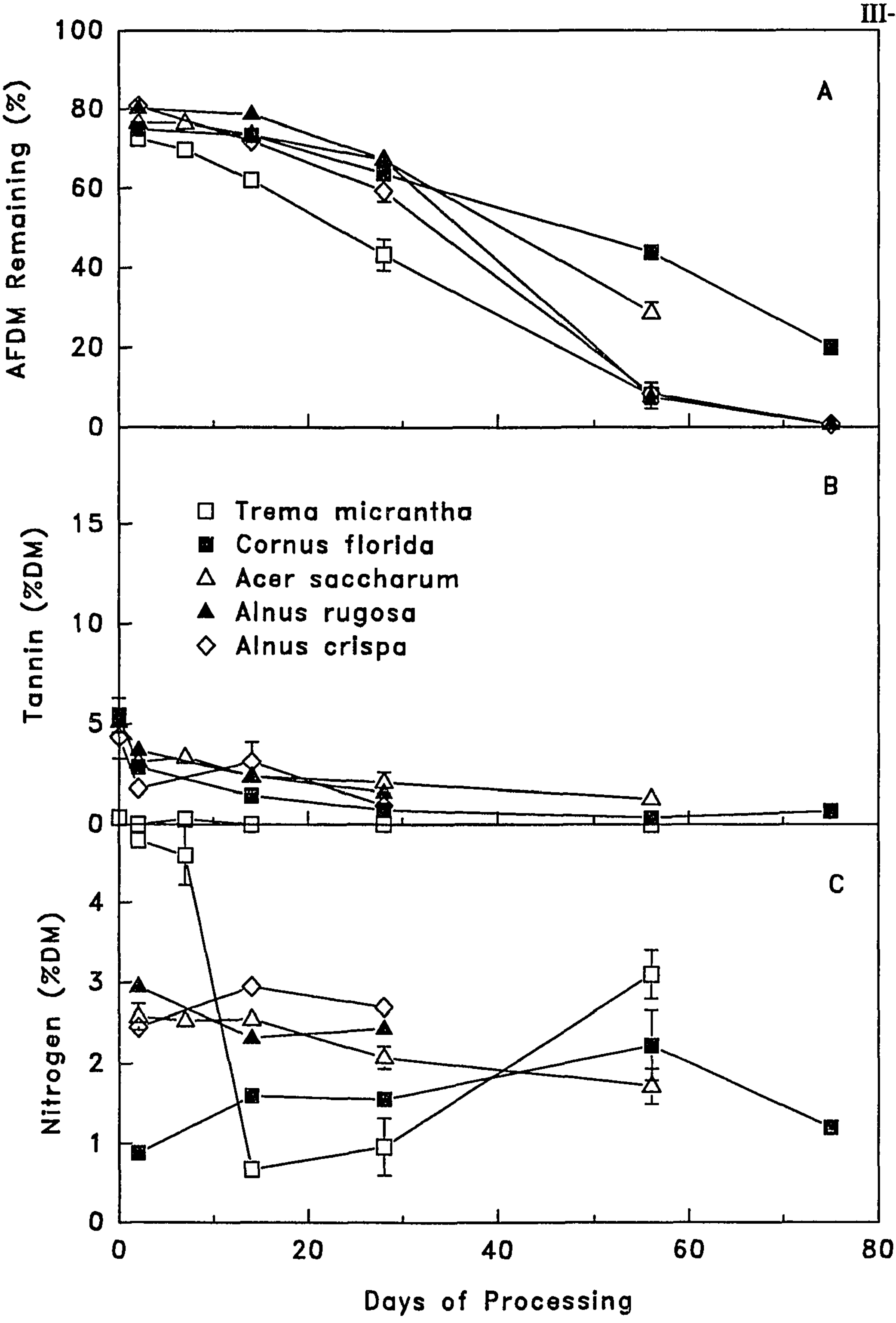

100
80
60
40
20
0
AFDM Remaining (%)
A
15
10
5
0
Tannin (%DM)
B
□ Trema micrantha
■ Cornus florida
△ Acer saccharum
▲ Alnus rugosa
◇ Alnus crispa
4
3
2
1
0
Nitrogen (%DM)
C
0
20
40
60
80
Days of Processing

Figure III-3

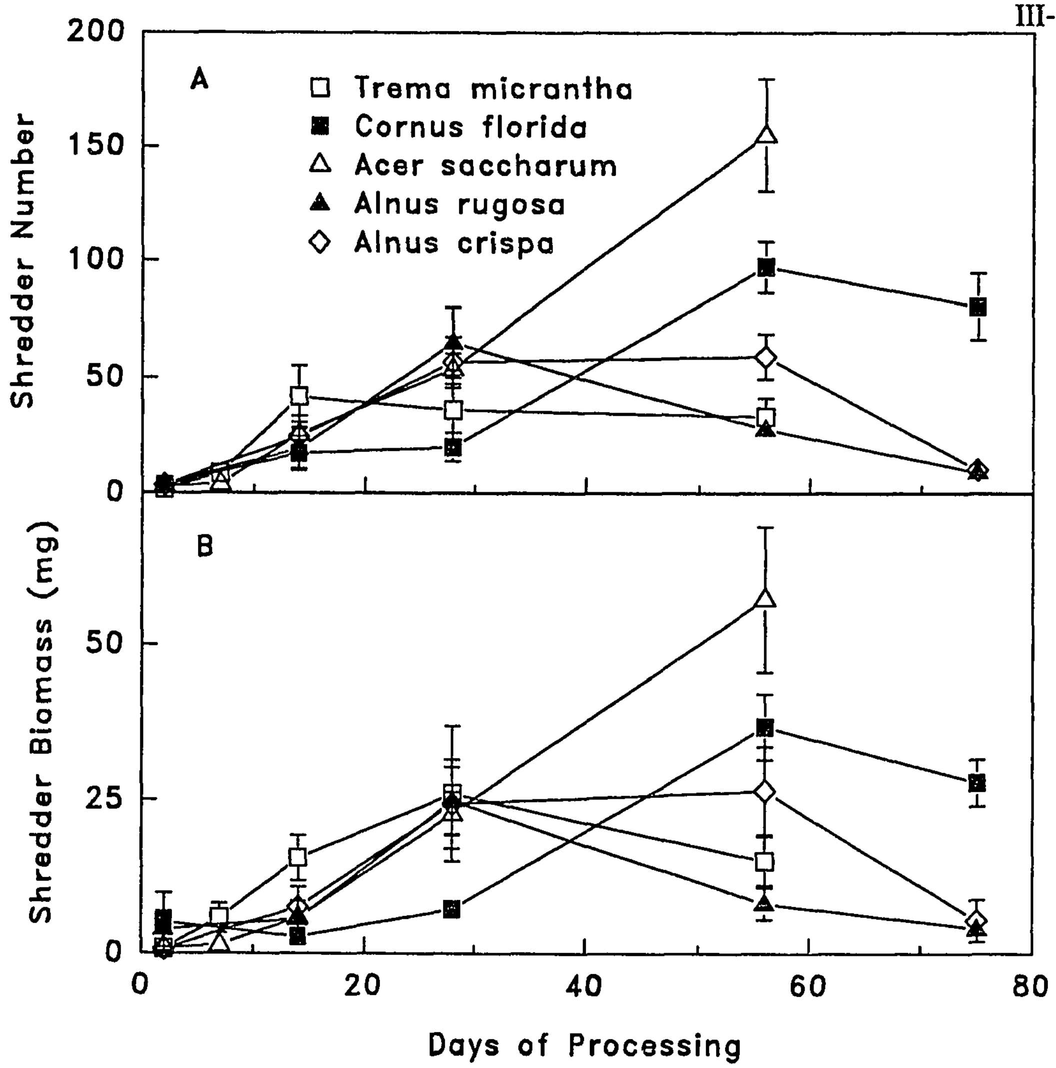

A
B
□ Trema micrantha
■ Cornus florida
△ Acer saccharum
▲ Alnus rugosa
◇ Alnus crispa
Shredder Number
Shredder Biomass (mg)
Days of Processing
0
50
100
150
200
0
25
50
0
20
40
60
80

Figure III-4

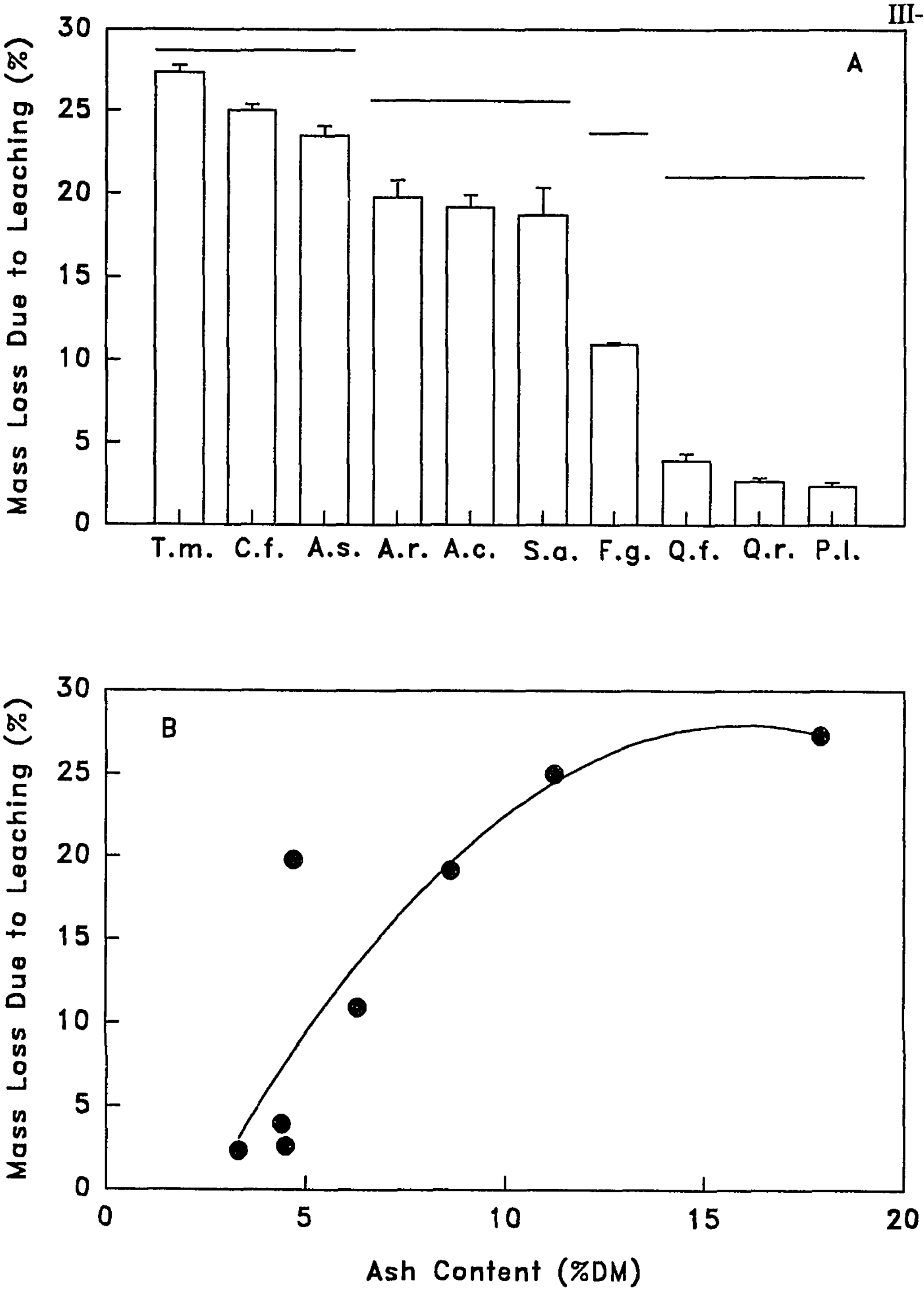

A
Mass Loss Due to Leaching (%)
0
5
10
15
20
25
30
T.m.
C.f.
A.s.
A.r.
A.c.
S.a.
F.g.
Q.f.
Q.r.
P.l.
B
Mass Loss Due to Leaching (%)
0
5
10
15
20
25
30
0
5
10
15
20
Ash Content (%DM)

Figure III-5

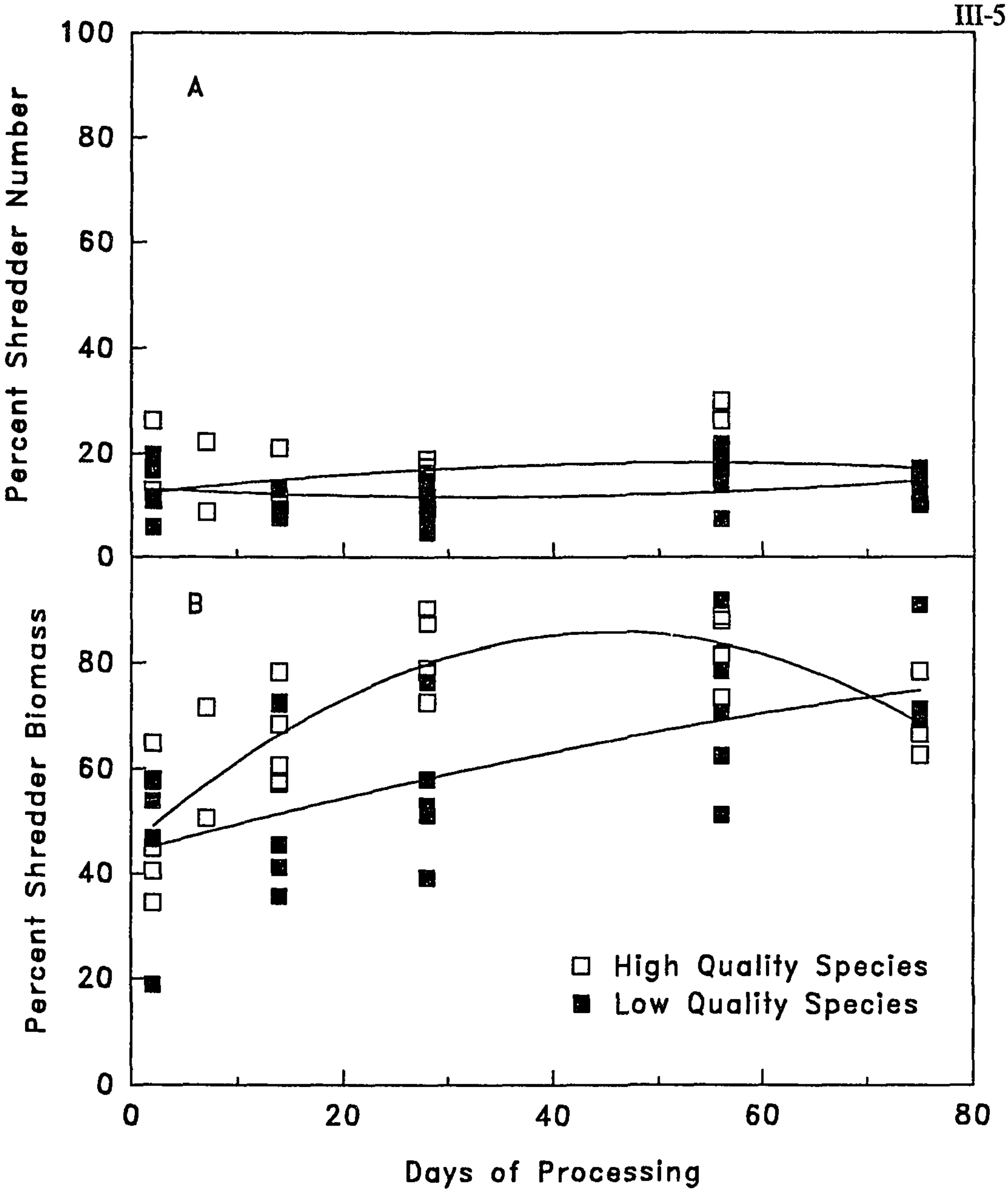

A
B
Percent Shredder Number
Percent Shredder Biomass
Days of Processing
0
20
40
60
80
100
□ High Quality Species
■ Low Quality Species

Figure III-6

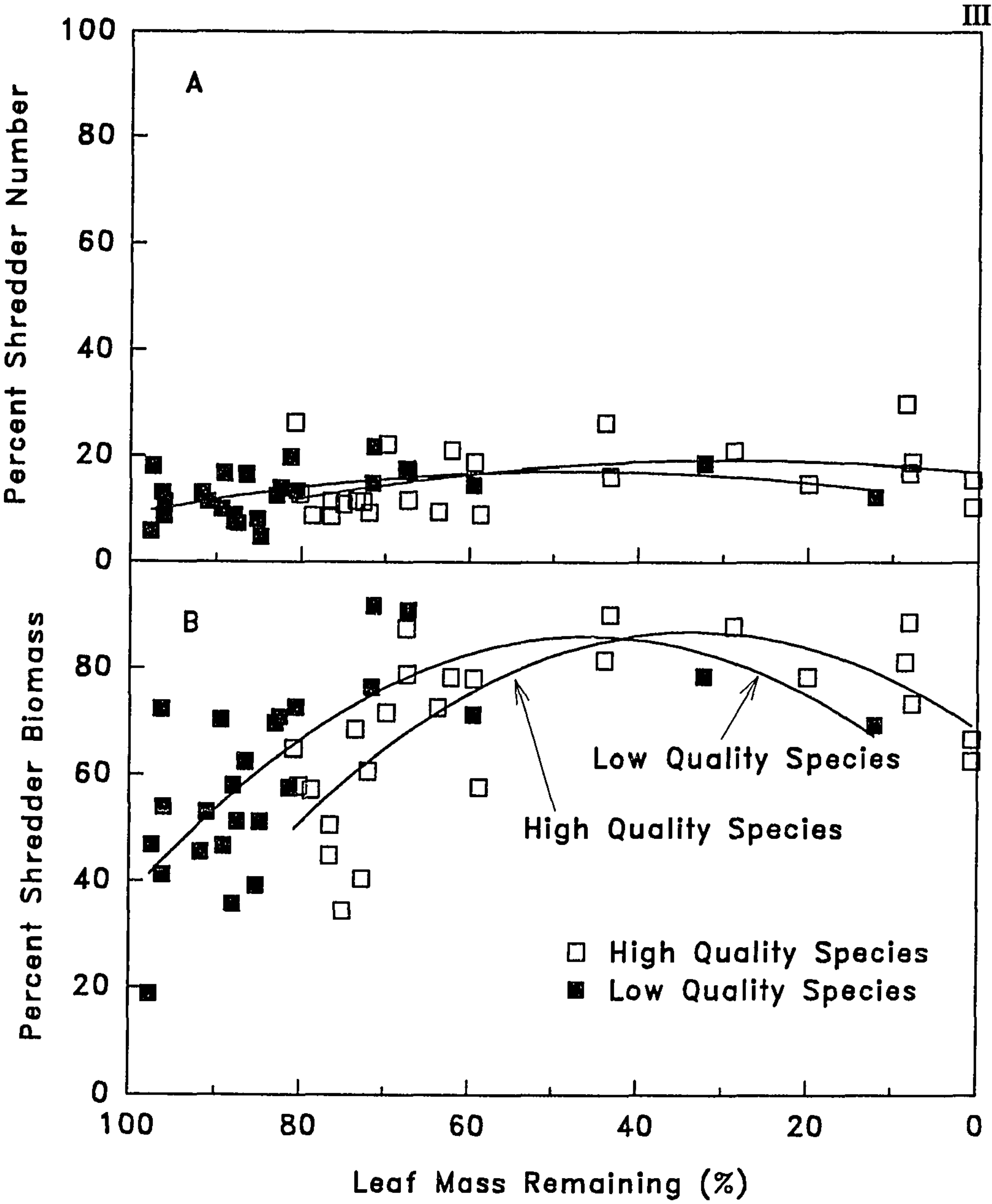

A
B
100
80
60
40
20
0
Percent Shredder Number
Percent Shredder Biomass
Low Quality Species
High Quality Species
□ High Quality Species
■ Low Quality Species
100
80
60
40
20
0
Leaf Mass Remaining (%)

Figure III-7

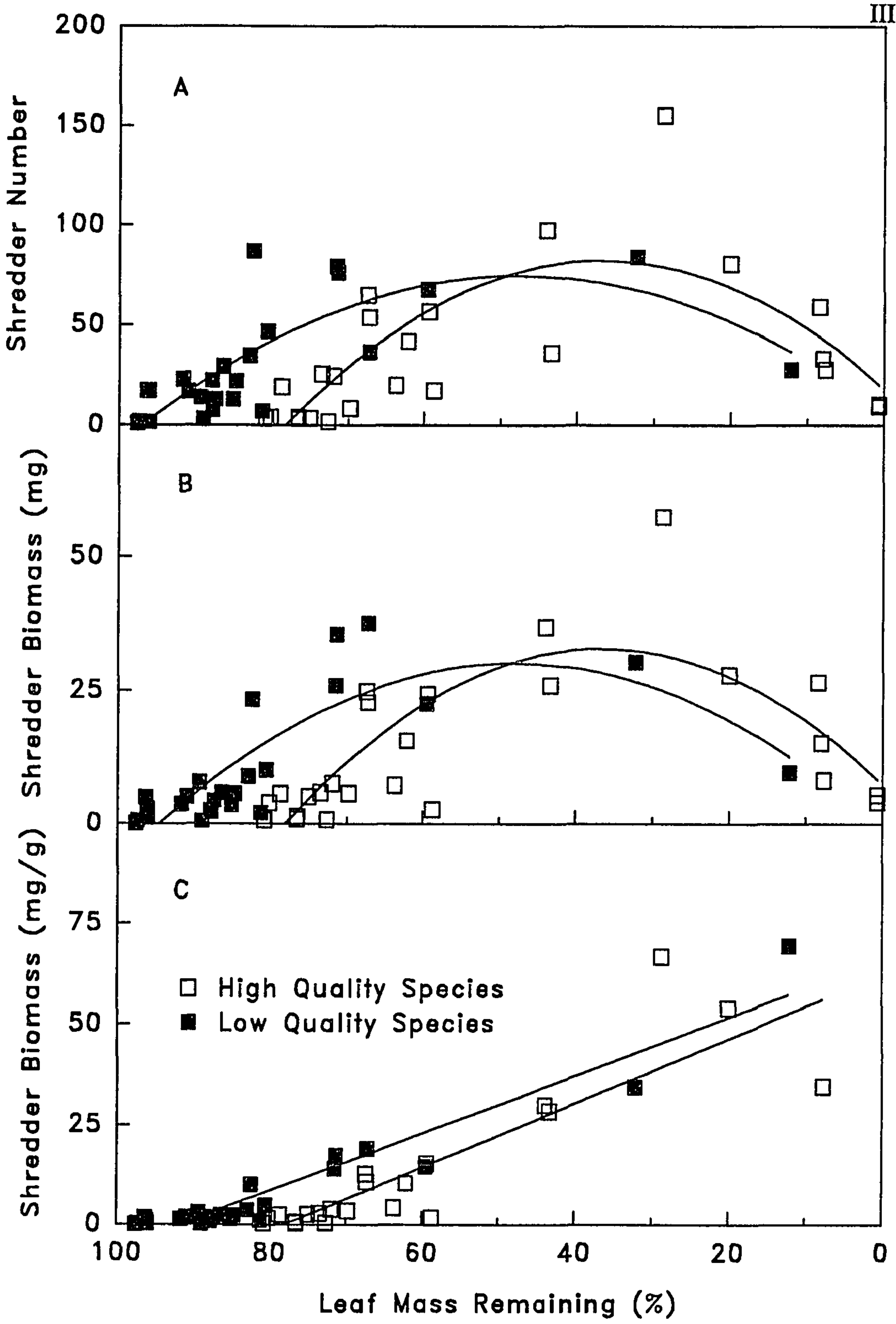

A
B
C
Shredder Number
Shredder Biomass (mg)
Shredder Biomass (mg/g)
200
150
100
50
0
50
25
0
75
50
25
0
100
80
60
40
20
0
Leaf Mass Remaining (%)
□ High Quality Species
■ Low Quality Species

Figure III-8

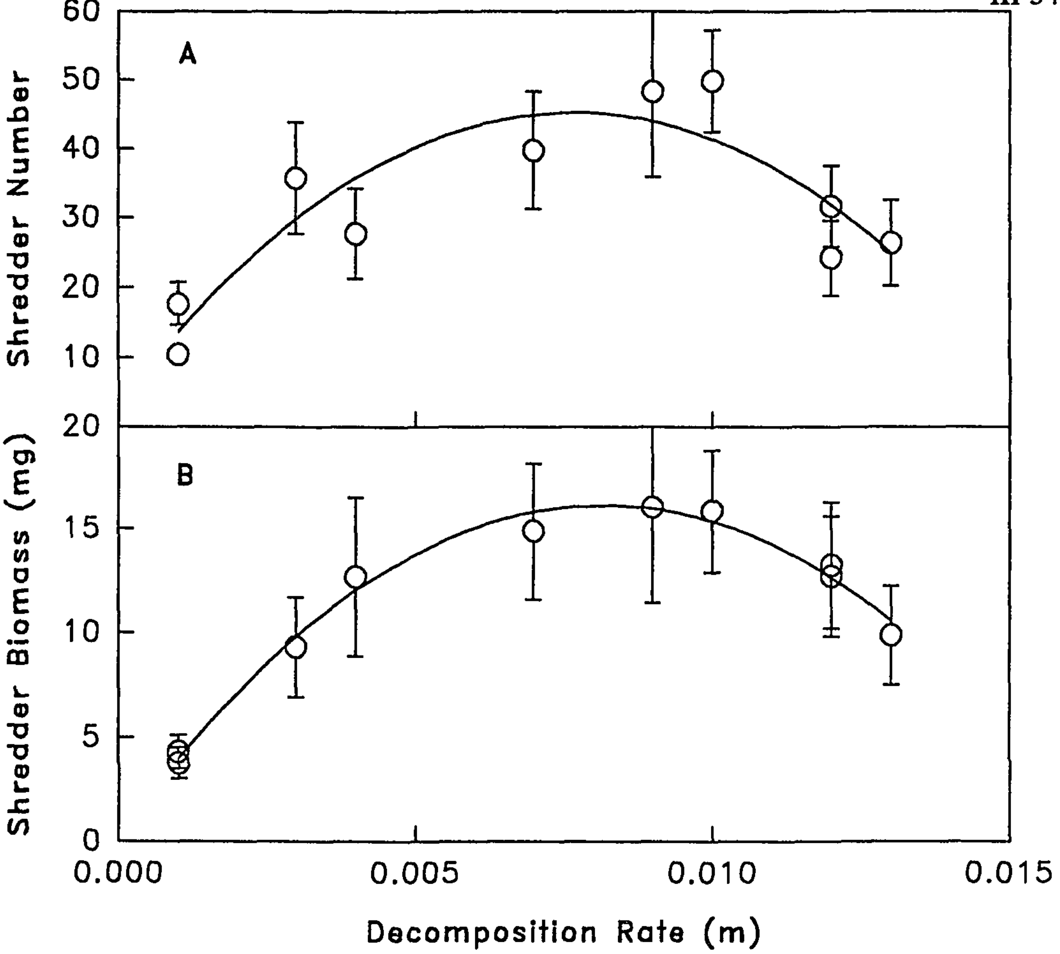

A
B
Shredder Number
Shredder Biomass (mg)
Decomposition Rate (m)
60
50
40
30
20
10
20
15
10
5
0
0.000
0.005
0.010
0.015

Figure III-9

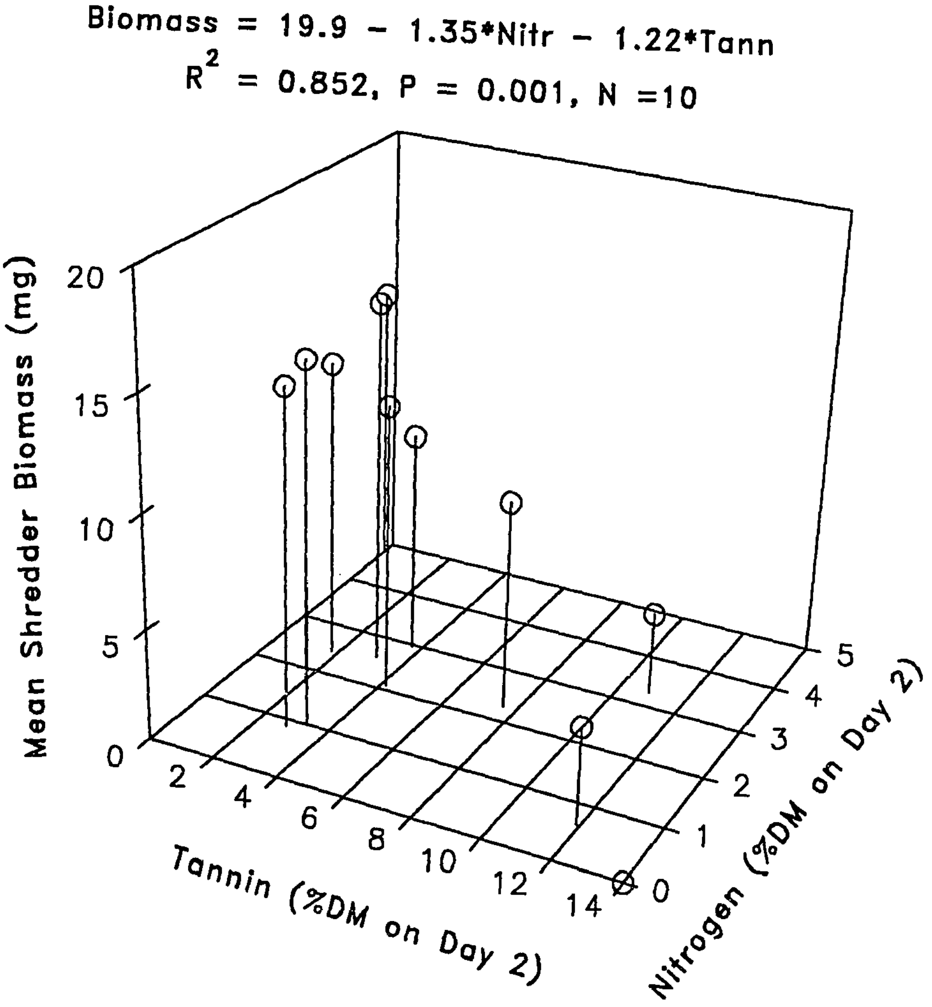


Figure III-10

Number = 56.60 − 5.93*Nitr − 2.40*Tann

R^2 = 0.501, P = 0.036, N = 10

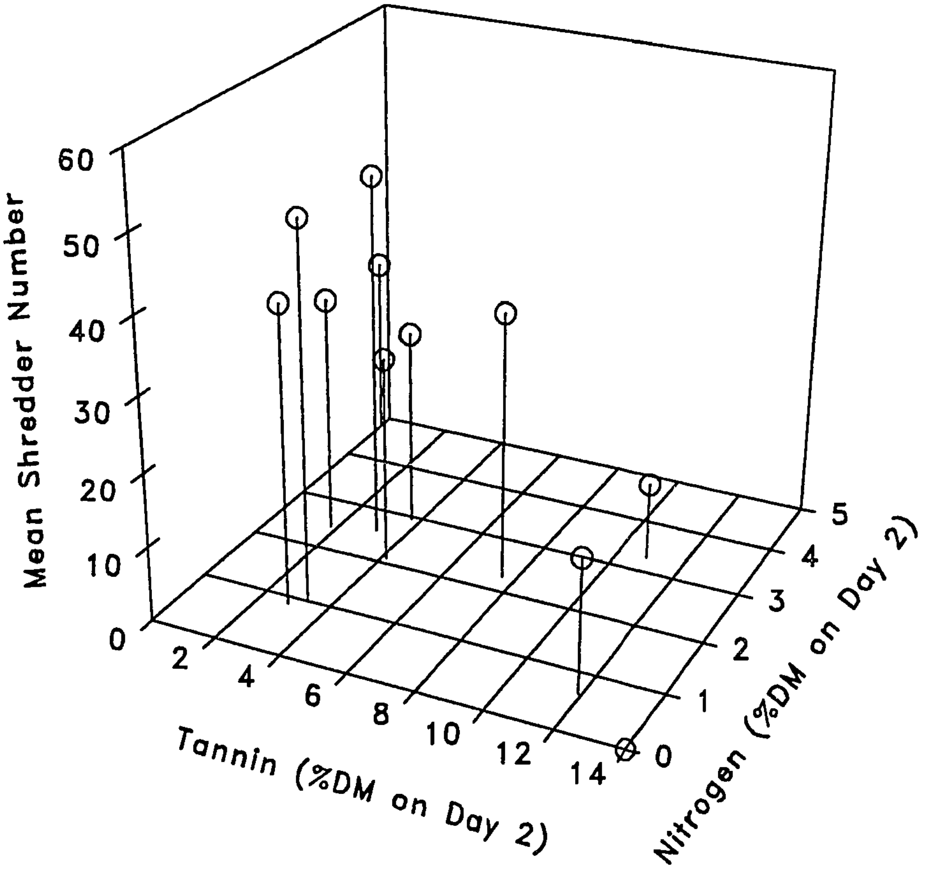


Figure III-11

LATITUDINAL PATTERNS IN LEAF LITTER DECOMPOSITION: IS TEMPERATURE REALLY IMPORTANT?

John G. Irons III[1,2]

Mark W. Oswood[1]

R.Jean Stout[3]

Cathy M. Pringle[4]

Submitted to Freshwater Biology

---

[1] Institute of Arctic Biology, University of Alaska, Fairbanks, AK, USA

[2] Author to whom correspondence should be sent. Current address: Institute of Northern Forestry, 308 Tanana Dr., Fairbanks, AK, USA

[3] Deptartment of Entomology, Michigan State University, E. Lansing, MI, USA

[4] Institute of Ecology, University of Georgia, Athens, GA, USA

SUMMARY

1. Stream food webs in forested regions depend to a large degree on input of dead riparian zone leaves for their energy, which is converted into living biomass by microbes, macroinvertebrates, and fish.

2. Temperature has been invoked as important in controlling decomposition rates, and aquatic biologists have suggested that by normalizing processing rates to degree-days rather than days, one can "factor out" the effect of temperature and compare processing rates in streams with different thermal histories (e.g different seasons or study sites in different biomes).

3. We examined processing rates (k) along a latitudinal (i.e. thermal) gradient by using reciprocal transplants of leafpacks. We placed leafpacks of ten tree species (representing a large range of leaf litter quality) in streams in Costa Rica, Michigan, and Alaska using coarse-mesh litter bags. We then examined both the "per day" (k_{day}) and "per degree-day" ($k_{degreeday}$) models of leaf litter processing. While processing rates (per day) were fastest in Costa Rica (as expected), rates in Alaska and Michigan were similar to each other, which we would not predict if temperature were the principal factor controlling decomposition rate. If using degree-days eliminates any effect of differing thermal regimes, rates should be similar across latitudes; however, rates in Alaska were much faster (per degree-day) than rates in either Costa Rica or Michigan.

4. We compared our data to studies in the literature. Regression analysis of k_{day} and

$k_{degreeday}$ against latitude of the study revealed that processing rates of leaves from a wide range of tree species in a wide range of streams types do indeed decrease with increasing latitude. However, when normalized for temperature ($k_{degreeday}$), there is a strong positive correlation between processing rates and latitude, causing us to reject the hypothesis that normalizing processing rates to cumulative degree-days removes the effect of temperature.

5. We suggest three hypotheses: a) Shredding insect populations have adapted to the thermal regime of their geographic area, and invertebrate-mediated processing rates are either similar between regions (showing no latitudinal pattern), or invertebrate-mediated processing rates increase with latitude, b) Microbial populations have less ability to remain active at colder temperatures, and the rate of microbially-mediated processing of leaf litter will show a latitudinal gradient, and c) The relative importance of invertebrate versus microbial processing changes on a latitudinal gradient, with invertebrates being more important at high latitudes.

INTRODUCTION

Decomposition of leaf litter in mid-latitude streams has been studied for several decades (e.g. Kaushik & Hynes, 1968, 1971; Anderson & Sedell, 1979; Webster & Benfield, 1986). Following a period of mass loss due to leaching (24 to 48 hours), leaves in streams begin to be colonized by decomposer microbes, primarily aquatic hyphomycetes. These microbes both degrade the leaf litter themselves, and condition the litter for macroinvertebrates by softening the leaf tissue and increasing the palatability and nitrogen concentration. Shredding macroinvertebrates then consume the leaf-microbe complex, further hastening the breakdown process. Many factors have been invoked as important in controlling rates of litter breakdown: temperature, tree species, microbial abundance, shredder abundance, exposure technique, dissolved nutrients, dissolved oxygen, acidity, and site (Webster & Benfield, 1986).

Water temperature has often been invoked as one of the most important variables controlling rates of litter decomposition (e.g. Kaushik & Hynes, 1971; Reice, 1974; Iversen, 1975; Suberkropp, Klug, & Cummins 1975; Cummins, 1979; Paul, Benfield & Cairns, 1983; Barnes, McArthur, & Cushing, 1986). However, studies have shown that litter can break down rapidly at temperatures close to or at 0°C (Short, Canton, & Ward,1980; Cowan *et al.*, 1983). Other studies have found that temperature does not explain the difference in breakdown rates between sites or seasons with differing thermal regimes (e.g. Hart & Howmiller, 1975; Griffith & Perry, 1991; Stewart, 1992). A number of aquatic biologists have suggested that, by normalizing decomposition (or processing) rates on a per-degree-day basis rather than on a per-day basis, one can "factor out" the effect of temperature and compare processing rates in streams with differing thermal histories (e.g. Cummins, 1979; Hanson *et al.*, 1984; Webster & Benfield, 1986; McArthur *et al.*, 1988; Cummins *et al.* 1989). Anomalies in this model have been noted, however, that are generally explained by differences in the shredder community (e.g. Paul *et al.*, 1983; Short *et al.*, 1984; Griffith & Perry, 1991).

In this study, we examined the contention that rates of leaf litter decomposition in streams are temperature-dependant; that is, that they vary along a latitudinal gradient. We carried out the experiment using a reciprocal transplant of leaf litter at study streams along the latitudinal gradient from Costa Rica (tropical) to Michigan (temperate) to Alaska (subarctic). In this paper, we begin by reporting the decomposition dynamics, normalized by degree-days, for the three sites. We then explore the data in more detail by using regression analysis with latitude as the independent variable. Finally, we suggest a conceptual model of the manner in which temperature affects leaf litter decomposition in streams.

METHODS

We chose study sites in Costa Rica (CR), Michigan (MI), and Alaska (AK) to be similar to each other in stream size, depth, and velocity. El Salto Creek in Costa Rica is located at 10°N latitude and 83°W longitude near the La Selva Biological Station, operated by the Organization for Tropical Studies. This stream is a second order stream about 45 m above sea level and the study site was about 2 km from the stream origin. The Ford River, a third order stream on the upper peninsula of Michigan, is located at 46°N latitude and 87°W longitude. The study site was about 25 km from the source. Monument Creek (65°N latitude, 146°W longitude) is a second order tributary of the Chena River, near Fairbanks, Alaska, and the study site was located 1 km upstream from the Chena Hot Springs Resort at an elevation of about 380 m, 14 km from the stream origin. All streams had moderate riparian canopy (10-30% canopy cover), and the experimental sites were located in riffles of moderate depth and velocity (approximately 30-50 cm deep and 0.5 m/sec). Detailed study site descriptions, methods, and results of the foliar chemistry aspect of the study can be found in (chapter II).

We placed leaves of ten different tree species in each study stream. Pairs of species, one chosen to be high in condensed tannin concentration (i.e. low litter quality: Stout, 1989; Irons, Bryant & Oswood, 1991) and one low in tannin concentration (i.e. high litter quality), were collected from five locations in North and Central America (Table 1), and leaves of each species were shipped to each stream study site. Twenty-five litter bags of each species (3 g of leaves, 2 cm mesh) were placed in each stream in late summer (CR, MI) or early autumn (AK), and five replicates collected on each of five dates. Lengths of the processing studies were 84 days (CR), 112 days (MI), and 75 days (AK). Water temperature was recorded for determination of accumulated degree-days above zero Celcius.

Processing coefficients were calculated using a negative exponential model:

$$M_t/M_i = (M_0/M_i)e^{-kt}$$

where M_i is the initial mass (approximately 3 g in this study), M_t is the mass remaining at time t (thus, M_t/M_i is the proportion of the initial mass remaining at time t), k is the rate constant, and the intercept, M_0/M_i, represents the proportion of the original mass which would remain at time t=0 if the mass lost to leaching were removed instantaneously. These equations were calculated using linear regression on $\ln((M_t/M_i) + 1))$-transformed data using SYSTAT (Wilkinson, 1990). For degree-day calculations, we substituted for time (t) the thermal sum in degree-days above 0°C on the collection day (i.e. the sum of each daily mean water temperature over the period that the leafpacks were in the water). Some species were completely gone before the study period ended (especially in Costa Rica): for these species we used the first collection date with zero mass remaining as a data point, but not subsequent ones. Rate coefficients based on days were abbreviated k_{day} and coefficients based on thermal sums were abbreviated $k_{degreeday}$. Coefficients using days of processing as the independent variable can be found in (chapter II), coefficients from regressions using degree-days above zero are tabulated here.

Workers investigating the breakdown of leaf litter in streams have used a variety of mathematical models to describe breakdown curves. Most have used the negative exponential model (e.g. Petersen & Cummins, 1974); however, there are several ways to fit this model. Two of the most common differences arise when investigators 1) either calculate an intercept (M_0) or force the curve through 1.0, and 2) they either use the mass remaining at time t (M_t) or the proportion of the original mass left at time t (M_t/M_i). When comparing our results to published decomposition coefficients, we attempted to ascertain whether or not the investigators used mass or proportion in their calculations, and we converted those equations using mass to proportions by dividing the reported k by the initial mass of the leafpack. We did not attempt to correct for the use of a calculated intercept or an equation forced through $M_0/M_i=1.0$. A rough estimate of $k_{degreeday}$ often was possible in those studies that did not report it: if mean daily temperature was reported, we divided k_{day} by mean temperature; if the length of the study and the total thermal sum were reported, we divided k_{day} by the ratio of degree-days to days (which equals the daily mean temperature). We then compared the resulting decomposition coefficients (including our own), on both a per day and a per degree-day basis, with latitude (as a surrogate for temperature). We also plotted estimates of the relative proportion of mass loss attributable to microbial processing and biomass of shredders per gram of leaf material against latitude, using several studies from the literature (Petersen & Cummins, 1974; Short & Ward, 1980; Wallace, Webster & Cuffney, 1982; Mutch *et al.*, 1983; Mulholland *et al.*, 1987). We used this subsample of the literature to build a conceptual, testable model. All comparisons were made using regression analysis in SYSTAT (Wilkinson, 1990).

RESULTS

Processing rates, when degree-days above freezing are used as the independent variable, are an order of magnitude faster in Alaska than in Michigan or Costa Rica (Table 2). When based on days, rates in Costa Rica were fastest, and rates in

Michigan and Alaska were similar (chapter II). Although the Alaskan, and to a lesser extent, the Michigan data fit a linear model better than an exponential, only the negative exponential coefficients are reported here to facilitate comparisons with other studies. Leafpacks in Alaska accumulated only about 22 degree-days above zero in 75 days, while those in Michigan accumulated about 950 in 112 days (Figure IV-1). The Costa Rican study lasted for 84 days (2200 degree-days); however, all leafpacks in the high litter quality group were completely gone by day 28 (750 degree-days) and most leafpacks in the low quality group were gone by day 40 (1100 degree-days).

In Figure IV-2, the dotted lines represent the cut-off points for the divisions between decomposition categories of slow, intermediate, and fast decomposing species, based on days (Petersen & Cummins, 1974) and on degree-days (Cummins *et al.*, 1989). The five bars on the left side of each site in Figure IV-2 are species with low quality litter (from left to right: *Pithecellobium longifolium*, *Quercus falcata*, *Fagus grandifolium*, *Quercus rubra*, and *Salix alaxensis*), and the five bars on the right side are species with high quality litter (from left to right: *Trema micrantha*, *Cornus florida*, *Acer saccharum*, *Alnus rugosa*, and *Alnus crispa*). When based on days, species chosen to have poor litter quality (five bars on the left) were classified as fast species in Costa Rica (except *Pithecellobium longifolium*, which was classified as medium) while the same species were classified as slow species in Michigan and Alaska (except *Salix alaxensis*, which was classified as medium in Alaska) (Figure IV-2A). Leaves of higher quality (five bars on the right) broke down extremely fast in Costa Rica, and were either slow or intermediate in Michigan and Alaska (one species, *Trema micrantha*, was fast in Michigan. When compared on a degree-day basis, however, patterns were reversed: all species were classified as fast in Alaska, all species as slow in Michigan, and only one as fast and one as intermediate in Costa Rica (Figure IV-2B). Regression analysis showed that latitude explained a significant amount of the variance, both on a per day basis (45%: Figure IV-3A) and on a per degree-day basis (67%: Figure IV-3B) (log-transformed data).

Using 252 processing coefficients obtained from 28 studies in the literature (see Appendix), we found that there was a slight but statistically significant negative correlation between latitude and k_{day} that explained only 3.8% of the variance (Figure IV-4A). These literature values came from more than 40 tree species (with associated differences in litter quality), from permanent and intermittent streams, from a wide variety of habitats, elevations, precipitation regimes, and from biomes across North America. Conversely, there is a strong positive correlation between latitude and $k_{degreeday}$ (Figure IV-4B). Because of the leverage exerted by the 10 points from Costa Rica and the 10 points from Alaska, we ran the regression analyses excluding the data points from out study (resulting in n=222) and neither the regression on raw data ($P = 0.091$) nor the regression on log-transformed data ($P = 0.861$) based on k_{day} was significant. However, both were significant on a per degree-day ($k_{degreeday}$) basis ($F = 35.5$ and 32.9, $P < 0.0005$, $n = 217$). Thus, rather than the expected relationship of a negative correlation between k_{day} and latitude (i.e. slower decomposition with increasing latitude and decreasing temperature), which one would expect if temperature is a determining variable in leaf litter decomposition, there was little or no correlation. Conversely, when the regressions were based on thermal sums rather than elapsed time, there was a strong positive correlation between latitude and decomposition.

Several studies done at different latitudes have estimated the relative contribution of microbes versus shredding macroinvertebrates to leaf litter processing rates in streams (e.g. Petersen & Cummins, 1974; Short & Ward, 1980; Wallace, Webster, & Cuffney, 1982; Mutch *et al.*, 1983; Mulholland *et al.*, 1987). As one goes farther north and probably to higher elevations, the relative contribution of microbes to leaf litter breakdown decreased and the biomass of shredders found on leafpacks increased (Figure IV-5). We feel that a testable model regarding the relative contributions of microbial and invertebrate processing to leaf litter breakdown can be built from these trends. We propose the following: the absolute amount of the leaf litter that is processed by macroinvertebrate shredders in a given time period increases with increasing latitude and elevation (and hence decreasing thermal resources). Conversely, the absolute amount of microbial processing of leaf litter decreases with latitude and elevation and decreasing thermal resources. When these two trends are combined, the rate of processing per day (k_{day}) is a function of latitude that declines steeply at first, then plateaus or increases at higher latitudes (Figure IV-6). This model would result in the patterns of breakdown rates seen in Figure IV-2A.

Given the preceding model, one can predict patterns of $k_{degreeday}$ across latitudes. On a thermal sum basis, total processing rates increase with latitude, as does the contribution of macroinvertebrates to overall leaf litter breakdown, while the contribution of microbes decreases both proportionally and in grams of litter mass lost.

DISCUSSION

Latitudinal gradients have been long noted by ecologists, both on a continental (e.g. Pianka, 1966, 1978; MacArthur, 1972; Schall & Pianka, 1978 and a regional scale (e.g. MacLean, 1975; MacLean & Hodkinson, 1980). Gradients have been shown to exist in such traits as species richness and abundance, primary productivity, and body size of conspecific and congeneric taxa. Hypotheses advanced to explain these phenomena include time since glaciation, climate, and intensity of competition (Pianka, 1966). While the mechanisms generating these gradients remain hotly debated (temperature remains a leading contender), all agree that temperature is well correlated with latitude, thus allowing us to use latitude as a surrogate for the long-term (e.g. evolutionary time scale) thermal regime of a region.

Water temperature has been widely cited as an important controlling variable for stream ecosystem processes, including evolution and ecology of aquatic insects (e.g. Vannote & Sweeney, 1980; Ward & Stanford, 1982) and microbial dynamics (Suberkropp & Klug, 1976), and leaf litter breakdown rates (Kaushik & Hynes, 1971;

Anderson & Sedell, 1979; Webster & Benfield, 1986). The effect of differing thermal regimes in space and time on leaf litter decomposition in streams has been well-documented. For instance, there is often a very good correlation between water temperature and leaf litter decomposition rates in field (Reice, 1974; Hart & Howmiller, 1975; Iversen, 1975; 1980; Hildrew *et al.*, 1984) and laboratory studies (Hynes & Kaushik, 1969; 1971; Suberkropp *et al.*, 1975).

Conversely, many studies have shown that temperature may not be the overriding controlling factor. Mass loss rates of leaves in cold streams at high elevation (Short *et al.*, 1980 and high latitude (Cowan *et al.*, 1983) are as high as or higher than breakdown rates of similar species in warmer streams. Decomposer microbes have been shown to actively grow and respire at temperatures very close to freezing (Bärlocher & Kendrick, 1974; Buttimore *et al.*, 1984). Processing rates calculated on a degree-day basis are often faster at colder water temperatures than at warmer ones (Cummins, 1979; Short & Ward, 1980; Paul *et al.*, 1983; Short *et al.*, 1984). Some authors explain this "anomaly" by suggesting that the shredder community is more depauperate below an impoundment (Cummins, 1979; Short & Ward, 1980), in streams of early successional forests (Griffith & Perry, 1991), and in prairie streams of Texas (Short *et al.*, 1984). Suberkropp, Godshalk, & Klug (1976) expected an increase in processing rates as stream temperatures warmed in the spring, and attributed the lack of such an increase to the accumulation of refractory compounds that overrode the temperature effect.

Many orders of aquatic insects, especially those with many species of shredders, likely evolved in cool running waters (e.g. Hynes, 1970; Edmunds, 1972; Wiggins, 1977). Webster & Benfield (1986) suggested that temperature affects primarily microbes, and that invertebrates seem to be less affected, so that the relative effect of invertebrate feeding may at times overshadow the role of microbes in leaf litter breakdown. Previous studies corroborate this suggestion: breakdown rates of litter in two southern African streams were much more rapid in the stream with an abundant shredder fauna (Stewart, 1992). Likewise, elimination of shredders by insecticide in an Appalachian Mountain stream reduced breakdown rates (Wallace *et al.* 1982). We suggest that the "anomalous" results mentioned above be taken at face value, and that the reason that conclusions differ between studies is in part a function of the relative roles of microbes and macroinvertebrate shredders.

Cummins *et al.* (1989) proposed a model of shredders and leaf litter processing in which one of the inputs to the model is "categorization of riparian plant communities on the basis of temperature-specific, in-stream processing rates of their litter." The categories proposed (fast species > 0.0015, medium 0.001-0.0015, and slow < 0.001) were thought to be "transferable between streams in different watersheds, in different biomes, and on different continents." We suggest that this is not the case. When the same 10 species were tested in three different biomes (tropical, temperate, and subarctic), processing rates on a degree-day basis differed. One would expect that processing rates ($k_{degreeday}$) of the same species would fall into the same processing category if the temperature-specific processing rate model is valid; however, most individual species in our transfer experiment span the range from slow to fast (Figure IV-2).

We propose a slightly different model. We suggest that, while temperature seems to be very important in determining processing rates within a stream or a geographical location, different biological processes operate at different efficiencies or rates in widely separated areas with differing biota and thermal regimes. Thus, the microbial and insect components of litter breakdown may be influenced by temperature in different ways in different biomes, owing to their differing evolutionary histories. It is readily apparent that, when using degree-days as the independent variable, rates in subarctic Alaska are an order of magnitude faster than those of temperate Michigan and tropical Costa Rica (Figure IV-2). When comparing differing thermal regimes within a region, studies of biotic processes are drawing from the same pool of microbes and shredders, which are presumably adapted to the long-term thermal regime of the area. On the other hand, studies such as ours that compare differing thermal regimes across broad biogeographic regions are drawing their decomposer flora and fauna from species variously adapted to the local climate of each biogeographic region.

Macroinvertebrates are generally well-adapted to the thermal regimes of their parent streams, and shredders adapted to high latitude or high altitude conditions can process leaf litter at temperatures very close to freezing (Short *et al.*, 1980; Cowan *et* *al.*, 1983, this study). Indeed, shredder biomass on leafpacks showed an increase with increasing latitude (and decreasing temperature), both in numbers and biomass (Stout *et al.* unpublished data). The microbial community, on the other hand, appears to be less able to process leaf inputs efficiently at colder water temperatures. The amount of leaf litter mass loss attributable to microbial respiration in Monument Creek was only about 10% or less (Buttimore *et al.*, 1984), and presumably most of the litter breakdown was related to shredder activity (Cowan *et al.*, 1983). In Michigan, Petersen, Cummins, & Ward (1989) found that shredders only contributed about 10% to total leaf processing, while in the southern Appalachian Mountains of North Carolina the fraction was 27% (Webster, 1983). At a given water temperature, respiration of the Alaskan microbial community was much lower than that of temperate regions, although respiration continued at temperatures very close to freezing (Buttimore *et al.*, 1984). Thus, it appears that latitudinal gradients in leaf litter processing rates are related to the relative proportion of mass loss attributable to microbial decomposition versus the amount attributable to macroinvertebrate feeding.

These preliminary results suggest several testable hypotheses: 1) Shredder insect populations are evolutionarily adapted to the thermal regimes found in cool running waters (their habitat of origin), and insect-mediated processing rates for a given plant species increase with increasing latitude; 2) Shredder insects are adapted to the thermal regime of their geographic area, and insect-mediated processing rates for a given plant species are similar between regions, thus showing no latitudinal pattern; and 3) Microbial populations are physiologically less able to remain active at optimal metabolic rates at colder temperatures, and the rate of microbially-mediated processing of leaf litter will decrease with increasing latitude. We suggest that the relative importance of invertebrate versus microbial processing changes on a latitudinal gradient, with invertebrates being more important in the colder waters of high latitudes and high elevations.

ACKNOWLEDGMENTS

Funding to JGI, MWO, and JPB for this project was provided by the National Science Foundation Taiga Forest Long Term Ecological Research grant BSR-8702629, with additional assistance from the Institute of Arctic Biology and the Institute of Northern Forestry. Field help in Alaska was provided by J. Johnson, D. Kennedy, S. Peek, and M. Wagener, and S. Kennedy sewed the litter bags. We thank the Chena Hot Springs Resort for access to Monument Creek.

Funding for RJS was provided by the U.S. Department of the Navy, Contract #N000039-81-C-0357, as part of a project on potential effects of extremely low frequency (E.L.F.) electromagnetic fields in stream ecosystems. Help in the field was generously provided by Amy Babincheck and Bill Cooper.

CMP acknowledges support from the National Science Foundation, Grant BSR-87-17746 and BSR-91-07772 which partially supported data synthesis. Field help in Costa Rica was provided by R. Vargas-Ramirez, R. Tiffer-Sotomayor, and G.

Browder. We thank the Organization for Tropical Studies for providing logistical support.

REFERENCES

Anderson N.H. & Sedell J.R. (1979) Detritus processing by macroinvertebrates in stream ecosystems. *Annual Review of Entomology* **24**, 351-377.

Bärlocher F. & Kendrick B. (1974) Dynamics of fungal populations on leaves in streams. *Journal of Ecology* **62**, 761-791.

Barnes J.R., McArthur J.V. & Cushing C.E. (1986) Effect of excluding shredders on leaf litter decomposing in two streams. *Great Basin Naturalist* **46**, 204-207.

Buttimore C.A., Flanagan P.W., Cowan C.A. & Oswood M.W. (1984) Microbial activity during leaf decomposition in an Alaskan subarctic stream. *Holarctic Ecology* **7**, 104-110.

Cowan C.A., Oswood M.W., Buttimore C.A. & Flanagan P.W. (1983) Processing and macroinvertebrate colonization of detritus in and Alaskan subarctic stream. *Holarctic Ecology* **6**, 340-348.

Cummins K.W. (1979) The natural stream ecosystem. In: *The ecology of regulated streams* (Eds J.V. Ward and J.A. Stanford), pp. 7-24. Plenum Press, New York.

Cummins K.W., Wilzbach M.A., Gates D.M., Perry J.B. & Taliaferro W.B. (1989) Shredders and riparian vegetation. *BioScience* **39**, 24-30.

Edmunds G.F. Jr. (1972) Biogeography and evolution of Ephemeroptera. *Annual Review of Entomology* **17**: 11-23.

Griffith M.B. & Perry S.A. (1991) Leaf pack processing in two Appalachian mountain streams draining catchments with different management histories. *Hydrobiologia* **220**, 247-254.

Hanson B.J., Cummins K.W., Barnes J.R. & Carter M.W. (1984) Leaf litter processing in aquatic systems: A two variable model. *Hydrobiologia* **111**, 21-29.

Hart S.D. & Howmiller R.P. (1975) Studies on the decomposition of allochthonous detritus in two southern California streams. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* **19**, 1665-1674.

Hildrew A.G., Townsend C.R., Francis J. & Finch K. (1984) Cellulolytic decomposition in streams of contrasting pH and its relationship with invertebrate community structure. *Freshwater Biology* **14**, 323-328.

Hynes H.B.N. (1970) *The ecology of running waters.* University of Toronto Press, Toronto.

Hynes H.B.N. & Kaushik N.K. (1969) The relationship between dissolved nutrient salts and protein production in submerged autumnal leaves. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* **17**, 95-103.

Irons J.G. III, Bryant J.P. & Oswood M.W. (1991) Effects of moose browsing on decomposition rates of birch leaf litter in a subarctic stream. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 442-444.

Iversen T.M. (1975) Disappearance of autumn-shed beech leaves placed in bags in small streams. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* **19**, 1687-1692.

Iversen T.M. (1980) Densities and energetics of two streamliving larval populations of Sericostoma personatum (Trichoptera). *Holarctic Ecology* **3**, 65-73.

Kaushik N.K. & Hynes H.B.N. (1968) Experimental study on the role of autumn-shed leaves in aquatic environments. *Journal of Ecology* **56**, 229-243.

Kaushik N.K. & Hynes H.B.N. (1971) The fate of the dead leaves that fall into streams. *Archiv für Hydrobiologia* **68**, 465-515.

MacArthur R.A. (1972) *Geographical ecology*. Harper and Rowe, New York.

MacLean S.F. Jr. (1975) Ecological adaptations of tundra invertebrates. In: *Physiological adaptations to the environment* (Ed J. Vernberg), pp. 269-300. Intext Phys. Publ., New York.

MacLean S.F. Jr. & Hodkinson I.D. (1980) The distribution of psyllids (Homoptera: Psyloidea) in the arctic and subarctic Alaska. *Arctic and Alpine Research* **12**, 369-376.

McArthur J.V., Barnes J.R., Hansen B.J. & Leff L.G. (1988) Seasonal dynamics of leaf litter breakdown in a Utah alpine stream. *Journal of the North American Benthological Society* **7**, 44-50.

Mulholland P.J., Palumbo A.V., Elwood J.W. & Rosemond A.D. (1987) Effects of acidification on leaf decomposition in streams. *Journal of the North American Benthological Society* **6**, 147-158.

Mutch R.A., Steedman R.J., Berte S.B. & Pritchard G. (1983) Leaf breakdown in a mountain stream: A comparison of methods. *Archiv für Hydrobiologia* **97**, 89-108.

Paul R.W. Jr., Benfield E.F. & Cairns J. Jr. (1983) Dynamics of leaf processing in a medium-sized river. In: *Dynamics of lotic ecosystems* (Eds T.D. Fontaine III and S.M. Bartell), pp. 403-423. Ann Arbor Press, Ann Arbor, Michigan.

Petersen R.C. & Cummins K.W. (1974) Leaf processing in a woodland stream. *Freshwater Biology* **4**, 343-368.

Petersen R.C. Jr., Cummins K.W. & Ward G.M. (1989) Microbial and animal processing of detritus in a woodland stream. *Ecological Monographs* **59**, 21-39.

Pianka E.R. (1966) Latitudinal gradients in species diversity: a review of the concepts. *American Naturalist* **100**, 33-46.

Pianka E.R. (1978) *Evolutionary ecology*. Volume 2. Harper and Row, New York.

Reice S.R. (1974) Environmental patchiness and the breakdown of leaf litter in a woodland stream. *Ecology* **55**, 1271-1282.

Schall J.J. & Pianka E.R. (1978) Geographical trends in numbers of species. *Science* **201**, 679-686.

Short R.A. & Ward J.V. (1980) Leaf litter processing in a regulated Rocky Mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 123-127.

Short R.A., Canton S.P. & Ward J.V. (1980) Detrital processing and associated macroinvertebrates in a Colorado mountain stream. *Ecology* **61**, 727-732.

Short R.A., Smith S.L., Guthrie D.W. & Stanford J.A. (1984) Leaf litter processing rates in four Texas streams. *Journal of Freshwater Ecology* **2**, 469-473.

Stewart B.A. (1992) The effect of invertebrates on leaf decomposition rates in two small woodland streams in southern Africa. *Archiv für Hydrobiologia* **124**, 19-33.

Stout R.J. (1989) Effects of condensed tannins on leaf processing in mid-latitude and tropical streams: a theoretical approach. *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 1097-1106.

Suberkropp K. & Klug M.J. (1976) Fungi and bacteria associated with leaves during processing in a woodland stream. *Ecology* **57**, 707-719.

Suberkropp K., Klug M.J. & Cummins K.W. (1975) Community processing of leaf litter in woodland streams. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* **19**, 1653-1658.

Suberkropp K., Godshalk G.L. & Klug M.J. (1976) Changes in the chemical composition of leaves during processing in a woodland stream. *Ecology* **57**, 720-727.

Vannote R.L. & Sweeney B.W. (1980) Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *American Naturalist* **115**, 667-695.

Wallace J.B., Webster J.R. & Cuffney T.F. (1982) Stream detritus dynamics: regulation by invertebrate consumers. *Oecologia* **53**, 197-200.

Ward J.V. & Stanford J.A. (1982) Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology* **27**, 97-117.

Webster J.R. & Benfield E.F. (1986) Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics* **17**, 567-594.

Wiggins G.B. (1977). *Larvae of the North American caddisfly genera (Trichoptera).* University of Toronto Press, Toronto.

Wilkinson L. (1990) *SYSTAT: The system for statistics*. SYSTAT, Inc., Evanston, IL.

Table IV-1. Species and origin of leaves used at each of the stream study sites.

TREE SPECIES	COLLECTION LOCATION	COLLECTOR
Pithecellobium longifolium	Costa Rica	C.M. Pringle
Trema micrantha	Costa Rica	C.M. Pringle
Cornus florida	North Carolina	S.R. Reice
Quercus falcata	North Carolina	S.R. Reice
Acer saccharum	New York	W.H. McDowell
Fagus grandifolia	New York	W.H. McDowell
Alnus rugosa	Michigan	R.J. Stout
Quercus rubra	Michigan	R.J. Stout
Alnus crispa	Alaska	J.G. Irons and M.W. Oswood
Salix alaxensis	Alaska	J.G. Irons and M.W. Oswood

Table IV-2. Coefficients of leaf litter mass loss (proportion of DM remaining) through time on a per degree-day basis ($k_{degreeday}$) for ten species of leaves placed in streams in Alaska (Monument Creek), Michigan (Ford River), and Costa Rica (El Salto Creek) in autumn of 1988. The coefficient is the decay constant (k) from $M_t = M_0e^{kt}$, where t is the cumulative degree-days above 0°C, calculated via linear regression on log-transformed data $[\ln((M_t/M_i)+1)]$. H = High Quality Litter Group, L = Low Quality Litter Group.

		Coefficients of Decay		
		Alaska	Michigan	Costa Rica
SPECIES	H/L	k	k	k
Pithecellobium	H	-0.00246	-0.00017	-0.00025
Quercus falcata	H	-0.00353	-0.00030	-0.00050
Fagus grandifolia	H	-0.00687	-0.00024	-0.00098
Quercus rubra	H	-0.00855	-0.00040	-0.00043
Salix alaxensis	H	-0.02473	-0.00034	-0.00039
Trema micrantha	L	-0.02885	-0.00094	-0.00143
Cornus florida	L	-0.01596	-0.00042	-0.00187
Acer saccharum	L	-0.01830	-0.00042	-0.00089
Alnus rugosa	L	-0.03449	-0.00022	-0.00084
Alnus crispa	L	-0.03382	-0.00049	-0.00078

FIGURE CAPTIONS

Figure IV-1. Processing curves for 3 gram leafpacks from five tree species with low quality leaf litter in three streams of differing latitude: Costa Rica, 10°N; Michigan, 43°N; and Alaska, 65°N.

Figure IV-2. Processing curves for 3 gram leafpacks from five tree species with high quality leaf litter in three streams of differing latitude: Costa Rica, 10°N; Michigan, 43°N; and Alaska, 65°N.

Figure IV-3. Processing coefficients (k) for the ten species and three study sites shown in Figure IV-1, on a per day basis in panel A and a per degree-day basis in panel B. Dotted lines are the cutoff values for the slow, medium and fast processing categories proposed by Petersen and Cummins (1974) (panel A) and Cummins *et al.* (1989) (panel B). Data for top panel (A) taken from (chapter II), Table 3.

Figure IV-4. A) Regression of processing coefficients from this study on a per day basis (from chapter II) against latitude. B) Regression of processing coefficients from this study on a per degree-day basis (Table 2) against latitude. All data were natural log-transformed.

Figure IV-5. A) Regression of processing coefficients on a per day basis from this study and 28 other North American studies (see Appendix) against latitude. B) Regression of processing coefficients on a per degree-day basis of this study and 28 other North American studies (see Appendix) against latitude. All data were natural log-transformed.

Figure IV-6. A) Percent of total leaf litter breakdown that is attributable to microbial processing along a latitudinal gradient. B) Biomass of shredders on leafpacks on a per gram of leaf material remaining basis. Data were take from several studies in the literature (see text for references).

Figure IV-7. Conceptual model of the relative contributions of microbial and invertebrate processing to total leaf litter breakdown rates on a per day basis.

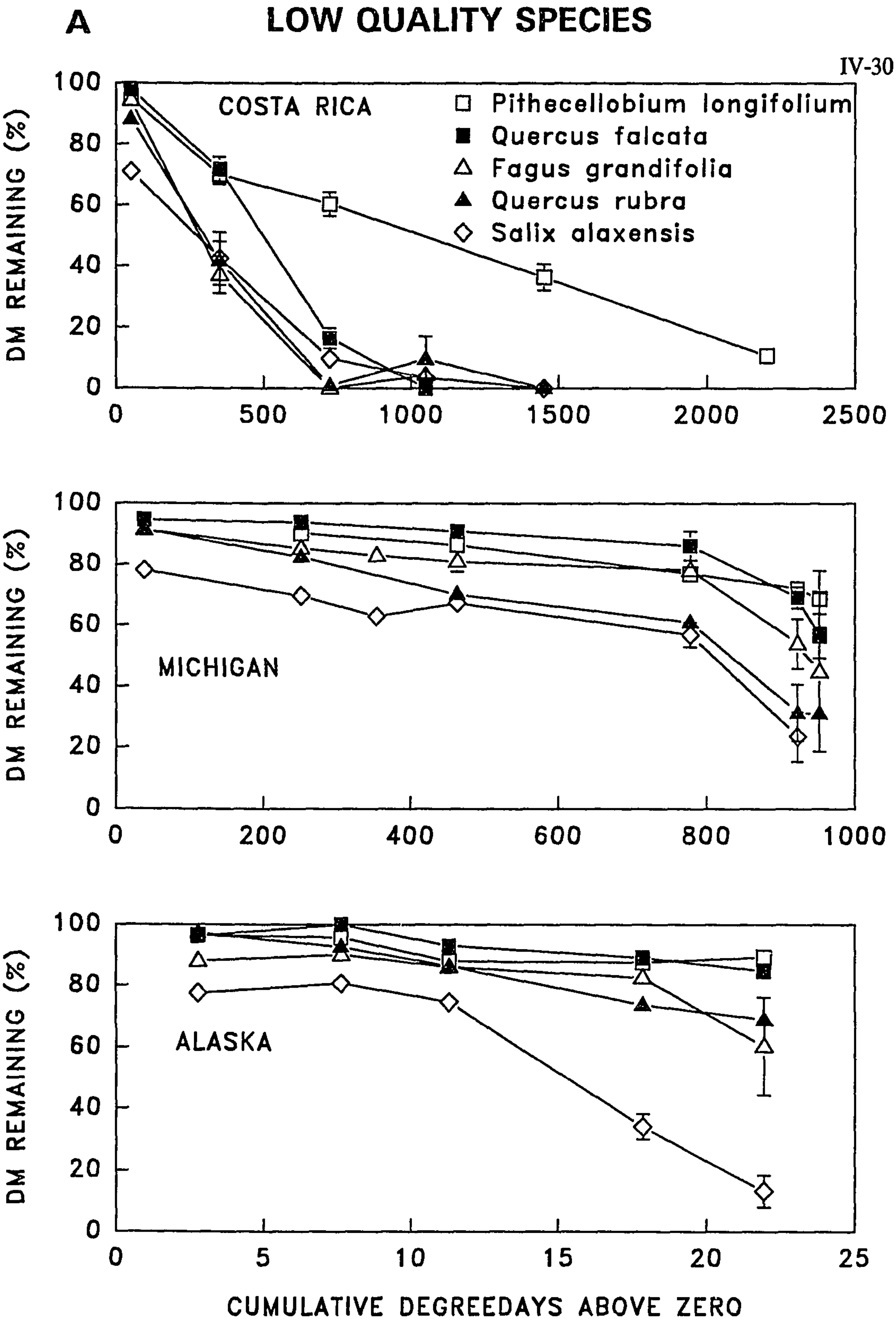

A
LOW QUALITY SPECIES
COSTA RICA
□ Pithecellobium longifolium
■ Quercus falcata
△ Fagus grandifolia
▲ Quercus rubra
◇ Salix alaxensis
DM REMAINING (%)
0
20
40
60
80
100
0
500
1000
1500
2000
2500
MICHIGAN
DM REMAINING (%)
0
20
40
60
80
100
0
200
400
600
800
1000
ALASKA
DM REMAINING (%)
0
20
40
60
80
100
0
5
10
15
20
25
CUMULATIVE DEGREEDAYS ABOVE ZERO

Figure IV-1

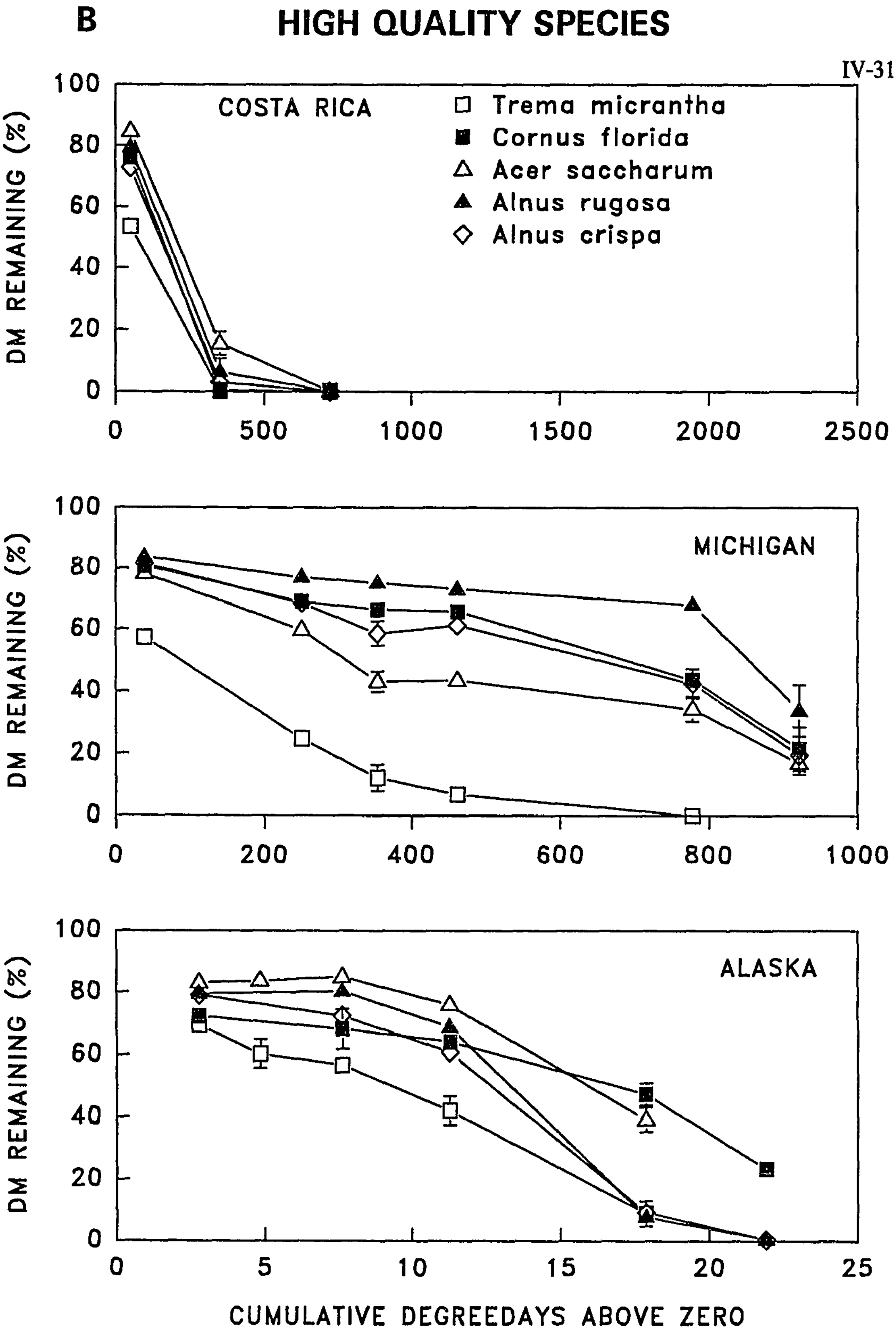

B
HIGH QUALITY SPECIES
COSTA RICA
□ Trema micrantha
■ Cornus florida
△ Acer saccharum
▲ Alnus rugosa
◇ Alnus crispa
DM REMAINING (%)
100
80
60
40
20
0
0
500
1000
1500
2000
2500
MICHIGAN
DM REMAINING (%)
100
80
60
40
20
0
0
200
400
600
800
1000
ALASKA
DM REMAINING (%)
100
80
60
40
20
0
0
5
10
15
20
25
CUMULATIVE DEGREEDAYS ABOVE ZERO

Figure IV-2

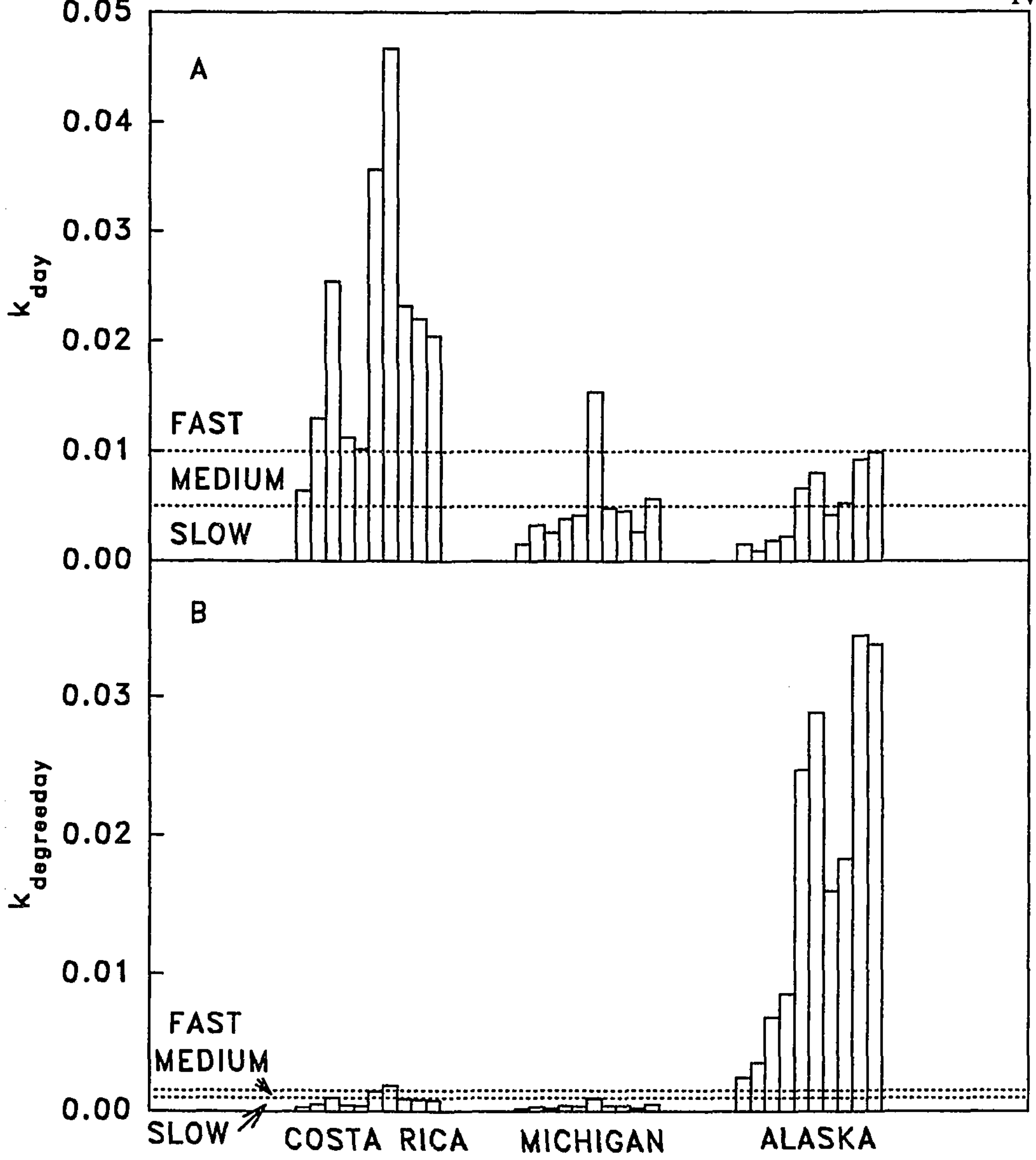

0.05
0.04
0.03
0.02
0.01
0.00
k_{day}
A
FAST
MEDIUM
SLOW
B
0.03
0.02
0.01
0.00
$k_{degreeday}$
FAST
MEDIUM
SLOW
COSTA RICA
MICHIGAN
ALASKA

Figure IV-3

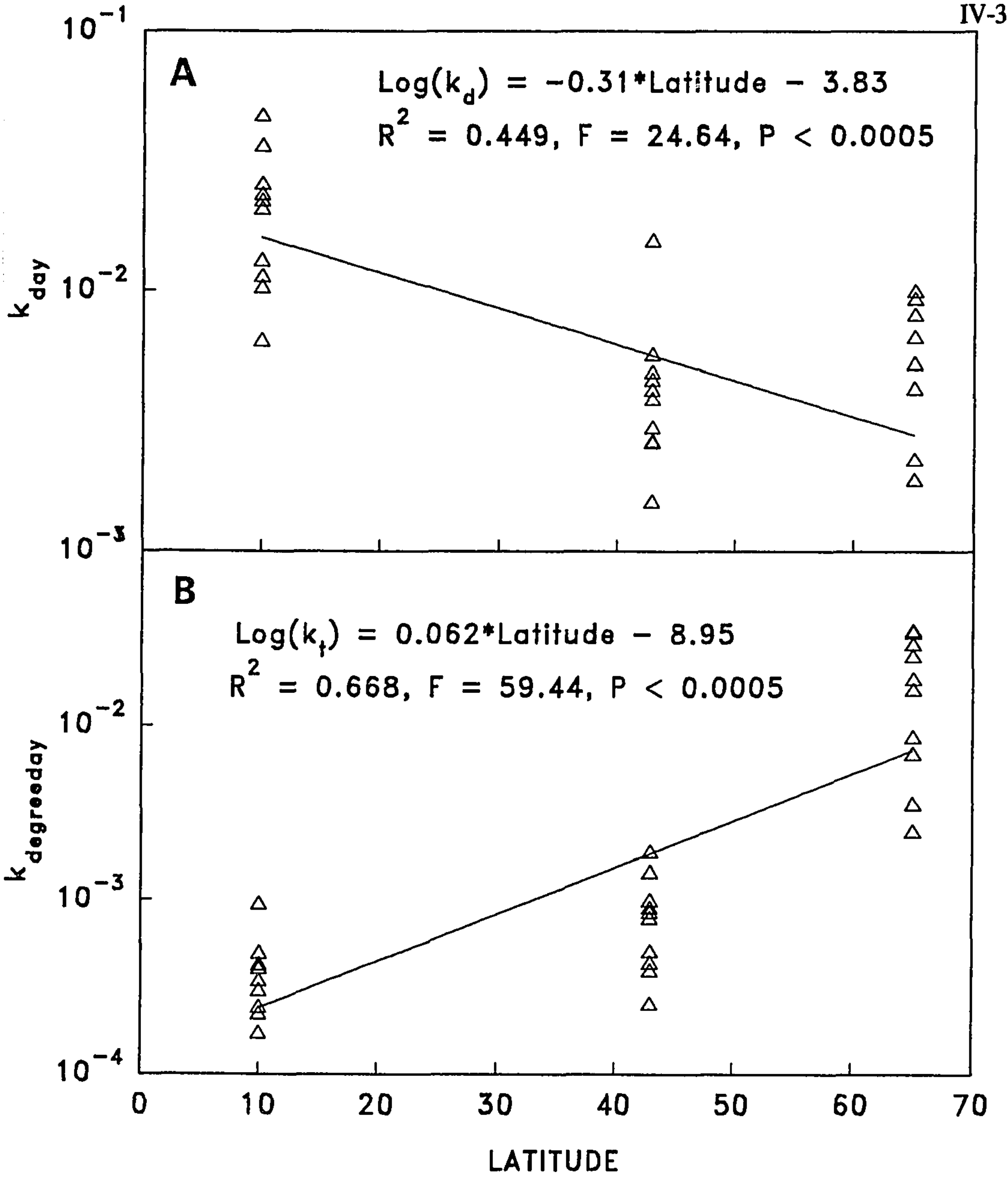

A
$\text{Log}(k_d) = -0.31*\text{Latitude} - 3.83$
$R^2 = 0.449$, F = 24.64, P < 0.0005
B
$\text{Log}(k_t) = 0.062*\text{Latitude} - 8.95$
$R^2 = 0.668$, F = 59.44, P < 0.0005
k_{day}
$k_{degreeday}$
10^{-1}
10^{-2}
10^{-3}
10^{-2}
10^{-3}
10^{-4}
0
10
20
30
40
50
60
70
LATITUDE

Figure IV-4

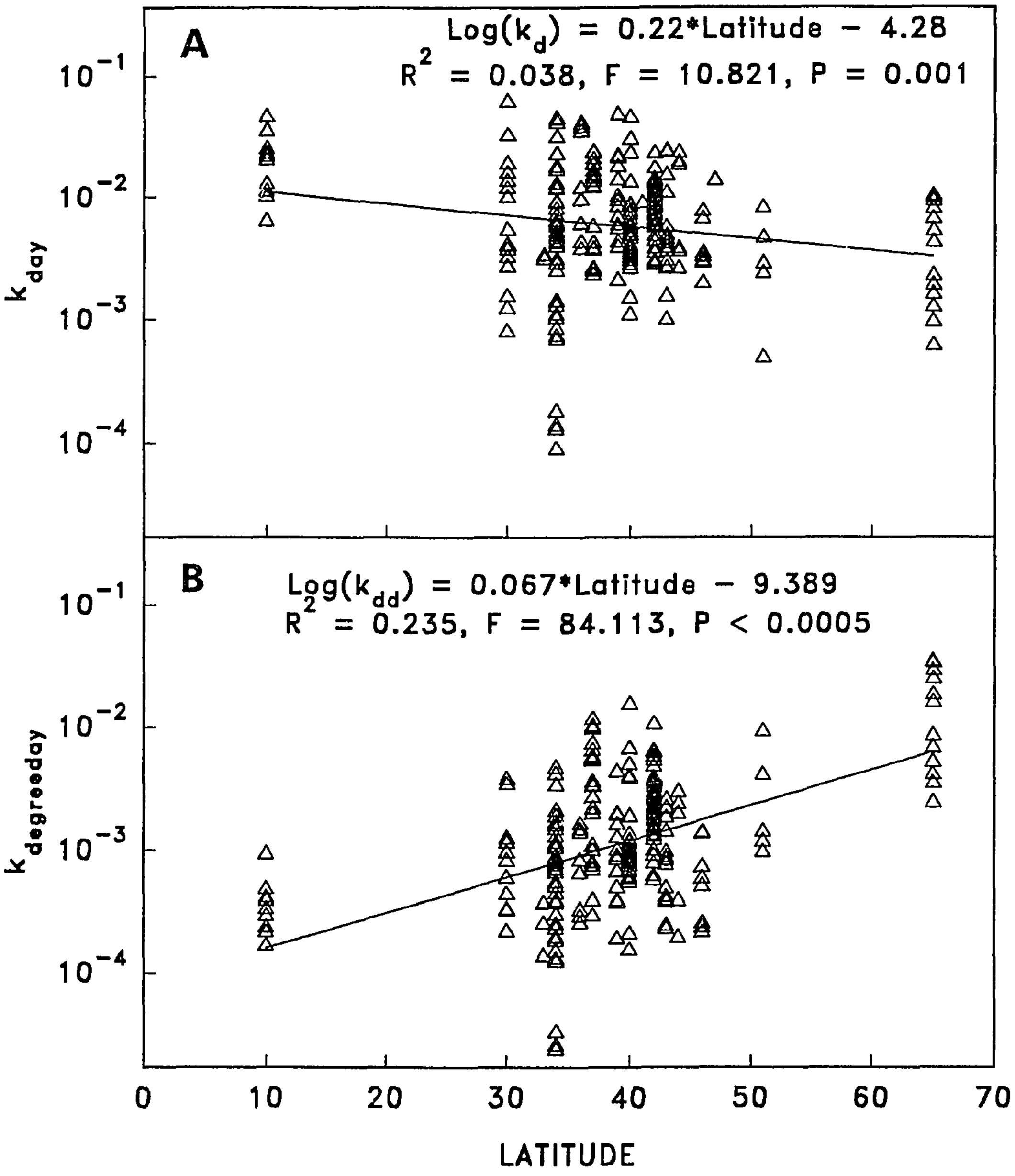

A
$\mathrm{Log}(k_d) = 0.22*\mathrm{Latitude} - 4.28$
$R^2 = 0.038, F = 10.821, P = 0.001$
k_{day}
10^{-1}
10^{-2}
10^{-3}
10^{-4}
B
$\mathrm{Log}(k_{dd}) = 0.067*\mathrm{Latitude} - 9.389$
$R^2 = 0.235, F = 84.113, P < 0.0005$
$k_{degreeday}$
10^{-1}
10^{-2}
10^{-3}
10^{-4}
0
10
20
30
40
50
60
70
LATITUDE

Figure IV-5

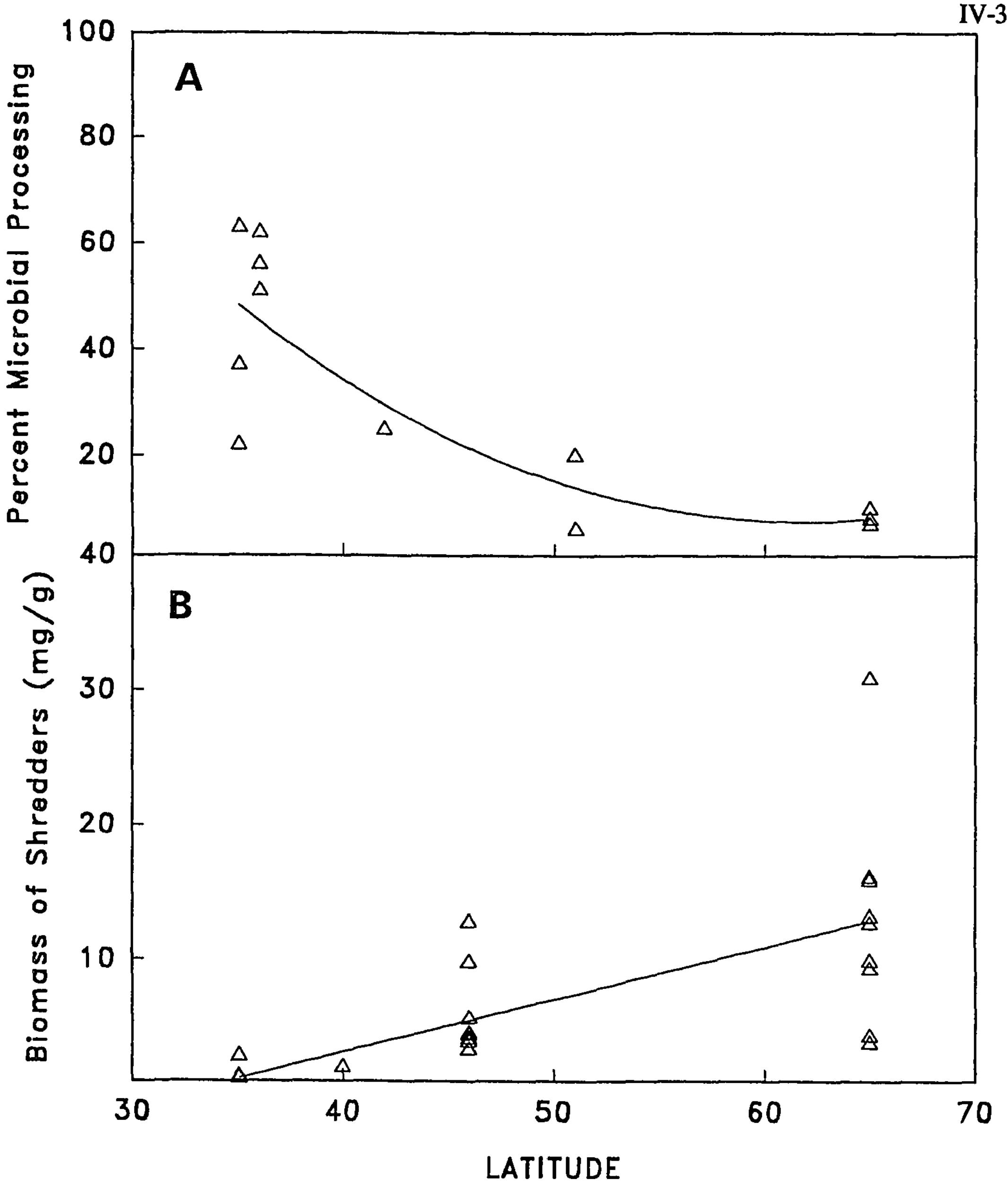

A
B
Percent Microbial Processing
Biomass of Shredders (mg/g)
100
80
60
40
20
40
30
20
10
30
40
50
60
70
LATITUDE

Figure IV-6

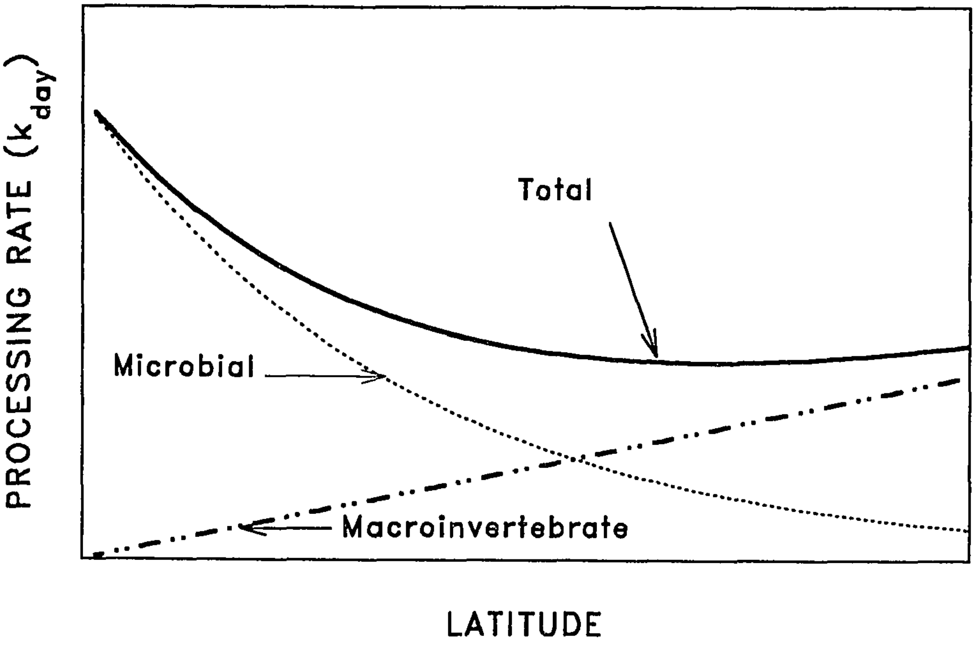

PROCESSING RATE (k_{day})
Total
Microbial
Macroinvertebrate
LATITUDE

Figure IV-7

APPENDIX

Citations for the 28 studies used in latitudinal gradient analyses.

Barnes J.R., McArthur J.V. & Cushing C.E. (1986) Effect of excluding shredders on leaf litter decomposing in two streams. *Great Basin Naturalist* **46**, 204-207.

Bartodziej W. & Perry J.A. (1990) Litter processing in diffuse and conduit springs. *Hydrobiologia* **206**, 87-97.

Beiser M.C., Testa S. III & Aumen N.G. (1991) Macroinvertebrate trophic composition and processing of four leaf species in a Mississippi stream. *Journal of Freshwater Ecology* **6**, 23-33.

Benfield E.F. & Webster J.R. (1985) Shredder abundance and leaf breakdown in an Appalachian Mountain stream. *Freshwater Biology* **15**, 113-120.

Benfield E.F., Jones D.S. & Patterson M.F. (1977) Leaf pack processing in a pastureland stream. *Oikos* **29**, 99-103.

Bird G.A. & Kaushik N.K. (1987) Processing of maple leaf, grass and fern packs and their colonization by invertebrates in a stream. *Journal of Freshwater Ecology* **4**, 177-190.

Brussock P.P., Willis L.D. & Brown A.V. (1988) Leaf decomposition in an Ozark cave and spring. *Journal of Freshwater Ecology* **4**, 263-270.

Canton S.P. & Martinson R.J. (1990) The effects of varying current on weight loss from willow leaf packs. *Journal of Freshwater Ecology* **5**, 413-415.

Cowan C.A., Oswood M.W., Buttimore C.A. & Flanagan P.W. (1983) Processing and macroinvertebrate colonization of detritus in and Alaskan subarctic stream. *Holarctic Ecology* **6**, 340-348.

Garden A. & Davies R.W. (1988) Decay rates of autumn and spring leaf litter in a stream and effects on growth of a detritivore. *Freshwater Biology* **19**, 297-303.

Garden A. & Davies R.W. (1989) Decomposition of leaf litter exposed to simulated acid rain in a buffered lotic system. *Freshwater Biology* **22**, 33-44.

Griffith M.B. & Perry S.A. (1991) Leaf pack processing in two Appalachian mountain streams draining catchments with different management histories.

Hydrobiologia **220**, 247-254.

Guthrie D.W. & Short R.A. (1982) Leaf litter processing in two Texas streams. In: *Proc. Symp. Recent Benth. Invest. Texas Adjacent States* (Ed J.R. Davies), pp. 9-19. Texas Academy of Science, Austin.

Hassage R.L. & Harrel R.C. (1986) Allochthonous leaves as a substrate for macrobenthos. *Journal of Freshwater Ecology* **3**, 453-466.

Hill B.H., Gardener T.J. & Ekisola O.F. (1988) Breakdown of gallery forest leaf litter in intermittent and perennial prairie streams. *Southwestern Naturalist* **33**, 323-331.

Hill B.H., Gardner T.J., Ekisola O.F. & Henebry G.M. (1992) Microbial use of leaf litter in prairie streams. *Journal of the North American Benthological Society* **11**, 11-19.

Horton R.T. & Brown A.V. (1991) Processing of green American elm leaves in first, third, and fifth order reaches of an Ozark stream. *Journal of Freshwater Ecology* **6**, 115-119.

Leff L.G. & McArthur J.V. (1990) Effect of nutrient content on leaf decomposition in a coastal plain stream: a comparison of green and senescent leaves. *Journal of Freshwater Ecology* 5, 269-278.

McArthur J.V. & Barnes J.R. (1988) Community dynamics of leaf litter breakdown in a Utah alpine stream. *Journal of the North American Benthological Society* 7, 37-43.

McArthur J.V., Leff L.G., Kovacic D.A. & Jaroscak J. (1986) Green leaf decomposition in coastal plain streams. *Journal of Freshwater Ecology* 3, 553-558.

McArthur J.V., Barnes J.R., Hansen B.J. & Leff L.G. (1988) Seasonal dynamics of leaf litter breakdown in a Utah alpine stream. *Journal of the North American Benthological Society* 7, 44-50.

Mutch R.A. & Davies R.W. (1984) Processing of willow leaves in two Alberta Rocky Mountain streams. *Holarctic Ecology* 7, 171-176.

Paul R.W. Jr., Benfield E.F. & Cairns J. Jr. (1983) Dynamics of leaf processing in a medium-sized river. In: *Dynamics of lotic ecosystems* (Eds T.D. Fontaine III and S.M. Bartell), pp. 403-423. Ann Arbor Press, Ann Arbor, Michigan.

Petersen R.C. & Cummins K.W. (1974) Leaf processing in a woodland stream. *Freshwater Biology* **4**, 343-368.

Richardson W.B. (1990) A comparison of detritus processing between permanent and intermittent headwater streams. *Journal of Freshwater Ecology* **5**, 341-357.

Short R.A. & Ward J.V. (1980) Leaf litter processing in a regulated Rocky Mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 123-127.

Short R.A., Canton S.P. & Ward J.V. (1980) Detrital processing and associated macroinvertebrates in a Colorado mountain stream. *Ecology* **61**, 727-732.

Short R.A., Smith S.L., Guthrie D.W. & Stanford J.A. (1984) Leaf litter processing rates in four Texas streams. *Journal of Freshwater Ecology* **2**, 469-473.

CONCLUSIONS

Many factors interact to determine the breakdown rate of leaf litter in a given stream. Among these are tree species (e.g. differences in physical and chemical characteristics of leaves among species), water temperature, and the decomposer flora and fauna (i.e. aquatic fungi and macroinvertebrate shredders). Different plant species have evolved differing strategies to minimize the effect of plant pathogens and herbivores on their leaves. These include physical defenses such as highly lignified leaves, thick waxy cuticles, and various spines, hairs and thorns; and chemical defenses such as condensed tannins, phenolic glycosides, and alkaloids. The initial physical and chemical characteristics of the leaves set the stage for the decomposition process: leaves with high nutrient concentrations, low secondary compound concentrations, and that are poorly lignified with thin cuticles break down rapidly, while leaves with low nutrient concentrations and high secondary compound concentrations that are highly lignified with thick cuticles break down more slowly. Leaves of any given species have a suite of nutrient concentrations, and physical and chemical defenses.

The complex effects of these initial conditions on the leafpack biota begin with the decomposer microbes. Tannins are known to inhibit microbial colonization in terrestrial ecosystems, and may influence colonization of leaf litter in streams as well.

ecosystems, and on microbially conditioned and unconditioned litter. Thus, secondary compound concentration may have a direct effect on breakdown by microbes and invertebrates, and an indirect effect on invertebrates by affecting the microbial community.

In this study, we have shown that leaf litter breakdown rates and shredder numbers and biomass are more highly correlated with condensed tannin concentrations than with nitrogen concentrations in leaves. This could be a result of tannins acting as a deterrent to either microbes or shredders, or both. Further, we have shown that normalizing breakdown rates to cumulative degree-days above zero does not remove the influence of temperature; indeed, it seems to exacerbate it when comparing breakdown rates in streams in different biomes. We propose a model of the factors controlling leaf litter breakdown that includes latitude (i.e. temperature) and leaf litter quality as controlling variables, and that partitions breakdown into the contributions by microbes and invertebrate shredders. Breakdown rates are highest for high quality species at low latitudes, where virtually all the breakdown is done by microbes. In more northerly streams where leaf litter is present in the streams for longer periods, shredders have a more predictable resource, and shredders are more abundant and contribute more to leaf litter processing. Chronological breakdown rates may be as rapid in the subarctic as in temperate regions due to this increase in the importance of shredding macroinvertebrates. Thus, we suggest that two modifications need to be made to the current paradigm of controls of leaf litter breakdown in streams: 1) the inhibitory effect of secondary compounds may be as important as the stimulatory effect of high nutrient concentrations, and 2) differing thermal regimes affect microbes and invertebrates in different ways, and care must be taken when extrapolating breakdown rates between widely separated regions with different thermal regimes.

APPENDIX: DATA ARCHIVE

ABBREVIATIONS

Mass loss, foliar chemistry, and macroinvertebrate data used in this study are tabulated in this appendix. A period (".") represents missing data due to leafpacks being frozen into ice or to insufficient leaf material for analysis. Abbreviations are as follows:

REP	Replicate number of the leafpack.
DAY	Number of days of processing in Monument Creek.
AFDM%	Ash-free Dry Mass of leaf litter remaining as a proportion of the original mass (ca. 3 g).
AFDM_g	Ash-free Dry Mass of leaf litter remaining, in grams.
DM_g	Dry Mass of leaf litter remaining, in grams.
TANN%	Condensed tannin concentration in leaf litter as a proportion of dry mass remaining, in quebracho equivelants.
NITR%	Total Kjeldahl nitrogen in leaf litter as a proportion of dry mass remaining.
PHOS%	Total phosphorus in leaf litter as a proportion of dry mass remaining.
TOTAL#	Total number of macroinvertebrates on the leafpack.
SHR#	Number of shredders on the leafpack.
SCR#	Number of scrapers on the leafpack.

C-G#	Number of collector-gatherers on the leafpack.
C-FF#	Number of collector-filter feeders on the leafpack.
PRED#	Number of predators on the leafpack.
TOTmg	Total invertebrate biomass on the leafpack (in mg)
SHRmg	Biomass of shredders on the leafpack (in mg).
NONmg	Biomass of non-shredders on the leafpack (in mg).
CHIR	Number of Chironomidae.
CHEL	Number of Chelifera (Diptera: Empididae)
OREO	Oreogeton (Diptera: Empididae)
PERI	Number of Pericoma (Diptera: Psychodidae)
PROS	Prosimulium (Diptera: Simuliidae)
SIMU	Simulium (Diptera: Simuliidae)
UDIP	Unidentified Diptera larvae
BAET	Baetis (Ephemeroptera: Baetidae)
EPHE	Ephemerella (Ephemeroptera: Ephemerellidae)
CINY	Cinygmula (Ephemeroptera: Heptageniidae)
EPEO	Epeorus (Ephemeroptera: Heptageniidae)
UHEP	Unidentified Heptageniidae
AMEL	Ameletus (Ephemeroptera: Siphlonuridae)
CAPN	Capniidae (probably Mesocapnia)
CHLO	Chloroperlidae (probably Plumiperla)

ZAPA	Zapada (Plecoptera: Nemouridae)
NEMO	Unidentified Nemouridae nymphs
PERL	Perlodidae (probably Arcynopteryx and Isoperla)
TAEN	Taenionema (Plecoptera: Taeiopterygidae)
CHYR	Chyranda (Trichoptera: Limnephilidae)
ECCL	Ecclisomyia (Trichoptera: Limnephilidae)
HYDA	Hydatophylax (Trichoptera: Limnephilidae)
ONOC	Onocosmoecus (Trichoptera: Limnephilidae)
ULIM	Unidentified Limnephilidae larvae
RHYA	Rhyacophila (Trichoptera: Rhyacophilidae)
HYDR	Hydracarina (Arachnida: Acarina)
OLIG	Oligochaeta (marked as present with a "+": most specimens were broken).

Trema micrantha

REP	DAY	AFDM%	AFDM_g	DM_g	TANN%	NITR%	PHOS%	TOTAL#	SHR#	SCR#	C-G#	C-FF#	PRED#	TOTmg
1	2	0.730	1.764	2.050	0.000	0.049	0.003	32	2	0	1	29	0	2.900
2	2	0.739	1.833	2.130	0.000	0.047	0.003	9	1	0	3	4	1	1.700
3	2	0.731	1.741	2.010	0.000	0.019	0.001	37	4	0	6	27	0	1.900
4	2	0.720	1.793	2.040	0.000	0.025	0.001	7	2	0	2	3	0	1.700
5	2	0.713	1.816	2.170	0.000	0.008	0.000	27	0	0	3	24	0	1.000
21	7	0.688	1.768	2.010	0.001	0.047	0.002	43	10	0	21	11	1	5.800
22	7	0.729	1.833	2.040	0.003	0.052	0.002	23	6	0	15	2	0	5.500
23	7	0.704	1.757	2.000	0.003	.	.	37	9	0	25	2	1	4.400
24	7	0.671	1.609	1.830	0.002	0.039	0.001	33	7	0	10	15	1	17.600
25	7	.	1.159	1.310	0.005	.	.	63	10	0	25	28	0	3.800
6	14	0.635	1.554	1.690	0.000	0.008	0.001	245	51	0	166	27	1	19.300
7	14	0.590	1.412	1.570	0.000	0.006	0.000	616	90	0	457	43	26	42.300
8	14	0.673	1.625	1.830	0.000	0.006	0.000	97	16	0	66	11	4	9.800
9	14	0.646	1.591	1.770	0.000	0.007	0.000	109	25	0	82	1	1	19.800
10	14	0.564	1.348	1.500	0.000	.	.	88	27	2	46	12	1	11.100
11	28	0.329	0.792	0.940	0.001	0.006	0.000	420	102	0	245	66	7	75.100
12	28	0.501	1.180	1.340	0.001	0.007	0.000	191	34	2	153	0	2	19.400
13	28	0.439	1.040	1.150	0.000	0.006	0.000	82	11	0	65	6	0	7.700
14	28	0.359	0.874	1.010	0.000	0.005	0.000	88	11	0	77	0	0	16.900
15	28	0.536	1.294	1.710	0.000	0.024	0.001	172	22	1	144	0	5	24.100
16	56	0.012	0.030	0.030	.	.	.	66	14	0	52	0	0	3.500
17	56	0.074	0.175	0.230	.	.	.	265	50	0	215	0	0	25.700
18	56	0.205	0.496	0.730	.	0.034	0.001	194	18	2	169	1	4	12.100
19	56	0.063	0.154	0.190	.	0.028	0.001	171	31	1	139	0	0	18.500
20	56	0.049	0.120	0.140	.	.	.	268	53	0	203	5	7	24.400

Trema micrantha

REP	DAY	SHRmg	NONmg	CHIR	CHEL	PERI	PROS	SIMU	OREO	UDIP	BAET	EPHE	CINY	EPEO	UHEP
1	2	1.800	1.100	1			29								
2	2	0.500	1.200	2	1		4				1				
3	2	1.100	0.800	4			27				2				
4	2	0.900	0.800				3				2				
5	2	0.000	1.000	2			24								1
21	7	5.000	0.800	16			11				4				1
22	7	4.000	1.500	10			2				2				2
23	7	3.600	0.800	24			2				1				
24	7	15.100	2.500	9			15				1				
25	7	1.200	2.600	5			28				19				1
6	14	17.700	1.600	144	1		27				21				1
7	14	26.800	15.500	383		1	43				67				6
8	14	5.400	4.400	58			11				7				1
9	14	18.300	1.500	81			1								
10	14	9.900	1.200	22			12				24		2		
11	28	68.600	6.500	185			66				59			1	
12	28	17.800	1.600	152		1							2		
13	28	6.700	1.000	64			6				1				
14	28	15.200	1.700	76							1				
15	28	21.800	2.300	137	2						3		1	4	
16	56	3.100	0.400	50							2				
17	56	25.400	0.300	211							1			3	
18	56	9.300	2.800	166	2		1				2		2	1	
19	56	17.400	1.100	139									1		
20	56	20.800	3.600	199	1		5				4				

Trema micrantha

REP	DAY	AMEL	CAPN	CHLO	ZAPA	PERL	TAEN	CHYR	ECCL	HYDA	ONOC	ULIM	RHYA	HYDR	OLIG
1	2				2										
2	2				1										
3	2		2		2										
4	2				2										
5	2														
21	7		3	1	6				1						
22	7	1	1		5										
23	7		2	1	7										
24	7		4		2					1			1		
25	7		4		6										
6	14		4		41						6				
7	14		3	12	83	5					4		8	1	+
8	14		2	1	13	2					1		1		
9	14	1	5	1	7				13						
10	14		6	1	20						1				
11	28		5	2	86	1	2		7		2		4		
12	28		4	1	30									1	
13	28		2		9										
14	28		3		5				3						
15	28		5	2	13				4				1		
16	56				14										
17	56		11		28				6		5				
18	56		1	1	14				3				1		
19	56		1		29						1				
20	56		4	2	47						2		4		

Pithecellobium longifolium

REP	DAY	AFDM%	AFDM_g	DM_g	TANN%	NITR%	PHOS%	TOTAL	SHR#	SCR#	C-G#	C-FF#	PRED#	TOTmg
1	2	0.971	2.809	2.870	0.100	0.033	0.002	47	1	0	11	35	0	1.500
2	2	0.978	2.819	2.880	0.126	0.033	0.002	9	1	0	1	7	0	0.500
3	2	0.984	2.873	2.930	0.113	0.025	0.001	16	0	0	4	12	0	0.050
4	2	0.976	2.821	2.890	.	0.017	0.000	26	0	0	8	17	1	0.400
5	2	0.972	2.811	2.870	0.097	0.033	0.001	19	3	0	3	13	0	0.550
6	14	0.970	2.888	2.960	0.091	0.040	0.003	59	11	0	44	4	0	3.800
7	14	0.951	2.796	2.870	0.110	0.050	0.003	215	22	0	174	14	5	10.050
8	14	0.962	2.809	2.900	0.096	0.047	0.003	129	17	0	104	3	5	4.800
9	14	0.961	2.779	2.860	0.076	0.046	0.001	103	15	0	85	1	2	7.600
10	14	0.973	2.812	2.890	0.108	.	.	237	21	4	180	28	4	9.933
11	28	0.830	2.424	2.520	0.107	0.048	0.001	105	7	0	74	20	4	2.800
12	28	0.919	2.675	2.760	0.066	0.041	0.001	221	13	21	179	2	6	4.400
13	28	0.892	2.587	2.660	0.027	0.050	0.001	40	4	0	36	0	0	2.233
14	28	0.902	2.643	2.740	0.076	0.040	0.001	101	9	3	69	19	1	4.600
15	28	0.850	2.449	2.540	0.049	0.040	0.001	39	5	2	27	3	2	5.800
16	56	0.829	2.428	2.600	0.017	0.008	0.000	156	14	2	126	11	3	9.000
17	56	0.871	2.552	2.610	0.053	0.023	0.001	30	1	0	26	1	2	2.100
18	56	0.871	2.561	2.630	0.029	0.066	0.000	240	15	6	194	18	7	17.800
19	56	0.894	2.602	2.690	0.049	0.030	0.001	200	14	3	168	11	4	8.300
20	56	0.906	2.697	2.770	0.091	0.033	0.001	193	21	7	141	21	3	8.500
21	75	0.889	2.597	2.690	0.042	0.029	0.001	162	20	0	138	1	3	6.700
22	75	0.879	2.593	2.660	0.016	0.032	0.001	124	18	0	103	0	3	9.700
23	75	.	.	.	.	.	.	.	.	.	.	.	.	.
24	75	0.884	2.590	2.690	0.048	0.026	0.001	140	15	0	124	1	0	17.500
25	75	0.923	2.677	2.760	0.057	.	.	111	3	0	94	11	3	5.200

Pithecellobium longifolium

REP	DAY	SHRmg	NONmg	CHIR	CHEL	PERI	PROS	SIMU	OREO	UDIP	BAET	EPHE	CINY	EPEO	UHEP
1	2	0.400	1.100	9			35				2				
2	2	0.200	0.300	1			7								
3	2	0.000	0.050	2			12				2				
4	2	0.000	0.400	6			17				2				
5	2	0.150	0.400	3			13								
6	14	3.300	0.500	24			4				18				1
7	14	5.150	4.900	122			14				44				8
8	14	3.500	1.300	95	1		3				4				5
9	14	6.567	1.033	81			1				1			2	
10	14	6.400	3.533	114	1		26	1			63		4	3	
11	28	1.033	1.767	65	2		20				9				
12	28	2.567	1.833	165			2						21	14	
13	28	1.500	0.733	33							2			1	
14	28	2.700	1.900	62			19				7		3		
15	28	4.000	1.800	20			3				6		2	1	
16	56	7.100	1.900	125			11				1		2		
17	56	0.900	1.200	26			1								
18	56	5.000	12.800	178	1		18				14		6	2	
19	56	5.000	3.300	153			11				14		3	1	
20	56	3.900	4.600	108	1		21				33		7		
21	75	5.100	1.600	129			1				6				3
22	75	8.200	1.500	101	2						2				
23	75	.	.												
24	75	16.400	1.100	123			1				1				
25	75	1.400	3.800	70			11				23				1

Pithecellobium longifolium

REP	DAY	AMEL	CAPN	CHLO	ZAPA	PERL	TAEN	CHYR	ECCL	HYDA	ONOC	ULIM	RHYA	HYDR	OLIG
1	2				1										
2	2		1												
3	2														
4	2			1											
5	2		2		1										
6	14	1	7		2			1			1				
7	14		4	1	16	3						2	1		
8	14		6	3	11	1									+
9	14	1	3	2	6				5		1				
10	14		4	3	15		1				1				
11	28			1	7								1		
12	28		7	3	5		1						3		
13	28				4										
14	28		1		7				1					1	
15	28			1	5									1	
16	56		3		9				1		1		2	1	
17	56				1								2		
18	56			1	15								5		
19	56		1		11				1		1		2	2	
20	56		1		18							2	2		
21	75		6		13	1					1		2		
22	75		1		15						2			1	
23	75														
24	75		1		13				1						
25	75				3	1							2		

Cornus florida

REP	DAY	AFDM%	AFDM_g	DM_g	TANN	NITR	PHOS%	TOTAL#	SHR#	SCR#	C-G#	C-FF#	PRED#	TOTmg
1	2	0.752	1.991	2.160	0.029	0.008	0.001	33	4	0	11	17	1	25.800
2	2	0.748	2.000	2.170	0.020	0.009	0.001	5	0	0	2	3	0	0.500
3	2	0.737	1.964	2.130	0.041	0.035	0.001	19	4	0	6	8	1	1.100
4	2	0.761	2.061	2.250	0.028	0.011	0.001	7	0	0	3	4	0	0.300
5	2	0.752	2.030	2.190	0.025	0.019	0.001	42	9	0	19	13	1	4.100
6	14	0.763	2.033	2.250	0.014	0.016	0.000	112	5	0	107	0	0	1.800
7	14	0.000	1.185	1.330	0.013	0.016	0.000	267	19	0	220	23	5	8.000
8	14	0.697	1.857	2.100	0.016	0.016	0.000	244	45	0	189	10	0	5.600
9	14	0.719	1.941	2.140	0.022	0.016	0.000	89	7	1	72	6	3	3.700
10	14	0.757	2.050	2.500	0.007	.	.	141	10	1	120	5	5	3.300
11	28	0.666	1.822	2.060	0.008	0.015	0.000	150	15	0	127	8	0	.
12	28	0.646	1.734	1.960	0.008	0.015	0.000	339	27	4	288	10	10	14.200
13	28	0.649	1.758	1.970	0.011	0.017	0.000	89	6	0	81	1	1	5.200
14	28	0.628	1.696	1.950	0.007	0.015	0.000	97	12	2	79	3	1	7.100
15	28	0.599	1.606	1.840	0.004	0.016	0.000	381	40	8	317	7	5	15.100
16	56	0.476	1.280	1.600	0.003	0.029	0.000	720	129	2	563	17	9	39.900
17	56	0.354	0.953	1.340	0.004	0.018	0.000	.	.	.	.	.	.	.
18	56	0.433	1.166	1.060	0.003	0.030	0.000	175	87	0	83	2	3	57.000
19	56	0.464	1.250	1.600	0.004	.	.	552	94	1	440	8	9	39.200
20	56	0.467	1.260	1.600	0.003	0.012	0.001	380	79	3	270	21	7	42.800
21	75	0.215	0.576	0.810	0.003	0.013	0.001	610	76	0	525	1	8	37.200
22	75	0.202	0.540	0.720	0.010	0.012	0.001	263	42	0	211	5	5	22.100
23	75	.	.	.	.	.	.	.	.	.	.	.	.	.
24	75	0.241	0.656	0.830	0.007	0.011	0.001	682	101	0	571	3	7	37.800
25	75	0.143	0.380	0.470	.	.	.	643	103	0	449	80	11	46.100

Cornus florida

REP	DAY	SHRmg	NONmg	CHIR	CHEL	PERI	PROS	SIMU	OREO	UDIP	BAET	EPHE	CINY	EPEO	UHEP
1	2	23.900	1.900	6			17				2				1
2	2	0.000	0.500				3				1				1
3	2	0.500	0.600	4			8				1				1
4	2	0.000	0.300	3			4								
5	2	1.400	2.700	10			13				9				
6	14	0.700	1.100	104							1				2
7	14	5.000	3.000	183			22				33				4
8	14	4.000	1.600	178			10				9				2
9	14	2.500	1.200	70	2		6				2		1		
10	14	1.600	1.700	109	1		5				10		1	1	
11	28	20.300	.	115			8				11			1	
12	28	6.700	7.500	282	1	1	10						4	5	
13	28	4.100	1.100	78			1				1			2	
14	28	6.000	1.100	68			3				11		2		
15	28	12.100	3.000	310			7			4			8	7	
16	56	31.800	8.100	558	3		17				4		2	1	
17	56	.	.	0	0	0									
18	56	52.500	4.500	79			2							4	
19	56	33.800	5.400	436	2		7				1		1	3	
20	56	29.200	13.600	260	1		18	3			10		3		
21	75	30.400	6.800	518	5		1				4				3
22	75	16.900	5.200	193	1		5				16				2
23	75	.	.												
24	75	33.700	4.100	559	3		2				11	1			
25	75	30.600	15.500	403	3		80				46				

Cornus florida

REP	DAY	AMEL	CAPN	CHLO	ZAPA	PERL	TAEN	CHYR	ECCL	HYDA	ONOC	ULIM	RHYA	HYDR	OLIG
1	2	2	1		2					1			1		
2	2														
3	2		4	1											
4	2														
5	2		5		4								1		
6	14		2		3										
7	14		8	2	10	3					1				+
8	14		17		26						2				
9	14		2	1	4				1						+
10	14		4	4	6										
11	28		1		14										
12	28		2	4	23				1		1		4	1	
13	28		1	1	5										
14	28		3	1	8				1						
15	28		9	5	30				1						
16	56		6		117		1		2	1	2		5	1	
17	56														
18	56		9	2	74				3		1		1		
19	56		7	1	84		2		1				6		
20	56		4		71							4	6		
21	75		11		55			2	5		3		3		+
22	75		2	1	37						3		3		+
23	75														
24	75		2		93						6		3	1	
25	75		1	1	85	3					15	2	4		

Quercus falcata

REP	DAY	AFDM%	AFDM_	DM_g	TANN%	NITR%	PHOS%	TOTAL	SHR#	SCR#	C-G#	C-FF#	PRED#	TOTmg
1	2	0.958	2.739	2.870	0.096	0.006	0.000	8	0	0	2	6	0	0.600
2	2	0.965	2.749	2.880	0.093	0.007	0.000	6	2	0	2	1	1	2.300
3	2	0.947	2.734	2.860	0.129	0.017	0.000	65	3	0	2	60	0	2.900
4	2	0.960	2.744	2.870	0.147	0.032	0.001	19	2	0	3	14	0	2.000
5	2	0.972	2.835	2.980	0.130	0.018	0.001	12	1	0	7	3	1	1.600
6	14	0.958	2.785	2.920	0.124	0.018	0.001	143	20	0	76	44	3	7.900
7	14	0.000	3.153	3.380	0.118	0.014	0.001	188	16	0	103	66	3	9.500
8	14	0.969	2.780	2.970	0.160	0.013	0.001	252	19	0	211	19	3	8.200
9	14	0.945	2.683	2.880	0.103	0.017	0.001	281	24	3	86	167	1	6.900
10	14	0.974	2.813	2.940	0.107	.	.	141	7	1	130	2	1	3.400
11	28	0.949	2.730	2.870	0.110	0.016	0.001	128	25	0	71	29	3	7.000
12	28	0.899	2.612	2.780	0.139	0.013	0.001	101	6	0	74	21	0	1.500
13	28	0.919	2.645	2.810	0.134	0.010	0.001	101	15	0	83	1	2	9.600
14	28	0.928	2.643	2.860	0.104	0.016	0.001	290	30	7	235	10	8	14.000
15	28	0.856	2.447	2.650	0.085	0.016	0.001	138	9	0	107	19	3	9.700
16	56	0.893	2.578	2.800	0.093	0.010	0.001	346	43	3	286	3	11	15.000
17	56	0.801	2.290	2.450	0.087	0.018	0.001	194	32	1	154	0	7	7.000
18	56	0.922	2.617	2.820	0.109	0.006	0.000	63	13	1	46	0	3	5.000
19	56	.	.	.	.	.	.	.	.	.	.	.	.	.
20	56	0.841	2.404	2.580	0.074	0.009	0.000	.	.	.	.	.	.	.
21	75	0.860	2.491	2.690	0.078	0.007	0.000	229	27	0	182	13	6	13.700
22	75	0.827	2.403	2.560	0.058	0.009	0.000	382	44	0	320	6	7	17.100
23	75	0.801	2.305	2.440	0.079	.	.	229	33	0	184	5	6	7.200
24	75	.	.	.	.	.	.	.	.	.	.	.	.	.
25	75	.	.	.	.	.	.	.	.	.	.	.	.	.

Quercus falcata

REP	DAY	SHRmg	NONmg	CHIR	CHEL	PERI	PROS	SIMU	OREO	UDIP	BAET	EPHE	CINY	EPEO	UHEP
1	2	0.000	0.600				6				2				
2	2	1.700	0.600	2	1		1								
3	2	1.800	1.100	1			60				1				
4	2	1.300	0.700	1			14				2				
5	2	1.100	0.500	6			3				1				
6	14	2.800	5.100	65	1		44				11				
7	14	3.100	6.400	65			66				36				2
8	14	5.800	2.400	185	1		19				23				3
9	14	2.000	4.900	57			167				29		3		
10	14	1.300	2.100	123			2				7		1		
11	28	5.200	1.800	65	1		29				5			1	
12	28	0.200	1.300	71			21				2			1	
13	28	8.400	1.200	83	1		1								
14	28	10.000	4.000	220	1	1	8	2			14		7		
15	28	1.800	7.900	78			19				29				
16	56	9.500	5.500	264	2		3				18		3	2	
17	56	5.900	1.100	146	3						8		1		
18	56	2.000	3.000	36	1						8		1	2	
19	56	.	.												
20	56	.	.												
21	75	9.000	4.700	153	3		13				29				
22	75	12.400	4.700	288	1		6				28				4
23	75	5.100	2.100	171	1		5				9				4
24	75	.	.												
25	75	.	.												

Quercus falcata

REP	DAY	AMEL	CAPN	CHLO	ZAPA	PERL	TAEN	CHYR	ECCL	HYDA	ONOC	ULIM	RHYA	HYDR	OLIG
1	2														
2	2				2										
3	2				3										
4	2				2										
5	2			1	1										
6	14		2		18	1							1		
7	14			1	16								1	1	
8	14		6		10	1			1		2		1		
9	14		2	1	20		1		1						
10	14		4	1	3										
11	28		1		24	2									
12	28				6										
13	28				14						1			1	+
14	28		5	5	24						1		1	1	
15	28		1		5		3						3		
16	56	2	3	2	40								3	4	
17	56			1	31				1				1	2	
18	56		2		11								1	1	
19	56														
20	56														
21	75				23				1		3		3	1	
22	75		3		34	1					7		4	6	+
23	75		1	1	31						1		4	1	
24	75														
25	75														

Acer saccharum

REP	DAY	AFDM%	AFDM_g	DM_g	TANN%	NITR%	PHOS%	TOTAL#	SHR#	SCR#	C-G#	C-FF#	PRED#	TOTmg
1	2	0.779	2.321	2.520	0.048	0.024	0.001	49	2	0	7	40	0	1.000
2	2	0.769	2.367	2.570	0.020	0.027	0.001	20	6	0	9	5	0	1.400
3	2	0.757	2.256	2.460	0.030	.	0.001	23	3	0	6	12	2	4.400
4	2	0.746	2.239	2.440	0.023	0.027	0.001	60	2	0	6	50	2	2.600
5	2	0.776	2.359	2.540	0.034	0.023	0.001	42	3	0	6	33	0	1.700
21	7	0.757	2.256	2.460	0.042	0.027	0.001	57	4	0	49	4	0	2.500
22	7	0.789	2.461	2.670	0.016	0.026	0.001	17	3	0	8	4	2	1.200
23	7	0.774	2.298	2.530	0.040	.	.	107	9	0	84	12	2	5.000
24	7	0.764	2.222	2.430	0.030	0.023	0.001	59	2	0	47	6	4	4.200
25	7	0.741	2.217	2.440	0.040	.	.	28	2	0	9	15	2	2.100
6	14	0.769	2.315	2.540	0.028	0.024	0.001	318	27	0	269	19	2	11.000
7	14	0.721	2.119	2.340	0.021	0.027	0.001	305	41	0	232	22	10	17.900
8	14	.	.	.	0.026	0.025	0.000	341	31	0	229	75	6	10.500
9	14	0.739	2.218	2.410	0.023	0.026	0.001	115	16	0	99	0	0	5.100
10	14	0.711	2.126	2.340	0.022	.	.	102	13	0	87	1	1	2.700
11	28	0.672	2.137	2.390	0.019	0.023	0.000	456	64	18	256	115	3	37.200
12	28	0.702	2.149	2.400	0.017	0.024	0.001	535	51	26	445	4	9	22.600
13	28	0.685	2.096	2.370	0.039	0.017	0.001	368	48	5	305	5	5	24.700
14	28	0.645	2.038	2.310	0.023	0.018	0.001	379	34	6	338	1	0	22.300
15	28	0.664	2.097	2.390	0.008	0.022	0.001	553	72	16	433	23	7	36.000
16	56	0.243	0.713	1.070	0.018	0.023	0.001	653	107	2	535	4	5	.
17	56	0.346	1.025	1.470	0.008	0.010	0.001	1360	226	3	1115	1	15	82.400
18	56	0.272	0.817	1.150	0.005	0.015	0.001	751	114	2	605	22	8	28.900
19	56	0.227	0.677	0.790	0.007	0.019	0.001	702	203	3	483	4	9	80.900
20	56	0.347	1.048	1.370	0.027	0.019	0.001	445	125	6	308	1	5	66.000

Acer saccharum

REP	DAY	SHRmg	NONmg	CHIR	CHEL	PERI	PROS	SIMU	OREO	UDIP	BAET	EPHE	CINY	EPEO	UHEP
1	2	0.300	0.700	4			40				3				
2	2	0.900	0.500	7			5				2				
3	2	1.700	2.700	5			12				1				
4	2	1.000	1.600	4			50				2				
5	2	0.900	0.800	5			33				1				
21	7	1.700	0.800	48			3				1				
22	7	0.600	0.600	8	1		4								
23	7	3.300	1.700	71			12				13				
24	7	0.100	4.100	44			6				1				2
25	7	1.400	0.700	7			15				2				
6	14	8.400	2.600	253			19				15				1
7	14	9.600	8.300	197			21				29				6
8	14	4.900	5.600	169			75				53				5
9	14	4.300	0.800	95										3	
10	14	2.200	0.500	82			1				4			1	
11	28	31.900	5.300	229			115				22		18	5	
12	28	14.600	8.000	429	1		4				2	1	26	13	
13	28	18.400	6.300	294	1		5					10	5		
14	28	19.000	3.300	331		2		1			3		6	2	
15	28	30.400	5.600	398			23			2	23		16	12	
16	56	.	.	523	3	1	4				8		2	3	
17	56	72.500	9.900	1109	4		1				3		3	2	
18	56	24.000	4.900	572	5		22				33		2		
19	56	76.200	4.700	475	3		4				7		3	1	
20	56	57.100	8.900	294	1		1				13		6		

Acer saccharum

REP	DAY	AMEL	CAPN	CHLO	ZAPA	PERL	TAEN	CHYR	ECCL	HYDA	ONOC	ULIM	RHYA	HYDR	OLIG
1	2				2										
2	2		2		4										
3	2			1	2				1				1		
4	2			2	2										
5	2				3										
21	7		3		1										
22	7		1	1	2										
23	7		3	1	5	1						1			
24	7		1	3	1								1		
25	7			2	2										
6	14		7	1	20								1		
7	14		11	6	30	3							1		
8	14	2	10	3	20	3			1						+
9	14	1	11		3				1		1				
10	14		5	1	5		2		1						
11	28		12	2	45		1		5		1		1		
12	28		18	7	27		3				3		1		
13	28	1	10	3	35		1		1		1		1		+
14	28		12		18				3		1				
15	28		18	1	52	2			2				4		
16	56		20	1	81	1			5		1				
17	56	1	79	8	137				2		8			3	
18	56		29		80				1		4		1	2	
19	56		49	3	152		2						2	1	
20	56	1	16		99				4			6	4		

Fagus grandifolia

REP	DAY	AFDM%	AFDM_g	DM_g	TANN%	NITR%	PHOS%	TOTAL	SHR#	SCR#	C-G#	C-FF#	PRED#	TOTmg
1	2	0.888	2.513	2.650	0.078	0.022	0.001	27	1	0	6	20	0	1.300
2	2	0.890	2.475	2.610	0.064	0.023	0.001	14	5	0	9	0	0	1.600
3	2	0.896	2.484	2.600	0.085	0.032	0.001	41	1	0	5	35	0	1.100
4	2	0.890	2.567	2.710	0.083	0.018	0.001	30	4	0	13	13	0	0.800
5	2	0.889	2.497	2.650	0.069	0.010	0.001	14	4	0	5	5	0	0.900
6	14	0.867	2.445	2.730	0.060	0.009	0.001	333	21	0	215	93	4	5.500
7	14	0.851	2.385	2.570	0.047	0.006	0.001	160	10	0	90	54	6	3.500
8	14	0.891	2.488	2.720	0.065	0.009	0.001	685	54	0	592	32	7	15.500
9	14	0.882	2.496	2.710	0.053	0.009	0.001	152	9	0	136	5	2	2.100
10	14	0.904	2.551	2.780	0.039	.	.	149	17	4	123	1	4	2.900
11	28	0.848	2.400	2.630	0.030	0.010	0.001	940	71	12	647	194	16	27.400
12	28	0.861	2.388	2.610	0.045	0.010	0.001	224	15	10	186	3	10	5.500
13	28	0.842	2.382	2.540	0.095	0.008	0.001	162	5	1	148	1	7	4.500
14	28	0.821	2.291	2.480	0.042	0.010	0.001	322	2	13	292	6	9	8.200
15	28	0.865	2.463	2.660	0.030	0.031	0.001	292	17	8	203	62	2	7.800
16	56	0.819	2.301	2.450	0.022	0.006	0.000	458	58	27	356	4	13	30.700
17	56	0.886	2.566	2.740	0.036	0.024	0.001	447	62	36	335	3	11	25.300
18	56	0.790	2.249	2.400	0.020	0.024	0.001	685	110	25	534	8	8	33.700
19	56	.	.	.	.	.	.	.	.	.	.	.	.	.
20	56	0.804	2.267	2.430	0.027	0.025	0.001	888	117	21	705	20	25	46.300
21	75	0.720	2.037	2.200	0.021	0.025	0.001	412	95	0	303	3	11	43.900
22	75	0.801	2.296	2.430	0.027	0.026	0.001	849	76	0	751	4	15	21.700
23	75	0.264	0.743	0.860	0.021	.	.	275	32	0	199	28	15	24.100
24	75	.	.	.	.	.	.	.	.	.	.	.	.	.
25	75	.	.	.	.	.	.	.	.	.	.	.	.	.

Fagus grandifolia

REP	DAY	SHRmg	NONmg	CHIR	CHEL	PERI	PROS	SIMU	OREO	UDIP	BAET	EPHE	CINY	EPEO	UHEP
1	2	0.500	0.800	1			20				5				
2	2	1.400	0.200	7							1				1
3	2	0.400	0.700	1			35				4				
4	2	0.300	0.500	12			13				1				
5	2	0.300	0.600	4			5								
6	14	1.600	3.900	166			93				46				3
7	14	1.600	1.900	59			54				30				1
8	14	8.300	7.200	534	1	1	31				52				5
9	14	0.400	1.700	132			5				3			1	
10	14	0.900	2.000	120				1			2		4	1	
11	28	14.400	13.000	510	1		194				131		12	6	
12	28	3.000	2.500	166			3				20		10		
13	28	1.600	2.900	142									1	5	
14	28	5.300	2.900	281			6				3		13	8	
15	28	3.800	4.000	174			61	1			27		8	2	
16	56	24.600	6.100	337			4				8		27	11	
17	56	18.700	6.600	312	1		3				12		36	11	
18	56	25.700	8.000	479	1		8				42		25	13	
19	56	.	.												
20	56	24.500	21.800	644	2		19				52		21	9	
21	75	39.600	4.300	221	1		3				33				49
22	75	14.700	7.000	689	5		4				26				36
23	75	13.500	10.600	166	3		28				30				3
24	75	.	.												
25	75	.	.												

Fagus grandifolia

REP	DAY	AMEL	CAPN	CHLO	ZAPA	PERL	TAEN	CHYR	ECCL	HYDA	ONOC	ULIM	RHYA	HYDR	OLIG
1	2				1										
2	2		3		1					1					
3	2		1												
4	2		4												
5	2	1	3		1										
6	14		5	1	15	2					1		1		+
7	14				10	5							1		
8	14		28	4	23	1					3		1		+
9	14		6	2	3										
10	14		13	4	4										
11	28		9	3	53	4	7		2				8		
12	28		2	6	11	2	2						1	1	
13	28	1	2	6	2				1				1		
14	28		2	8									1		+
15	28		3		12		2						1	1	
16	56		8	9	49				1				1	3	
17	56		13	8	45		2		1		1		2		+
18	56		28	4	77		3	1			1		1	2	
19	56														
20	56		25	6	87			1	1		3		13	4	+
21	75		23	7	71	2					1		1		
22	75		24	5	49						3		5	3	+
23	75				27	6					5		6	1	
24	75														
25	75														

Alnus rugosa

REP	DAY	AFDM%	AFDM_g	DM_g	TANN%	NITR%	PHOS	TOTAL#	SHR#	SCR#	C-G#	C-FF#	PRED#	TOTmg
1	2	0.798	2.342	2.440	0.027	0.030	0.001	19	2	0	3	14	0	1.700
2	2	0.778	2.371	2.470	0.034	0.029	0.001	15	4	0	8	0	3	16.700
3	2	0.790	2.243	2.340	0.046	0.020	0.001	45	3	0	6	36	0	1.800
4	2	0.805	2.331	2.440	0.032	0.030	0.001	115	9	0	17	89	0	3.800
5	2	0.839	2.454	2.540	0.046	0.024	0.001	16	2	0	9	5	0	1.200
6	14	0.792	2.272	2.440	0.032	0.022	0.001	126	12	0	81	30	3	6.400
7	14	0.782	2.267	2.450	0.013	0.026	0.001	107	7	0	74	26	0	2.100
8	14	0.809	2.350	2.570	0.026	0.022	0.001	463	52	0	368	28	14	22.500
9	14	0.787	2.341	2.490	0.027	0.023	0.001	99	5	1	84	8	1	1.200
10	14	0.767	2.177	2.280	0.023	.	.	175	20	1	146	2	5	9.200
11	28	0.616	1.831	1.960	0.010	0.024	0.001	330	91	6	213	14	6	45.400
12	28	0.713	2.031	2.230	0.020	0.023	0.001	430	78	19	321	8	4	33.000
13	28	0.732	2.157	2.250	0.024	0.026	0.001	273	23	2	246	0	2	22.400
14	28	0.651	1.893	2.050	0.013	0.026	0.001	447	97	16	328	1	5	33.500
15	28	0.661	1.896	2.020	0.014	0.023	0.001	324	36	4	276	7	1	8.500
16	56	0.106	0.309	0.330	.	.	.	160	34	0	120	6	0	13.600
17	56	0.066	0.189	0.200	.	.	.	127	27	0	94	2	4	4.500
18	56	0.063	0.181	0.190	.	.	.	117	19	0	92	1	5	9.400
19	56	.	.	.	.	.	.	.	.	.	.	.	.	.
20	56	0.074	0.220	0.240	.	.	.	185	31	3	145	2	4	14.300
21	75	0.000	0.001	0.001	.	.	.	41	9	0	29	2	1	7.100
22	75	0.010	0.030	0.030	.	.	.	162	14	0	134	9	5	5.600
23	75	0.010	0.030	0.030	.	.	.	31	5	0	17	8	1	6.700
24	75	.	.	.	.	.	.	.	.	.	.	.	.	.
25	75	.	.	.	.	.	.	.	.	.	.	.	.	.

Alnus rugosa

REP	DAY	SHRmg	NONmg	CHIR	CHEL	PERI	PROS	SIMU	OREO	UDIP	BAET	EPHE	CINY	EPEO	UHEP
1	2	1.000	0.700	3			14								
2	2	15.400	1.300	7											
3	2	0.800	1.000	4			36				2				
4	2	2.000	1.800	12			89				5				
5	2	0.500	0.700	5			5				3				1
6	14	2.800	3.600	64			30				16				1
7	14	1.000	1.100	59			26				15				
8	14	16.400	6.100	318	3		28			1	50				
9	14	0.500	0.700	84			8						1		
10	14	7.400	1.800	140	1		2				5		1	1	
11	28	39.700	5.700	167	1		14				46		6		
12	28	25.000	8.000	289			8				19		19	12	
13	28	21.100	1.300	244									2	2	
14	28	31.500	2.000	327				1					16	1	
15	28	7.300	1.200	267			2	5			6		4	3	
16	56	12.200	1.400	115			6				5				
17	56	3.000	1.500	88			2				6				
18	56	4.300	5.100	75			1				17				
19	56	.	.												
20	56	13.100	1.200	131	2		2				14		3		
21	75	6.400	0.700	28	1		2				1				
22	75	3.400	2.200	116	3		9				18				
23	75	2.500	4.200	12			8				5				
24	75	.	.												
25	75	.	.												

Alnus rugosa

REP	DAY	AMEL	CAPN	CHLO	ZAPA	PERL	TAEN	CHYR	ECCL	HYDA	ONOC	ULIM	RHYA	HYDR	OLIG
1	2				2										
2	2	1	1	3	2					1					
3	2		2						1						
4	2				9										
5	2				2										
6	14			1	12	1							1		
7	14		1		5						1				
8	14		6	4	41	2					5		5		
9	14			1	5										
10	14		3	4	14				2		1			1	+
11	28		1		86	1					4		3	1	
12	28	1	18	1	53	2	5		2					1	
13	28		5	2	14				2		2				
14	28		14	1	79	3			3		1		1		
15	28		3		33								1		
16	56				32						2				
17	56		2	1	24				1				2	1	
18	56			1	15				1		3		4		
19	56														
20	56		1		21				3		6		1	1	+
21	75				6						3				+
22	75		1		11						2		2		
23	75		2		2						1		1		
24	75														
25	75														

Quercus rubra

REP	DAY	AFDM%	AFDM_g	DM_g	TANN%	NITR%	PHOS%	TOTAL	SHR#	SCR#	C-G#	C-FF#	PRED#	TOTmg
1	2	0.974	2.763	2.890	0.035	0.021	0.001	26	1	0	3	22	0	1.300
2	2	0.972	2.839	2.970	0.031	0.021	0.001	9	3	0	3	2	1	2.000
3	2	0.973	2.750	2.880	0.058	0.012	0.001	64	0	0	9	55	0	0.900
4	2	0.969	2.860	3.000	0.028	0.013	0.001	65	2	0	6	56	1	2.100
5	2	0.981	2.793	2.910	0.055	0.033	0.002	6	3	0	2	1	0	0.900
6	14	0.911	2.663	2.790	0.024	0.033	0.002	157	19	0	77	59	2	2.100
7	14	0.914	2.592	2.750	0.028	0.032	0.002	113	8	0	53	51	1	6.300
8	14	0.917	2.664	2.830	0.043	0.029	0.002	254	20	0	227	4	3	6.400
9	14	0.920	2.645	2.780	0.032	0.030	0.000	91	19	2	50	20	0	1.800
10	14	0.924	2.628	2.790	0.026	.	.	287	49	4	215	18	1	15.600
11	28	0.849	2.474	2.640	0.016	0.031	0.001	121	12	1	82	24	2	6.900
12	28	0.856	2.470	2.620	0.022	0.029	0.001	101	10	0	71	19	1	4.800
13	28	0.873	2.536	2.660	0.026	0.032	0.001	94	5	2	85	1	1	2.600
14	28	0.836	2.362	2.540	0.012	0.032	0.001	.	.	.	.	.	.	.
15	28	0.843	2.408	2.540	0.021	.	.	347	25	0	243	73	6	18.800
16	56	0.740	2.121	2.280	0.013	0.027	0.001	321	91	4	213	3	10	37.300
17	56	0.653	1.922	2.070	0.010	0.032	0.001	430	93	3	326	1	7	55.000
18	56	0.739	2.152	2.300	0.008	0.030	0.001	291	63	3	219	4	2	40.100
19	56	.	.	.	.	.	.	.	.	.	.	.	.	.
20	56	0.724	2.082	2.280	0.006	0.026	0.001	371	58	16	286	0	11	21.100
21	75	0.677	1.971	2.120	0.008	0.028	0.001	155	34	0	114	3	3	34.400
22	75	.	.	.	.	.	.	.	.	.	.	.	.	.
23	75	0.669	1.956	2.090	0.013	.	.	317	39	0	208	63	6	49.300
24	75	.	.	.	.	.	.	.	.	.	.	.	.	.
25	75	.	.	.	.	.	.	.	.	.	.	.	.	.

Quercus rubra

REP	DAY	SHRmg	NONmg	CHIR	CHEL	PERI	PROS	SIMU	OREO	UDIP	BAET	EPHE	CINY	EPEO	UHEP
1	2	0.400	0.900	1			22				2				
2	2	1.400	0.600	3			2								
3	2	0.000	0.900	7			55				2				
4	2	0.700	1.400	2			56				4				
5	2	0.900	0.000	2			1								
6	14	0.600	1.500	55			59		1		22				
7	14	1.900	4.400	35			51				17				1
8	14	2.800	3.600	220			4				5				2
9	14	0.800	1.000	44			20				6		2		
10	14	12.600	3.000	203			18				12		4		
11	28	2.300	4.600	70			24				12		1		
12	28	1.000	3.800	66			19				5				
13	28	1.300	1.300	85			1						2		
14	28	.	.												
15	28	9.900	8.900	196			73				45			2	
16	56	34.700	2.600	209	3		3				4		4		
17	56	52.400	2.600	305	1		1				19		3	2	
18	56	36.300	3.800	185	1		4				34		3		
19	56	.	.												
20	56	18.600	2.500	283	5						3		16		
21	75	33.300	1.100	100	2		3				14				
22	75	.	.												
23	75	41.900	7.400	177			63				28				3
24	75	.	.												
25	75	.	.												

Quercus rubra

REP	DAY	AMEL	CAPN	CHLO	ZAPA	PERL	TAEN	CHYR	ECCL	HYDA	ONOC	ULIM	RHYA	HYDR	OLIG
1	2				1										
2	2		2	1	1										
3	2														
4	2				2	1									
5	2		1		2										
6	14		2		16	1					1				
7	14				8								1		
8	14		9	2	8						3		1		+
9	14		2		16				1						
10	14		14	1	28		1		2		4				
11	28				12								2		
12	28				10								1		
13	28			1	5										
14	28														
15	28			1	24		1						4	1	
16	56		15		71				3		2		2	5	
17	56		5	2	77				9		2		3	1	
18	56		3		54				2		4		1		
19	56														
20	56		10		48								1	5	
21	75		1		21	1			6		6			1	
22	75														
23	75				31			1	5		2		5	2	+
24	75														
25	75														

Alnus crispa

REP	DAY	AFDM%	AFDM_g	DM_g	TANN%	NITR%	PHOS%	TOTAL	SHR#	SCR#	C-G#	C-FF#	PRED#	TOTmg
1	2	0.788	2.204	2.360	0.014	0.025	0.001	57	4	0	11	41	1	1.700
2	2	0.805	2.214	2.370	0.014	0.024	0.001	12	5	0	0	7	0	1.200
3	2	0.832	2.288	2.470	0.020	0.026	0.001	22	3	0	11	8	0	2.000
4	2	0.801	2.196	2.350	.	0.014	0.001	4	1	0	3	0	0	0.400
5	2	0.815	2.221	2.360	0.024	0.014	0.001	9	4	0	1	4	0	0.100
6	14	0.715	2.000	2.200	0.022	0.028	0.001	129	16	0	106	2	5	9.000
7	14	0.682	1.870	2.060	0.026	0.030	0.001	389	58	0	285	41	5	23.900
8	14	0.721	1.983	2.180	0.070	0.029	0.001	290	20	0	255	6	8	8.300
9	14	0.752	2.082	2.270	0.023	0.031	0.001	130	7	0	121	2	0	3.500
10	14	0.727	2.046	2.300	0.015	.	.	315	22	0	287	3	3	8.500
11	28	0.555	1.516	1.700	0.004	0.029	0.001	402	88	0	228	81	5	54.700
12	28	0.620	1.716	1.920	0.007	0.027	0.001	503	66	7	417	3	10	26.000
13	28	0.635	1.772	1.960	0.022	0.029	0.001	189	56	3	121	5	4	28.700
14	28	0.649	1.780	2.010	0.007	0.026	0.002	143	21	5	115	1	1	7.100
15	28	0.510	1.422	1.610	0.008	0.024	0.001	346	52	3	288	0	3	25.600
16	56	0.036	0.100	0.100	.	.	.	392	63	1	298	14	16	29.900
17	56	0.092	0.257	0.310	.	.	.	184	62	0	99	19	4	36.400
18	56	0.029	0.080	0.080	.	.	.	78	24	0	37	9	8	6.400
19	56	0.175	0.477	0.590	.	.	.	308	84	0	221	1	2	53.400
20	56	0.093	0.256	0.310	.	.	.	147	62	0	79	4	2	32.400
21	75	0.001	0.003	0.010	.	.	.	61	6	0	54	0	1	5.000
22	75	0.011	0.030	0.030	.	.	.	80	9	0	68	0	2	1.700
23	75	.	.	.	.	.	.	.	.	.	.	.	.	.
24	75	0.011	0.030	0.030	.	.	.	59	6	0	43	2	8	2.200
25	75	0.004	0.010	0.010	.	.	.	197	20	0	131	43	3	20.800

Alnus crispa

REP	DAY	SHRmg	NONmg	CHIR	CHEL	PERI	PROS	SIMU	OREO	UDIP	BAET	EPHE	CINY	EPEO	UHEP
1	2	0.700	1.000	10			41				1				
2	2	1.000	0.200				7								
3	2	2.000	0.000	7			8				4				
4	2	0.000	0.400	3											
5	2	0.100	0.000				4								1
6	14	4.300	4.700	101			2				3				2
7	14	20.400	3.500	201			41				82				2
8	14	5.500	2.800	236	2		6				12				6
9	14	1.000	2.500	120			2								
10	14	6.400	2.100	274			3				12			1	
11	28	47.400	7.300	189			81				38			1	
12	28	23.700	2.300	395	1		3				2		7	19	
13	28	26.700	2.000	112			5				5		3	3	
14	28	2.500	4.600	102				1			10		5	3	
15	28	21.600	4.000	271	1						6		3	11	
16	56	22.700	7.200	289	4		14				9		1		
17	56	31.300	5.100	82			19				17				
18	56	4.800	1.600	26	3		9				10			1	
19	56	48.600	4.800	215			1				2			4	
20	56	25.400	7.000	73			4				6				
21	75	4.100	0.900	52							1				1
22	75	0.800	0.900	67	2						1				
23	75	.	.												
24	75	1.400	0.800	38	7		2				5				
25	75	15.400	5.400	97	2		43				34				

Alnus crispa

REP	DAY	AMEL	CAPN	CHLO	ZAPA	PERL	TAEN	CHYR	ECCL	HYDA	ONOC	ULIM	RHYA	HYDR	OLIG
1	2		2	1	2										
2	2		1		3							1			
3	2				2							1			
4	2				1										
5	2		3		1										
6	14		3	2	10				3				3		+
7	14		7		41	3					10		2		
8	14	1	6	3	13	1					1		1	2	+
9	14	1	6		1										
10	14		9	3	11				1		1				
11	28				86				1		1		2	3	+
12	28	1	7	2	55				2		2		6	1	
13	28	1	5	4	51										
14	28		7	1	14										
15	28		6	1	43				3				1		
16	56			3	58				4		1		7	2	
17	56		1	3	54				6		1		1		
18	56		1	1	22						1		3	1	
19	56		2		76				5		1		2		
20	56				61	1						1	1		
21	75				5				1					1	
22	75				9									1	
23	75														
24	75				5						1		1		+
25	75				13				2		5		1		

Salix alaxensis (winter-picked leaves)

REP	DAY	AFDM%	AFDM_	DM_g	TANN%	NITR%	PHOS	TOTAL#	SHR#	SCR#	C-G#	C-FF#	PRED#	TOTmg	SHRm
1	2	0.830	2.157	2.370	0.033	0.011	0.001	35	6	0	9	20	0	3.300	2.100
2	2	0.816	2.120	2.330	0.018	0.010	0.001	20	5	0	12	3	0	1.100	0.500
3	2	0.763	2.002	2.220	0.042	0.023	0.001	66	15	0	20	30	1	7.500	6.100
4	2	0.795	2.059	2.270	0.034	0.027	0.001	18	3	0	10	4	1	1.800	0.700
5	2	0.861	2.275	2.470	0.035	0.018	0.000	35	6	0	17	11	1	1.700	1.000
6	14	0.830	2.172	2.550	0.030	0.024	0.001	347	71	0	259	15	1	9.500	7.200
7	14	0.771	2.011	2.320	0.021	0.024	0.001	522	62	0	391	59	9	21.500	15.000
8	14	0.807	2.091	2.390	0.025	0.021	0.001	354	52	0	294	3	5	20.800	15.800
9	14	0.810	2.105	2.440	0.028	0.017	0.001	103	8	1	92	1	1	4.200	2.800
10	14	0.813	2.177	2.460	0.022	.	.	333	41	0	265	22	5	12.800	9.600
11	28	0.780	2.034	2.280	0.015	0.029	0.001	551	84	5	356	93	13	34.400	20.400
12	28	0.704	1.854	2.260	0.010	0.022	0.001	911	85	15	801	5	5	38.800	31.100
13	28	0.697	1.818	2.170	0.020	0.022	0.001	406	77	5	307	11	6	38.500	33.400
14	28	0.750	1.949	2.290	0.010	0.022	0.001	313	51	6	236	12	8	14.700	9.700
15	28	0.648	1.686	2.200	0.021	0.025	0.001	672	99	5	547	13	6	39.200	35.300
16	56	0.377	0.977	1.380	0.006	0.018	0.000	549	82	3	454	2	8	48.700	41.800
17	56	0.250	0.655	0.970	0.011	0.025	0.001	233	47	0	181	2	3	12.800	9.100
18	56	0.347	0.898	1.130	.	.	.	599	114	0	472	2	11	63.900	55.900
19	56	0.252	0.656	0.960	0.005	0.011	0.001	365	50	1	305	3	6	24.400	17.200
20	56	0.384	1.011	0.650	0.007	0.010	0.001	495	126	2	327	26	14	35.500	27.700
21	75	0.230	0.603	0.780	0.006	0.012	0.000	233	37	0	193	0	3	7.800	5.100
22	75	0.174	0.460	0.550	.	.	.	298	35	0	252	6	5	13.700	7.300
23	75	.	.	.	.	.	.	.	.	.	.	.	.	.	.
24	75	0.046	0.123	0.190	.	.	.	144	16	0	121	2	5	11.100	10.000
25	75	0.036	0.092	0.100	.	.	.	217	23	0	162	27	5	23.000	15.800

Salix alaxensis (winter-picked leaves)

REP	DAY	NONmg	CHIR	CHEL	PERI	PROS	SIMU	OREO	UDIP	BAET	EPHE	CINY	EPEO	UHEP	AMEL	CAPN
1	2	1.200	8			20				1						
2	2	0.600	10			3				1	1					4
3	2	1.400	19			30				1						3
4	2	1.100	7			4				3						
5	2	0.700	13	1		11				4						2
6	14	2.300	234	1		15				18				7		15
7	14	6.500	358	4		59				27				5	1	5
8	14	5.000	282	1		3				7				5		12
9	14	1.400	92			1						1				3
10	14	3.200	249			22				14			2			6
11	28	14.000	317	4		93				39		5				2
12	28	7.700	783	2		5				1		15	13		4	15
13	28	5.100	297	1		10	1			5		5	5			6
14	28	5.000	220	3		11	1			15		6	1			3
15	28	3.900	526	3		13			2	12		5	8		1	8
16	56	6.900	443	6	2	2				7		3	2			8
17	56	3.700	174	2		2				7						1
18	56	8.000	467	7		2				3			2			10
19	56	7.200	289	4		2	1			16		1				4
20	56	7.800	282	6	1	22	4			42		2	2			
21	75	2.700	186	2						7						7
22	75	6.400	250	1		6				2						3
23	75	.														
24	75	1.100	116	3		2				5						
25	75	7.200	150	2		27				12						

Salix alaxensis (winter-picked leaves)

REP	DAY	CHLO	ZAPA	PERL	TAEN	CHYR	ECCL	HYDA	ONOC	ULIM	RHYA	HYDR	OLIG
1	2		6										
2	2		1										
3	2	1	11							1			
4	2	1	3										
5	2		3							1			
6	14		55				1		1				+
7	14	2	49	1					8		2	1	+
8	14	3	36				3		1		1		
9	14		5								1		
10	14	2	33		1		1				2	1	
11	28	1	81				1				8		
12	28	2	65				5				1		
13	28	1	70			1					3	1	
14	28		47	3			1				2		
15	28	3	90				1						
16	56	1	64				4		6		1		
17	56		46								1		
18	56		98			1	4		1		3	1	
19	56		44				1		1		2		
20	56		123	5			3				2	1	
21	75		25			1	3		1		1		
22	75		27				2		3		3	1	+
23	75												
24	75		15	1					1		1		
25	75		19				1		3		2	1	

Ledum goenlandicum

REP	DAY	AFDM%	AFDM_g	DM_g	TANN%	NITR%	PHOS	SHR#	SHRmg	Capn	Nemo	Taen	Limn
1	2	0.91207	2.6588	2.77	0.1926	0.0175	0.0012	4	2	2	2		
2	2	0.904892	2.62041	2.73	0.2001	0.0167	0.0011	2	0.9	1	1		
3	2	0.935354	2.71765	2.8	0.1987	0.0323	0.001	7	0.2	4	3		
4	2	0.926861	2.69297	2.82	0.1875	0.0302	0.0014	6	5.2	1	3		2
5	2	0.896405	2.60448	2.73	0.166	0.0172	0.001	4	0.9	3	1		
6	14	0.784291	2.27874	3.28	0.1402	0.0255	0.0011	48	3	3	45		
7	14	0.830566	2.40517	2.79	0.1525	0.027	0.0011	35	7.5	14	19		2
8	14	0.838933	2.4375	3	0.1608	0.0292	0.0012	53	9.6	22	28		3
9	14	0.900574	2.6166	2.86	0.1235	0.0262	0.0013	15	4.2	9	4		2
10	14	0.862033	2.50462	2.96	0.1144	.	.	50	13.4	20	26		4
11	28	0.824633	2.40391	3.31	0.09	0.0349	0.0013	50	16.3	3	46		1
12	28	0.819673	2.38154	3.12	0.0792	0.0309	0.0012	83	11	14	62	4	3
13	28	0.64279	1.87381	2.56	0.083	0.0315	0.0012	18	3.3	5	13		
14	28	0.816002	2.37875	3.46	0.119	0.0495	0.002	88	12.9	5	81		2
15	28	0.768027	2.22407	2.71	0.1229	0.0309	0.0012	60	5.4	21	39		
16	56	0.723876	2.1032	2.49	0.0449	0.0101	0.0006	.	.				
17	56	0.724189	2.10411	3.37	0.0535	0.0464	0.0013	130	26.1		129		1
18	56	0.507463	1.47442	2.03	0.0416	0.0365	0	55	7	1	51		3
19	56	0.653738	1.89311	2.56	0.0517	0.0191	0.001	95	22.4	6	87		2
20	56	0.738784	2.14652	2.85	.	0.0164	0.0007	.	.				
21	75	0.615275	1.78173	2.34	0.0373	0.0156	0.0007	72	42	10	53		9
22	75	0.679386	1.97394	2.49	0.0364	0.0187	0.001	87	10.9	8	75		4
23	75	.	.	.	.	.	.	.	.				
24	75	0.612511	1.78555	2.27	0.0455	0.0142	0.001	157	52.2	17	129		11
25	75	0.699859	2.02667	2.66	0.051	.	.	119	13	7	107		5

Salix pulcra

REP	DAY	AFDM%	AFDM_g	DM_g	TANN%	NITR%	PHOS%	SHR#	SHRmg	Capn	Nemo	Taen	Limn
1	2	0.65864	1.88365	1.94	0.2578	0.0272	0.00138	5	1.6		5		
2	2	0.70171	2.00016	2.06	0.2627	0.0275	0.00131	3	11.4	1	2		
3	2	0.69468	1.99333	2.07	0.2911	0.0067	0.00034	2	1.7		2		
4	2	0.69123	1.97029	2.03	0.2489	0.0204	0.00115	3	2.3		3		
5	2	0.71119	2.02717	2.07	0.2649	0.0204	0.00143	3	0		3		
6	14	0.64071	1.82629	1.88	0.1305	0.0212	0.00141	118	.	12	101		5
7	14	0.6306	1.79748	1.86	0.1349	0.0216	0.00167	55	.	7	45		3
8	14	0.63442	1.8144	1.89	0.1344	0.0247	0.00127	93	.	4	88		1
9	14	0.6253	1.78829	1.88	0.1512	0.024	0.0012	34	8.2	8	23		3
10	14	0.63954	1.82903	1.89	0.1543	.	.	31	8.7	4	24	1	2
11	28	0.56988	1.61356	1.7	0.0475	0.0215	0.00123	50	.	1	45	1	3
12	28	0.61257	1.74025	1.85	0.0608	0.0261	0.00134	57	26	5	47		5
13	28	0.60019	1.7222	1.79	0.0396	0.026	0.00104	54	21.3	13	39		2
14	28	0.6062	1.73368	1.83	0.0932	0.0248	0.00141	25	14.3	6	16		3
15	28	0.57557	1.65154	1.71	0.0733	0.0452	0.00106	52	22.4	7	44		1
16	56	0.25371	0.72558	0.78	0.0232	0.0262	0.00108	96	60.9	12	72		12
17	56	0.2904	0.825	0.87	0.0396	0.023	0.00065	125	116.2	11	76		38
18	56	0.3042	0.87	0.87	0.0364	0.027	0.0015	115	34.5	3	105	1	6
19	56	.	0.405	0.45	.	.	.	98	77.4	4	81		13
20	56	0.28184	0.80069	0.86	0.0302	0.031	0.00144	153	52.9	17	122		14
21	75	.	.	.	.	.	.	.	.				
22	75	0.19266	0.54915	0.6	.	.	.	148	36.5	25	105		18
23	75	.	.	.	.	.	.	.	.				
24	75	0.2569	0.73961	0.82	0	0.0302	0.00137	101	41.1	26	52		23
25	75	.	0.02	0.02	.	.	.	22	5.2		22		

Shepherdia canadensis

REP	DAY	AFDM%	AFDM_	DM_g	TANN%	NITR%	PHOS%	SHR#	SHRm	Capn	Nemo	Taen	Limn
1	2	0.72287	2.0432	2.17	0.1212	0.0218	0.0007	7	5.2	2	5		
2	2	0.76382	2.13736	2.27	0.0844	0.0204	0.0005	4	2.8	2	2		
3	2	0.76236	2.162	2.3	0.1008	0.029	0.0014	4	0.1		4		
4	2	0.72393	2.06667	2.2	0.1053	0.0146	0.0012	6	0.8	1	4		1
5	2	0.71475	2.01352	2.13	0.1026	0.0096	0.0007	4	0.7	2	1		1
6	14	0.66648	1.87754	2.16	0.0777	0.0122	0.0007	41	9.2	3	37		1
7	14	0.67262	1.93286	2.31	0.0467	0.0093	0.0007	48	6.5	1	47		
8	14	0.67997	1.93475	2.13	0.0728	0.0136	0.0009	76	14.2	13	49		14
9	14	0.68566	1.96388	2.39	0.0533	0.0131	0.0007	77	12.9	3	73		1
10	14	0.6187	1.74292	1.95	0.0575	.	.	25	12.2	10	11		4
11	28	0.58082	1.64716	1.91	0.0293	0.0107	0.0007	73	31.9	1	71		1
12	28	0.59002	1.67325	2.07	0.0265	0.0085	0.0007	88	29.5	3	84	1	
13	28	0.62472	1.76577	2	0.0452	0.0113	0.0007	30	16	6	22	2	
14	28	0.63301	1.79516	2.1	0.0349	0.0098	0.0006	59	9.3	5	54		
15	28	0.6377	1.79646	2.03	0.0435	0.0112	0.0006	37	9.6	7	29		1
16	56	0.27957	0.80074	1.21	0.0101	0.024	0.0009	109	49.3	1	98		10
17	56	0.35811	1.01895	1.21	0.0092	0.0111	0.0005	135	43.2	4	126		5
18	56	0.40102	1.13727	1.39	0.0068	.	.	126	26.6	4	121		1
19	56	.	.	.	.	.	.	.	.				
20	56	.	.	.	.	.	.	81	31.7	1	74		6
21	75	0.22865	0.64843	1.17	0.0052	0.0185	0.0002	104	21.9	2	97		5
22	75	0.22341	0.63568	0.98	0.009	0.023	0.0011	66	20	1	60		5
23	75	0.29266	0.83824	1	0.0154	.	.	55	8.7	2	51		2
24	75	.	.	.	.	.	.	.	.				
25	75	.	.	.	.	.	.	.	.				

Alnus crispa (autumn-picked leaves)

REP	DAY	AFDM%	AFDM_g	DM_g	TANN%	NITR%	PHOS	SHR#	SHRmg	Capn	Nemo	Taen	Limn
1	2	0.85477	2.20838	2.460	0.0021	0.0152	0.0001	0	0				
2	2	0.87745	2.29815	2.560	0.0103	0.0157	0.0002	2	0.6	2			
3	2	0.86648	2.23865	2.510	0.015	0.0297	0.0011	3	0.8	1	2		
4	2	0.86665	2.34681	2.610	0.0061	0.0304	0.0015	1	0.5		1		
5	2	0.864	2.25524	2.500	0.0052	0.0286	0.0009	1	0.7		1		
6	14	0.84673	2.33046	2.670	0.0019	0.0304	0.0009	30	4	10	18		2
7	14	0.83583	2.1743	2.470	0.0075	0.0263	0.001	10	7.6		9		1
8	14	0.85214	2.27727	2.660	0.0057	0.028	0.0009	14	1.5	2	12		
9	14	0.84796	2.32632	2.600	0.0024	0.0295	0.0008	5	0.9	4	1		
10	14	0.83977	2.31875	2.650	0.0068	.	.	16	3.1	3	12	1	
11	28	0.87313	2.34109	2.670	0.0029	0.0278	0.0009	7	31	1	6		
12	28	0.81258	2.13545	2.610	0.0048	0.029	0.0007	37	9.2	9	27	1	
13	28	0.80405	2.19156	2.500	0.0039	0.0343	0.0009	40	18.5	1	34		5
14	28	0.76504	2.08525	2.400	0.0034	0.0325	0.0009	23	8.3	7	16		
15	28	0.69809	1.79741	2.110	0.0052	0.0308	0.0014	28	12.1		28		
16	56	0.49115	1.28639	1.720	0.0038	0.0329	0.0009	101	19.9	7	88		6
17	56	0.63467	1.71864	1.990	0.0043	0.0073	0.0001	77	13.6	7	65		5
18	56	0.53407	1.4557	1.770	0.0048	0.0182	0.0002	60	24.5	8	49		3
19	56	0.65436	1.77195	2.030	0.0058	0.0179	0.0001	79	38.5	7	65		7
20	56	.	0.88516	1.030	0.0039	0.018	0.0004	76	32.5	7	64		5
21	75	.	.	.	.	.	.	.	.				
22	75	0.18207	0.46878	0.620	0.0047	0.0042	0.0002	46	13.7	3	40		3
23	75	.	.	.	.	.	.	.	.				
24	75	0.39156	1.07769	1.630	0.0043	0.0165	0.0003	88	26.5	26	46		16
25	75	0.01544	0.04167	0.050	.	.	.	9	3.2		8		1

Salix alaxensis (unbrowsed)

REP	DAY	AFDM%	AFDM_g	DM_g	TANN%	NITR%	PHOS%	SHR#	SHRmg	Capn	Nemo	Taen	Limn
1	2	0.68566	1.886	2.04	0.1249	0.0134	0.0014	3	0.8		3		
2	2	0.69797	1.89525	2.05	0.1387	0.0129	0.0014	4	2	2	2		
3	2	0.71156	1.91333	2.05	0.1989	0.0111	0.001	3	1.4		3		
4	2	0.65966	1.84357	2.03	0.0837	0.0114	0.0012	7	2.9	1	6		
5	2	0.72768	1.97592	2.12	0.2224	0.0097	0.001	8	2.9	2	6		
6	14	0.6806	1.82409	1.98	0.0401	0.0122	0.001	20	2.1	3	16		1
7	14	0.5875	1.6419	1.78	0.0784	0.0111	0.001	10	1.9	1	8		1
8	14	0.65727	1.76157	2.03	0.0687	0.0109	0.001	18	7.3	2	16		
9	14	0.6697	1.84211	2	0.0537	0.0115	0.0011	9	3.4		9		
10	14	0.66023	1.83935	2.02	0.071	0.01	0.0008	14	6.1	1	11		2
11	28	0.55054	1.45125	1.62	0.0212	0.013	0.0011	63	30.9		55	1	7
12	28	0.62584	1.64974	1.86	0.0259	0.0131	0.0012	38	19.2		38		
13	28	0.63324	1.66924	1.91	0.0401	0.0122	0.001	24	20.1	3	15	1	5
14	28	.	1.01864	1.72	0.0178	0.0136	0.0011	49	23.1	1	46		2
15	28	0.56583	1.52647	1.73	0.0283	0.0133	0.0011	51	15.5	1	48		2
16	56	0.44347	1.20419	1.33	0.013	0.013	0.001	108	20.1	4	100	3	1
17	56	0.27498	0.74182	1.2	0.0085	0.0088	0.0008	50	14.2	2	41		7
18	56	0.33083	0.91	0.91	0.0057	0.0112	0.0009	53	17.4	1	48		4
19	56	.	.	.	.	.	.	.	.				
20	56	0.34302	0.9405	0.99	0.0164	0.0127	0.0009	.	.				
21	75	0.13921	0.36818	0.54	.	.	.	53	21.5		46		7
22	75	0.18221	0.48673	0.53	.	.	.	54	21.9	2	44		8
23	75	0.05025	0.136	0.17	.	.	.	17	10.9		14		3
24	75	.	.	.	.	.	.	.	.				
25	75	.	.	.	.	.	.	.	.				

Salix alaxensis (browsed)

REP	DAY	AFDM%	AFDM_	DM_g	TANN	NITR%	PHOS	SHR#	SHRmg	Capn	Nemo	Taen	Limn
1	2	0.66031	1.79702	1.89	0.1816	0.0098	0.0005	4	1	3	1		
2	2	0.6323	1.74948	1.84	0.18	0.0102	0.0006	3	1.1		3		
3	2	0.65278	1.84167	1.95	0.243	0.0081	0.0007	0	0				
4	2	0.67799	1.89433	1.99	0.0893	0.0116	0.0007	5	1.8	1	4		
5	2	0.72237	1.97901	2.07	0.1951	0.0104	0.0012	1	0.9		1		
6	14	0.6871	1.88238	2.09	0.0492	0.0105	0.0008	25	8.4	3	19		3
7	14	0.68088	1.853	2.18	0.0288	0.0116	0.0008	30	7.1	8	22		
8	14	0.70348	1.90812	2.13	0.0701	0.0096	0.0006	21	4.8	14	7		
9	14	0.67116	1.84479	2.01	0.0475	0.0101	0.0006	7	1.5	2	4		1
10	14	0.67123	1.86935	2.03	0.0472	0.0088	0.0007	34	10.8	5	24	1	4
11	28	0.59391	1.64864	1.84	0.014	0.0137	0.0008	41	22.9	3	37		1
12	28	0.59879	1.61872	1.77	0.0192	0.0102	0.0007	23	8.3	1	20		2
13	28	0.60037	1.62298	1.75	0.0152	0.015	0.0009	13	7.5		12		1
14	28	0.58451	1.58543	1.79	0.0135	0.0148	0.0009	21	8	2	18		1
15	28	0.65536	1.82515	2.4	0.0152	0.0095	0.0007	15	7.3	1	12		2
16	56	0.24378	0.66345	0.74	0.0053	0.0135	0.0008	72	46.2	2	66		4
17	56	0.27812	0.76447	0.83	0.0056	0.014	0.0009	76	26.6		73		3
18	56	0.28494	0.78581	0.84	0.0071	0.0127	0.0008	84	42.6		78		6
19	56	0.40567	1.10769	1.28	0.0211	0.0122	0.0007	63	27.3	2	56		5
20	56	0.36357	1.00924	1.19	0.0152	0.0114	0.0008	75	33	5	67	1	2
21	75	0.17017	0.46312	0.57	.	.	.	59	52.7	3	38		18
22	75	0.10726	0.29189	0.36	.	.	.	17	12.8	1	10		6
23	75	.	.	.	.	.	.	.	.				
24	75	0.05551	0.1536	0.24	.	.	.	11	3.6		11		
25	75	0.12791	0.35391	0.44	.	.	.	56	30.7	4	42		10

Betula papyrifera (unbrowsed)

REP	DAY	AFDM%	AFDM_	DM_g	TANN%	NITR%	PHOS%	SHR#	SHRmg	Capn	Nemo	Taen	Limn
1	2	0.87112	2.4948	2.620	0.2169	0.0084	0.0012	0	0				
2	2	0.85621	2.42814	2.550	0.1742	0.0082	0.0011	1	1.3		1		
3	2	0.87097	2.47812	2.600	0.2589	0.0084	0.0012	5	2.9		4		1
4	2	0.85594	2.47529	2.610	0.1846	0.009	0.0016	3	1.7		3		
5	2	0.87664	2.50244	2.620	0.2394	0.0075	0.0013	1	0.5	1			
6	14	0.79872	2.30236	2.420	0.1854	0.0093	0.0008	35	16.7	8	25		2
7	14	0.77618	2.19394	2.330	0.1569	0.0087	0.0008	15	10.4	1	12		2
8	14	0.78515	2.20465	2.370	0.0742	0.0084	0.0011	20	2.3	3	17		
9	14	0.78636	2.20071	2.370	0.0949	0.0095	0.0013	22	9.8	7	9		6
10	14	0.76805	2.1638	2.310	0.0894	0.0104	0.0013	34	3.3	8	26		
11	28	0.74257	2.12667	2.320	0.0259	0.0096	0.0009	58	23	4	53		1
12	28	0.71124	2.0303	2.230	0.0368	0.0092	0.0008	39	14.9	12	23		4
13	28	0.7223	2.08209	2.250	.	0.0106	0.0011	21	8.6	3	15		3
14	28	0.71895	2.03218	2.230	0.0491	0.0096	0.0009	24	12.6	7	16		1
15	28	0.69495	1.96433	2.140	.	0.0111	0.0009	52	25.9	5	45		2
16	56	0.2593	0.73778	0.830	0.0124	0.0112	0.0008	111	53.3	5	98		8
17	56	0.17465	0.48714	0.660	0.015	0.0119	0.0008	95	36.3	7	79		9
18	56	0.44056	1.23295	1.630	0.0095	0.0123	0.0008	51	12.6	7	43		1
19	56	0.33986	0.97017	1.080	0.0125	0.0125	0.0009	121	63.3	5	112		4
20	56	0.25981	0.7271	0.920	0.0092	0.0123	0.0009	116	35.2	12	100		4
21	75	.	.	.	.	.	.	.	.				
22	75	0.36326	1.0234	1.190	0.0135	0.0134	0.001	87	16.2	14	69		4
23	75	.	.	.	.	.	.	.	.				
24	75	0.24269	0.6973	0.860	0.0114	0.0133	0.0009	81	10.9	9	65		7
25	75	0.05328	0.15111	0.170	.	.	.	17	7.4		12		5

Betula papyrifera (browsed)

REP	DAY	AFDM%	AFDM_	DM_g	TANN%	NITR%	PHOS%	SHR#	SHRmg	Capn	Nemo	Taen	Limn
1	2	0.801	2.251	2.390	0.0887	0.0108	0.0013	5	1.4	1	4		
2	2	0.807	2.260	2.400	0.0273	0.0158	0.0013	3	0.9	1	2		
3	2	0.812	2.201	2.370	0.0368	0.0122	0.0017	0	0				
4	2	0.808	2.204	2.360	0.0312	0.013	0.0013	2	1		1		1
5	2	.	1.329	1.380	0.0378	0.0121	0.001	3	0.4		3		
6	14	0.768	2.166	2.390	0.0039	0.0151	0.0011	51	14.7	8	35		8
7	14	0.764	2.171	2.360	0.0121	0.0126	0.0007	32	9.4	9	20		3
8	14	0.767	2.156	2.380	0.0124	0.0148	0.0008	30	16.6	3	25		2
9	14	0.774	2.191	2.400	0.0183	0.0129	0.0011	15	8.1	4	11		
10	14	0.821	2.362	2.600	0.0125	0.0128	0.0012	38	6	5	33		
11	28	0.726	2.116	2.370	0.0101	0.011	0.001	42	17.7	7	35		
12	28	0.663	1.869	2.080	0.0159	0.0152	0.0011	69	27.8	12	51		6
13	28	0.647	1.806	2.010	0.0033	0.0143	0.001	66	29.1	4	60		2
14	28	0.662	1.818	2.020	0.0101	0.0142	0.0009	54	26.3	20	32		2
15	28	0.652	1.821	2.020	0.0063	0.0151	0.0012	76	33.8	9	65		2
16	56	0.094	0.259	0.290	.	.	.	47	15.1	1	42		4
17	56	0.111	0.308	0.350	.	.	.	59	33.9	2	49		8
18	56	0.200	0.565	0.640	0.0116	0.014	0.001	90	31.8	10	76		4
19	56	0.087	0.242	0.280	.	.	.	23	13	1	16		6
20	56	0.109	0.310	0.340	.	.	.	98	20	1	89		8
21	75	.	.	.	.	.	.	.	.				
22	75	0.146	0.401	0.460	.	.	.	58	12.7	3	51		4
23	75	.	.	.	.	.	.	.	.				
24	75	0.071	0.200	0.210	.	.	.	31	18.5	1	19		11
25	75	0.015	0.044	0.050	.	.	.	8	2.7		8		