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THE UNIVERSITY OF ALBERTA

EFFECT OF CONTINUOUS FORAGE PRODUCTION ON SOME PROPERTIES OF A GRAY LUVISOLIC SOIL

BY

© TIMOTHY C. MARTIN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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Date: April 7/87

Euery thyng that werketh naturelly ... enduceth the fourme of it seluen.

G. de Guilleville, 1413
The pilgrimage of the sowle

The soil does not consist of one factor or of a sum of factors, but represents a complicated and interdependent tissue of factors in which every single factor stipulates and influences the others .... Almost all the decisive factors are contained in the micromorphology, or correlate with characteristics expressed by it. A close collaboration of soil micromorphology and soil fertility therefore promises fruitful results.

Kubiena, 1964

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled EFFECT OF CONTINUOUS FORAGE PRODUCTION ON SOME PROPERTIES OF A GRAY LUVISOLIC SOIL submitted by TIMOTHY C. MARTIN in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

J. A. Robertson .....

Neil Gal - G. Jame .....

.....

.....

Date: 1987-04-07

DEDICATION

In memory of Lou Hendrigan, one of the creative thinkers of the world of the past generation.

For Miriam, to whom the world of the next is given.

ABSTRACT

Soils under forage stands three, eight, 26, and 49 years old were compared with nearby virgin forest soil at a site near Winfield, Alberta (Canada). Cultivation destroyed the LFH horizons and the bandad fabric of the Ae, creating an Ap horizon with a matrigranic fabric sequence in all agricultural soils. A thick moder turf layer developed with time under forage. Bulk density of the Ap horizon increased under continuous forage. Soil total C, N, and biomass were least in the forest A horizons, and greatest in the Ap horizon under 49 year old forage.

Faunal populations were greatest and most diverse in the forest soil, and least under the youngest forage stand. Meso and macrofaunal activity was limited almost exclusively to the turf layer under the older stands, and was dominated by oribatid mites. Enchytraeids were present only in organic layers; earthworms were not observed.

Frequent craze planes, channels, and aggrotubules were found in the upper Ap horizon of the 3 year old forage stand. A dense vughy porphyric Ap horizon, with very fine root channels and few planar voids or aggrotubules, developed with time under continuous forage. There were no visible signs of the formation of a significant (Chernozem-like) mull horizon. Introduction of a continuous forage stand has not induced mull-forming biological processes to replace the physico-chemical lessivage processes characteristic of the Gray Luvisolic soils.

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1. INTRODUCTION

Gray Luvisols are the dominant soil of Alberta, but they represent only 15% of the province's agricultural land, with 1.6 million hectares in cultivation (Bentley et. al., 1971). This is not only because of landscape and infrastructural limitations, and a marginal growing season in most of the Gray Luvisolic zone, but also because of limiting soil characteristics. The leached Ae horizon of Gray Luvisols presents the grain producer with significant tilth-related management problems. The weak soil aggregates cannot withstand the direct impact of rain or intense cultivation; puddling and crusting are common. A low nutrient status and limited buffering against acidification increase the energy investment required for agriculture on these soils, while tilth-related limitations and a dense B horizon reduce crop yields.

Lessivage processes are instrumental in the development of the Ae and Bt horizons of Gray Luvisols (Howitt and Pawluk, 1985b). The translocation of micaceous clays, as well as small amounts of Al, Fe, and organic constituents, from the A to the B horizon is the dominant pedogenic process in a Gray Luvisol. The lack of a strong granular structure in the upper solum of Gray Luvisols may be attributed to low organic matter content, frequent leaching of soluble organics and colloidal material to lower horizons, little annual root turnover, and minimal microbial and faunal activity. Ice lens formation during periods of freeze-thaw reinforce the weak platy structure (Howitt and Pawluk, 1985).

If one could improve the structural characteristics of the A horizon, the costs and risks of agronomic management of Gray Luvisols would be greatly reduced. A high organic matter content and active microbial and faunal populations are important to the formation of a mull structure. In the Black Chernozems of Alberta these are maintained by a large root exudate production and annual root turnover. Barratt (1971) observed a substantial regeneration of mull structure by continuous grass stands on deteriorated, cultivated soils of New Zealand. An interesting question is whether a continuous forage stand, with the development of a protective turf layer and without the interruptions of cultivation, might encourage mull formation in Gray Luvisols.

The conventional management system for grain production on Gray Luvisols involves a grain/forage rotation. At the Breton Plots a grain/forage rotation and the use of farmyard manure on a Gray Luvisol has resulted in increased organic matter and soil biomass, and improved tilth characteristics compared with a grain/fallow rotation (McGill et al., 1986). However mull fabric formation has been limited largely to aggrotubules (Pawluk, 1980). Matrigranic components formed by cultivation are unstable, and readily coalesce to form a vughy porphyric fabric.

In the early 1930's at about the time Wyatt was establishing the Breton Plots (Robertson, 1979), the late Lou Hendrigan, of Winfield,

Alberta, 30 km southwest of Breton, had decided that grain production was ill-suited to his Luvisolic soil, and that a management system with continual soil cover was required. He established continuous forage stands as the basis of a beef production system; some of his fields have been under continuous forage without cultivation for over a half-century. The Hendrigan farm is well suited to the study of the effects of a continuous forage system on Gray Luvisolic properties.

The purposes of this study are: 1. to compare some properties of a Luvisol under continuous forage stands of varying ages with the properties of adjacent undisturbed forest soil; 2. to compare some properties of a Luvisol under continuous forage stands of varying ages with the properties of adjacent soil under conventional grain/forage rotation management; and 3. to determine whether a continuous forage stand has encouraged mull formation on a Gray Luvisolic soil. Properties considered include soil density and acidity, carbon and nitrogen contents, biomass, and macrofaunal and microarthropod populations, as well as micromorphology. The focus of the study is on the upper solum; the factors chosen are indicative of the biological fertility and static bio-pedology of the soil.

2. LITERATURE REVIEW

2.1 Soil Fertility

2.1.1 Disparate Concepts

A significant disparity exists in the scientific community's concepts of soil fertility. At a recent symposium on Acarology, Purrini and Bukva (1984) made a statement which expresses a view held by many soil zoologists; "It is well known that the activity of soil arthropods in agrobiocenoses and forests largely determines the fertility of soil". Yet there was no mention of soil arthropods in any of the titles of papers presented at the 1985 Annual Meetings of the Soil Science Society of America[1*] (American Society of Agronomy, 1985). Given the physical, chemical, biological and ecological complexity of soil, a three dimensional body studied in spatial units ranging from cubic microns to metres deep by thousands of square kilometres, it is not surprising that in the study of soil fertility, defined by Viets (1977) as "...all processes in soil that affect the availability of essential and toxic elements, (and) their transport from the soil into the plant", one's approach may lead one to overemphasize or to neglect the role of a given group of actors.

In 1912 Sir John Russell observed that the study of

> ...soil as a medium for plant life... has grown up very unsystematically. Chemists, botanists, bacteriologists, geologists, and agriculturalists have all contributed something, but usually in connection with their own special problems, and not with the idea of developing a new subject.... Suggestions thrown out by men (sic) eminent in

* See notes at end of chapter.

> some other branch of science have been accepted without much serious examination... have acquired the force of established facts... have come to be believed for no better reason than that people have talked a great deal about them.
>
> In recent years, however, its recognition as a basis of national wealth has given the soil a high degree of technical importance.... (quoted in Bradfield, 1961).

Kevan, in his review of the history of soil zoology, observed (1985),

> a sort of 'two solitudes' attitude on the part of self-styled soil scientists on the one hand, and of zoologists, on the other, seems to be traceable to this period. The former, for a long time, seldom paid attention to animals smaller than earthworms (which they ignored if they could), whilst the few zoologists who deigned to get their hands dirty were considerably retarded in their recognition of the pedological significance of the soil fauna.

2.1.2 The "Soil Science" View

The development of the Soil Science Society of America's approach to soil fertility, which has dominated soil science in the western world, is well documented in addresses commemorating the 25th anniversary of the Society (Soil Sci. Soc. Am. Proc., 1961) and the American bicentennial (Soil Sci. Soc. Am. J., 1977). The technical bias observed by Russell was more pronounced in America, where soil science did not really develop until soil degradation and the limits of exploitable and fertile new land were experienced in the early 1900's, and especially in the "dirty thirties". Kellogg (1961) saw the enormous increase in fertilizer use and improved soil management practices as the major achievement of soil science to 1961. Observing the limited applicability of typically site-specific fertility research, Bradfield set as a goal the identification of critical

parameters and the development of a "set of equations" to efficiently and accurately diagnose the fertility status of any specific soil-crop system, and to elucidate how to best rectify any deficiencies. Viets (1977) reviewed the progress of research on "how plants feed", since Bradfield's review, and concluded

> From all this theory have come better explanations for what we do, even though we do not or cannot measure many of the critical parameters needed to put them to use on a field-by-field basis in a truly scientific agriculture.

Soil Fertility frequently is seen to be "... the highest development of soil science... built upon the information supplied by.... soil physics, chemistry, microbiology and pedology" (Bradfield, 1961). Such lists of foundational fields rarely if ever include soil zoology, in the American Society's literature. Kellogg (1961) did not even explicitly recognize zoology as one of the fields neglected by the Society, when he stated that "some important basic research appears to some to fall outside of our society", then mentioned "soil engineering", "common problems between soil science and geology", "applications of soil science to horticulture and to problems of range and forest management", and "other examples (which) will occur to most of you" as neglected fields or lightly treated issues.

Microbiology generally is included in lists of disciplines essential to soil fertility, commonly for the role of microorganisms in the "organic N-mineral N cycle" (Viets, 1977). Allison (1961) argued that soil microbiologists may be overemphasizing the role of fungal filaments and microbial polysaccharides in soil aggregation, suggesting

that the observed effects as likely are caused by the physical forces of water dynamics, root growth, freeze-thaw cycles, and cultivation. By the mid-seventies, the study of soil aggregation generally had been given over to soil physicists (Clark, 1977).

2.1.3 The "Soil Zoology" View

The soil zoologist, when addressing the question of soil fertility, is not so much asking "How can I make this soil, with these given fertility characteristics, produce maximum crop yields most economically?", but rather "what are the factors which result in the fertility status of a soil, in a given (natural or disturbed) ecosystem?", or more explicitly "What is the role of the fauna in the development of the fertility status of a soil in a given ecosystem?".

Interest in the role of fauna in soil formation has developed slowly. Some researchers in the nineteenth century, including Darwin, Muller, and Keller, observed a faunal role; however it was not until the 1950's that the study of soil zoology emerged as a discipline. In 1958 Kevan wrote

> Entomologists, as a general rule, have chiefly investigated larger soil insects--mainly those whose mature stages occur above ground or whose larvae are of direct economic importance--so that investigations have, till recently, been somewhat piecemeal.

Since the fifties there has been an enormous increase in studies of the role of soil fauna in organic matter decomposition and soil formation. Until recently this work generally has gone unnoticed by

"soil science". And as the Biological Survey of Canada (1982) noted, "...knowledge of soil arthropods in Canada is strikingly deficient.... fewer than half of our estimated 18,000 or more species have been described even in the adult stage."

Two factors probably have been most instrumental in the development of the notion of a role for soil fauna in the fertility of the soil. First is the observation, by Muller and later developed by Kubiena, of the role of fauna in "humusform" formation. Most important is the dramatic (albeit geographically limited) example of the major role of some species of earthworms in the formation of the spongy mull fabric so important to the fertility of many soils. Second is the observation that large and diverse faunal populations are found under the most productive and stable plant communities. Organisms are interdependent, and modify their environment "to get the best living conditions for (themselves) that the material environment will allow" (Jacks, 1963). Furthermore, the

> complex society of the soil (cannot) exist in equilibrium unless a compromise, which satisfies no individual or species completely, can be established between the conflicting interests of the society.
>
> Is is commonly agreed that the so-called climax plant association with its associated fauna ... is the social organism which makes the fullest use of the environment; the plants and animals have made the best possible living conditions for themselves, and the productivity of the soil is then the highest possible under the prevailing conditions. (Jacks, 1963).

These ecological principles suggest the existence of roles for the fauna in the overall fertility of the soil, without suggesting what those roles may be. Several have been proposed, promoted and

subsequently discarded. The fauna are not the primary decomposers: total faunal respiration usually accounts for less than five percent of total decomposition respiration (Petersen and Luxton, 1982); arthropod respiration may be less than one p cent (Crossley, 1977a), or even 0.1% of the total, while arthropods may represent 26% of the total decomposer biomass (Wallwork, 1983). The fauna are not a major nutrient sink, compared with the microflora and the soil organic matter pools. While some fauna consume large amounts of litter or soil material, assimilation rates are often very low, so that the excreta are chemically little different from the original material. Clements (1978) showed that the chemical removal of the total fauna (above and below ground) led to a nine to 40% increase in crop yields in eight consecutive years (largely because of the removal of plant consumers).

Due to the great heterogeneity of soil ecosystems in the world, any general statements about the role of soil fauna or of a specific faunal group in soil fertility must be interpreted relative to the system under consideration. Neglect of this principle can lead to confusion or to unwarranted conclusions. Lebrun's (1979) assertions that "saprophagous mites are responsible for the indispensable process of antiphotosynthesis" and that "it is clear that mites play an essential part in the biological fertility of the soil" may (or may not) be true of "the classic model of a deciduous forest published by Duvigneaud"; they may not be true of an earthworm-dominated deciduous forest, of an arctic tundra soil, or of a cultivated Gray Luvisol in Alberta.

2.1.4 Toward a Synthesis

The role of the fauna in soil fertility is via their roles in decomposition and in soil structural modifications; both of these are aspects of the development of the "humusform"[2] (Kubiena, 1955; Bal, 1982). Bal (1982) considered soil fertility ("an estimation of the suitability of a site for natural or agricultural plants") to be composed of an extrinsic component (climate, etc.) and an intrinsic component, which he called the "buffer capacity". He defined buffer capacity as

> ... an intrinsic parameter of the soil indicating the absolute amount of mineral resources including the rate of their release into an available form to plants, amount of available water (capacity), capability of draining surplus of surface water, air permeability, etc. The compound buffer capacity is thus composed of single values of chemical and physical characteristics.... Buffer capacity is not a constant parameter, as it may depend on the way in which a soil is used.

The humusform is indicative of the fertility of a soil; "Usually... mull humusforms are highly appraised in contrast with mor forms" (Bal, 1982). This is not always the case; some mull humusforms do not have a high buffer capacity. Others are "marginal humusforms", easily changed

> through the introduction of another vegetation or small ecological alterations. As opposed to marginal forms, in 'stable' forms the vegetation is not decisive at short notice (Bal, 1982).

A fertile soil is one which requires only minimal inputs of energy (tillage, chemical amendments, pesticides, etc.) to maintain a

productive plant community without significant loss of productivity with time. Characteristic of fertile soils is a diverse and active microbial and faunal community, and a resilient microstructure of complexed organic and mineral components, rich in nutrients, moisture holding capacity and porosity.

2.2 Soil Fauna

2.2.1 Diversity

The soil fauna are a diverse group of organisms. Considering only the invertebrates, the group may include as many as one million species, from the single-celled, aquatic Protozoa to organisms hundreds of millimetres in length, with individual body weights ranging over six orders of magnitude. The phyla represented include Protozoa, Platyhelminthes, Rotatoria (or rotifera), Nematoda, Nematerina, Nematomorpha, Tardigrada, Mollusca, Onychophora, Annelida, and Arthropoda. Numbers of individuals per square metre of soil commonly are on the order of hundreds of millions of Protozoa, several millions of nematodes, tens of thousands to hundreds of thousands of arthropods, and several thousands to tens of thousands of annelids, with biomasses ($g\ m^{-2}$) on the order of 10, 10, 10, and 2-40, respectively (Villee et al, 1973; Hole, 1981; Petersen and Luxton, 1982).

There is no simple, broadly useful way to classify soil fauna. Grouping the fauna by feeding type is conceptually attractive, especially in studies of faunal roles in decomposition and nutrient

cycling. In practice however, the task of separating and quantifying members of different feeding groups is difficult even when the feeding types are known. Many of the soil arthropods have not yet been described; feeding preferences are known for relatively few species. The Prostigmata (a sub-order of the order Acarina) includes predators, fungal and bacterial feeders, and detritus feeders; many individual species of acari vary their feeding habits seasonally (Anderson, 1978b). Some insects have dramatically different feeding habits in different life stages.

Classifications based on size or activity are limited by generality or arbitrariness. A useful distinction is that between aquatic, or hydrophilous forms (requiring at least a capillary film of water for locomotion) and aerophilous forms (able to traverse air-filled cavities). This approximates a distinction between microfaunal and mesofaunal classes, provided one does not strictly define the size delineation; nematodes may be mesofaunal by size but aquatic by habit. Similarily, a distinction between macrofauna and mesofauna may correspond with the distinction between fauna which can burrow and those which are limited to available pore space. This distinction does not hold rigorously as collembola and mites have been observed channelling in the soil (Haarlov, 1960). Also there is a categorical difference between burrowing in mineral soil and burrowing in organic material.

Taxonomy of the soil fauna does not well reflect soil activity.

At the phylum level quite different organisms are grouped together: the Arthropoda includes aquatic microfaunal Ostracoda and Copepoda and macrofaunal Insecta and Myriapoda. Enchytraeids have quite different effects in soil development than have lumbricid Oligochaeta. At lower levels of classification the number of taxonomic groups quickly becomes unmanageable. A taxonomic-based grouping which is not restricted to a particular level of classification, but considers lower levels only as required by faunal numbers or group complexity, can be useful and manageable (Table 1). In this way, Kuhnelt (1961) listed 68 distinct, important groups, Wallwork listed 101 (in Kuhnelt, 1961), Hole (1981) 50, and Petersen and Luxton (1982) 49 groups.

2.2.2 Distribution

Typical frequencies of soil faunal groups by biome are shown in Table 2. The literature is fraught with widely divergent population numbers for similar biomes, as much due to sampling, extraction and counting methods as to the high variability of population sizes. General trends have been emerging, however, and the review by Petersen and Luxton (1982) is the best recent summary of these.

Smaller organisms generally are present in much larger numbers than are the larger species, while on a biomass basis the larger species may be dominant. In their study of the arthropods and olygochaetes of a Swedish grassland, Persson and Lohm (1977) found a total of 247,000 individuals m^{-2}; Collembola and Acari made up 87% of this total, but less than 13% of the total biomass. Typical biomass

Table 1. A summary of major soil faunal groups. (Adapted from Hole, 1981; Petersen and Luxton, 1982)

Group	Body length (mm, approx.)	Common food sources (habits)
Protozoa	.02-.3	fungi, bacteria, algae, microfauna, detritus; some are autotrophs
Turbellaria	3	microfauna, algae, bacteria, litter
Rotifera	.05	microfauna, algae, bacteria, litter
Tardigrada	1	microfauna, algae, bacteria, litter
Nematoda	1	microfauna, algae, bacteria, litter
Acari: Oribatei	.6	litter, microflora
Gamasida		micro/mesofauna, microflora, litter
Actinedida		(predaceous), microflora, detritus
Acaridida		litter, microflora
Collembola	.5-4	litter, bacteria, fungi
Protura	5	detritus, mycorrhiza
Diplura	5	(predaceous)
Pauropoda and Symphyla	1-4	detritus, microflora, roots
Thysanura	5	(omnivorous)
Isopoda	5	litter, microflora
Gastropoda	20	plants, litter, fungi
Enchytraeidae	10+	litter, detritus, mycelia
Earthworms	10-100+	litter, microflora
Arachnomorpha	5+	(predaceous)
Diplopoda	5+	litter, microflora
Chilopoda	30+	(predaceous)
Diptera (larvae)	2-20+	litter, plants, fungi, (predaceous)
Lepidoptera (larvae)	10-30+	litter, plant roots
Coleoptera	3-20+	litter, fungi, roots, (predaceous)
Formicoidea	5-10+	plants, fungi, (predaceous)
Isoptera	5-10+	plants, litter, fungi
Hemiptera	2-10	plants, fungi, (predaceous)
Other insecta		

Table 2. Typical frequencies of soil faunal groups, by biome (1000's of individuals per m^2). Adapted from Petersen and Luxton, 1982; Hole, 1981; Anderson et al, 1984.

Group	Tundra	Temperate Grassland	Tropical Grassland	Temperate Coniferous	Temperate Deciduous	Tropical Forest	General
Protozoa	-	-	-	-	-	-	500,000
Rotifera	0.2-6.4	32-94	51	29-510	680	196	20
Tardigrada	2.4-5	4-29	27	42-50	4-150	38	-
Nematoda	1000-6000	1000-15000	-	1000-4000	4000-6300	1500-1900	300-30000
Oribatei	1.5-70	15-70	3	50-400	20-150	-	-
Gamasida	0.7-10	10	1.5	7-11	3-10	-	-
Actinedida	0-50	-	-	50-210	7-15	0.2-3	0-200
Acaridida	<1	1	-	-	-	16	0-10
Total Acari	2-100	10-200	10-80	50-600	80-200	20-600	60-150
Collembola	4-600	3-100	1-10.5	10-250	30-70	3-50	-
Protura	-	1.4-7	-	2-51	0.3-6.5	-	0.6
Diplura	-	0.1	0-2.6	0.1	0.1	-	0-1
Pauropoda	-	-	0.02-0.2	-	-	-	0.3-2
Symphyla	-	-	1.2-6.2	-	-	-	0.2-0.6
Isopoda	0	0.01-0.4	-	5×10^{-4}	0-0.6	0.01	-
Enchytraiedae	10-200	1-50	0.5	10-100	6-80	-	-
Earthworms	.005-0.3	.001-0.3	0.02-0.3	0-0.15	0.02-0.3	0-0.1	0-0.5
Araneae	.002-0.3	0.01-0.1	0.01-0.03	0.01-0.8	0.01-0.8	0.01-0.03	0.02
Diplopoda	-	.002-0.1	.001-0.1	.002-0.8	.008-0.2	.004-0.1	0.1
Chilopoda	0.001	0.01-0.1	0.002	.009-0.15	.008-0.18	.002-0.1	-
Diptera larvae	.01-2	.001-1	-	0.01-0.3	0.01-1	-	0-10
Coleoptera	-	0.5-2.5	-	-	-	-	0.1-4
Formicoidea	-	.001-5	0.05-0.5	-	0.03	0.02-0.8	0-5

estimates are listed in Table 3. The larger organisms have a lower respiration rate per unit body weight than the smaller individuals. Persson and Luhm estimated the Lumbricidae represented 56% of the total biomass, but only 27% of the total respiration of the faunal groups considered.

Harsh environments, for example the tundra biome or reclaimed sites, tend to be dominated by Enchytraeids, Collembola and/or Diptera larvae, while oribatid mites or earthworms tend to dominate more protected and stable environments. Temperate grasslands are dominated by nematodes and enchytraeids, or by earthworms. Forest mulls usually are earthworm dominated, while moders are dominated by oribatid mites, collembola, and enchytraeids. Eighty to 95% of the microarthropods of most soils are Acari and Collembola, with Acari usually outnumbering Collembola in mor and moder soils, but numbering about equal in grasslands. Of the Acari the Oribatei are most common, especially in coniferous forests (Curry and Ganley, 1977; Persson and Luhm, 1977).

Temperate soils have larger faunal biomasses than either arctic or tropical biomes. Faunal biomass is not related to annual litter fall, but litter accumulation is negatively related to total faunal biomass, which means there is a positive correlation between decomposition rate and faunal biomass (Petersen and Luxton, 1982).

The zoogeographic distribution of soil fauna is related to the taxonomic level of the group being considered, their ease of dispersal,

Table 3. Typical estimates of biomass of soil faunal groups, by biome ($mg\ m^{-2}$.) Adapted from Petersen and Luxton, 1982; Raw, 1967.

Group	Tundra	Temperate Grassland	Tropical Grassland	Temperate Coniferous	Temperate Deciduous Mor	Temperate Deciduous Mull	Tropical Forest
Nematoda	160	440	50	120	(330)[1]		50
Oribatei	60	110	20	450	700	180	-
Gamasida	20	60	10	80	(40)		-
Actinedida	10	40	50	30	(10)		-
Total Acari	90	120	80	500	520-900	220-300	100
Collembola	150	90	10	80	130-180	75-110	20
Isopoda	-	-	-	-	30	150	-
Gastropoda	0	100	10	20	(270)		10
Enchytraeidae	1800	330	20	480	520	340	20
Earthworms	330	3100	170	450	200	5300	340
Araneae	10	30	30	50	80	50	20
Diplopoda	0	100	10	50	160	680	20
Chilopoda	20	140	5	70	210	50	5
Diptera larvae	470	60	10	260	470	190	0
Predaceous Coleoptera	50	80	10	120	20	160	10
Formicoidea	0	100	300	10	(10)		30
Total fauna	3300	5800	1900	2400	3500	8000	1800

[1] Numbers in parentheses are from temperate deciduous forests; without destinction between humus types.

and individual size. Smaller organisms are more cosmopolitan than larger species. While many species are not eurytopic, orders and families are much more so (Anderson, 1977).

2.2.3 Factors Affecting Population Size and Structure

Physical factors which influence soil faunal populations include soil atmospheric conditions, humidity, temperature, and soil structure. Chemical factors such as pH and salinity also will influence the structure of the soil community (Morency, 1980). Each taxon of organisms has its own optimum range for each of these parameters, as well as threshold tolerance limits. Some collembola are able to remain active at temperatures well below freezing, however low temperatures slow arthropod development rates (Bloszyk et al, 1984). Enchytraeids are highly susceptible to desiccation, but less bothered by low temperatures or acidic soils than are most earthworm species, which can avoid desiccation by burrowing to depth. In a study of northern European grasslands, Curry (1978) found acarine communities to be correlated to organic matter, moisture, and base status characteristics of soils, while Collembola species were eurytopic. In a similar study of the microarthropods dwelling in the mosses on a forest rock, humidity and temperature were found to be important factors in community structure (Bonnet et al, 1975).

Temperature has a direct effect on rates of physiological activities including respiration, ingestion, assimilation, egestion,

growth and secondary production, and survival. Ceratozetes gracilis development takes 36 weeks at 15C and 19 weeks at 20C, under laboratory conditions. Respiration Q_{10} values are 2.8-4.0 and growth rate Q_{10} values are 3.5-4.0 for some oribatid species. Temperature also affects potential transpiration rates, and microbial population dynamics, thereby affecting desiccation potential and food availability (Mitchell, 1979).

Factors such as base status and soluble nutrients are related to faunal populations indirectly, via their influence on floral and microfloral populations. Food availability is a major factor in determining faunal population size. Forest clearcutting results in an increase in the total soil population because of the great increase in litter; Huhta (1976) found that the faunal biomass remained larger than normal for up to 13 years after forest clearcutting in Finland. Within an environment, microarthropod density varies with foliage and root densities, microbial activities, and nutrient quality of the foodstuffs; these are dependent on the nutrient status of the soil (Seastedt, 1984).

2.2.4 Variability

Soil faunal populations have high spatial and temporal variability.

Seasonal fluctuations in soil faunal population sizes are related

to temperature, moisture and litter production trends. The degree of fluctuation depends on the biome and the faunal taxon considered. In savannas, most faunal groups have high seasonal population fluctuations, up to 100-fold. In forested biomes the fluctuations are less than in non-wooded systems in similar climatic zones. In temperate and northern zones, enchytraeid and collembolan populations fluctuate more than acarine (up to 25-fold vs. six to ten-fold); populations of oribatid and gamasid mites are more stable than are those of Actinedida and Acaridida (usually less than six-fold vs. 16-fold or greater seasonal fluctuations) (Petersen and Luxton, 1982).

Biological development often is correlated to seasonal changes. For example low temperature may slow growth, while egg hatching and molting may be stimulated by warming temperatures in spring (Błoszyk et al, 1984).

The vertical distribution of soil fauna is related to soil horizonation. Most fauna are found in the upper few centimetres of most soils (Petersen and Luxton, 1982), where food supplies are abundant and porosity is greatest. Deep burrowing animals use this activity as a strategy for avoiding of desiccation, temperature extremes or predators. Non-burrowing fauna are limited by soil pore size. An often observed positive correlation between pore and insect (especially collembolan) size distributions within a soil is because of the competitive benefits and predation avoidance associated with such a distribution (Raw, 1967; MacFadyen, 1969).

Faunal populations tend to be highly aggregated. Collembola and mites often are found in "localized points of very high density" (Ford, 1938). This gregarious habit of collembola is not related primarily to low mobility from the site of egg clusters (Poole, 1961); aggregation pheromones are involved. The activity may be to optimize use of non-evenly distributed food resources, moisture conditions, and breeding and overwintering sites (Norton, 1985).

Species composition of soil populations is not strongly correlated with plant distribution within a given ecosystem, but faunal numbers often are. In grasslands, plant communities are seemingly unrelated to the microarthropod community (MacFadyen, 1969; Curry and Ganley, 1977). On a broad zoogeographic scale however, Blackith and Blackith (1975) found plant cover to be more significant than soil type in Europe, in locations where contradictions occur between soil type and plant cover. Exceptions also occur at the species level. The distribution of the mi[illegible] Tectocepheus velatus shows a strong preference for Pinus silvestris over Quercus robur, in a mixed forest site. Oribatei generally aggregate around tree trunks, while some collembolan populations increase with distance from trunks (Schenker, 1984). The relationship between plant species and microarthropods seems more an "overlapping mosaic" than a sequence of communities, and may be related more to plant biochemistry than to plant species (Anderson, 1977).

2.2.5 Microhabitats

Soil zoologists have long wondered at the apparent lack of niche specificity amongst microarthropod populations. Feeding selectivity sometimes is observed. Often however, organisms of very similar size with similar, very broad feeding habits--often several species of a single genus--will share habitats.

Part of this mystery can be solved by a recognition of scale. The apparently large microarthropod populations actually represent 0.01 to 0.02% of the organic layer volume and 0.003% or less of the upper mineral layer (Murphy, 1955). Haarlov (1955) found one microarthropod or fewer per 100 cm^2 of cavity wall, in the 0-4 cm depth. This, and recent electron microscopic evidence that the vast majority of the bacteria in mineral soils are associated with roots (Brewer et al., 1983), suggest that, to a microarthropod, the litter layers are fair pastures at best; the mineral soil, a sparcely vegetated desert with occasional food oases.

A macroscopically homogenous soil is, microscopically, highly heterogenous. Organic layers are a complex network of pores and channels between highly varied physical and chemical structures. In the F layer of moder soils, plant fragments in various stages of decomposition are intermixed with mineral grains, decaying carcasses and fecal material; all are overgrown with tangled microbial colonies. The moist atmosphere is thick with a continually changing array of volatile organics; pheromones, bodily excretions, and by-products of

decay. Anderson used gelatin-embedded soil sections and point count techniques to show a strong correlation (r=0.70) between microhabitat diversity and species diversity in the L, F, and H layers of forest soils (Anderson and Hall, 1977; Anderson, 1978a, 1978b).

Wallwork, in a 1983 review, suggested three probable factors, any or all of which may be involved in oribatid species distributions: feeding selectivity, microclimatic preferences, and physical microhabitat structural constraints. Usher (1978) suggested that interspecific competition in grassland microarthropod populations may be kept low by microstructural limitations, aggregation behavior, predation and physical or chemical gradients.

2.2.6 Acari

Soil Acari are classified in four suborders: Oribatei (or Cryptostigmata), Gamasida (or Mesostigmata), Actinedida (or Prostigmata) and Acaridida (or astigmata). Members of all four groups can be found in most soils, however the Oribatei usually are by far the dominant group, 80-90% of the total mite population). The Gamasida commonly are less than 20% of the population, often about five percent. Actinedida populations vary greatly, from near absent to dominant in number; because of their small body size the actinedid population often is underestimated. The Acaridida are insignificant or nearly absent in most soils. Acari prefer humid soils over aquic or arid conditions, and are more numerous in organic than in mineral layers.

Oribatid populations are largest in coniferous forest soils. They are larger in boreal and temperate soils than in tropical or tundra soils. Forest populations outnumber grassland populations in similar climatic zones. The Oribatei are decomposers; most are fungal feeders, some feed on plant detritus or wood litter, a few are herbivores. Predation and carrion feeding are rare oribatid activities. Many oribatids are resistant to desiccation, despite their small body size, because of their thick integument. This thick, often smooth dorsal integument gives them the appearance of minute beetles; they commonly are called "beetle-mites". Dry weights of individuals usually are 3-5 µg.

Most gamasids (members of the Gamasina sub-group) are predators of nematodes, other arthropods or Protozoa. Members of the sub-group Uropodina, rare in most soils, feed on fungal protoplasm. All are liquid feeders. The Gamasida are more frequent in forests than in open lands, and are insignificant in deserts and in some tundra soils. Their populations sometimes are very large in tropical forests. Gamasida size varies greatly; individual dry weights of most species are 3-5 µg, some weigh as much as 270 µg.

The Actinedida and Acaridida are less well known, the former because of neglect due to small body size (1µ g or less individual dry weight), the latter because of small population size. Actinedida are common in woodland and in open land, and are the dominant Acari in some

tundra, deserts and savanna soils. Some are predaceous, others are fungal feeders. Acaridida rarely number more than 1000 individuals m^{-2}, with individual dry weights of 0.7-2.1 µg. They feed on detritus, wood, fungi and algae, and are most numerous in soils with deep organic horizons. (Wallwork, 1967; Petersen and Luxton, 1982; Norton, 1985).

Many studies of oribatid feeding preferences have been carried out, to see whether trophic specialization can help explain the coexistence of large numbers of individuals of similar species in a single habitat. These studies have been of four types, each with its inherent limitations. Laboratory feeding preference tests, in which the organisms are given choice between two or more foodstuffs, are artificially simple, and do not correlate well with observed feeding in the field. Studies of the gut contents of field specimens overemphasize the importance of the least digestable foodstuffs. Studies of gut enzyme complements show which compounds an organism is able to digest; however these are carried out on whole body homogenates because of the small body size of the Oribatei; the source of the enzymes is not distinguished (Norton, 1985). Pande and Berthet (1973) used 2 mm thick serial gelatin sections of pine litter layers to observe oribatids in situ, and the marks of feeding activity on foodstuffs. This method resulted in useful observations of some species which feed on or in decaying wood and needle material; it was unable to distinguish the feeding preferences of species found in the well-decomposed soil layers, or to distinguish whether the litter feeders were decomposing plant material directly, or were feeding on

fungal material within the plant litter.

Several general observations of oribatid feeding habits have emerged. Soil Oribatei do not feed on fresh litter; some leaching and fungal attack of the material must occur first. Immatures are the most important feeders; adult feeding rates are slower (Luxton, 1972).

There is little evidence of trophic specialization by oribatid species. Marked seasonal variations in gut contents have been observed in a number of species. Liacarus xylariae is strictly mycophagous at the time of litterfall, non-specialized during summer, and feeds on decayed leaf litter immediately before litterfall. It is not uncommon to find separate food boluses of two or three different food types (fungi, bacteria, plant litter, detritus) in a single organism (Anderson, 1977; Luxton, 1984). Gut contents reflect microsite foodstuff availability more than species preferences (Anderson, 1978a).

Individual size and foodstuff are correlated. The smallest species feed more on amorphous material, medium sized species on fungal material and larger species more on higher plant material (Anderson, 1977). Also, the percentage microbial content of food boluses has been observed to increase with depth in soil in some species (Luxton, 1984). Observations of mite size and foodstuff relationships may be related to mite size distribution with depth. Larger species are confined to upper litter layers (Pande and Berthet, 1975). Ceratozetes gracilis is found nearer the surface than the smaller C. kananaskis; immatures tend

to be restricted to the F layer (Mitchell, 1979).

Oribatid digestion seems to be dependent on an active gut microflora, which changes as feeding substrate changes (Norton, 1985). Haq (1984) showed that Heptacarus hirsutus has glucosidase, galactosidase and cellulase enzymes in the gut. The enzymes probably are from the gut microbial population, since H. hirsutus feeds only on wood which has been colonized by microbes, and its fecal pellets have an active microbial population.

Forest oribatid daily food consumption is 1-13% of their dry body weight, with assimilation rates reported to range from 3-65%, commonly over 40%. Most of these estimates are from laboratory studies, with temperatures much higher than normal field temperatures, and there is a strong effect of temperature on both feeding and assimilation rates. The lower estimates may be more typical of field conditions (Wallwork, 1983).

Oribatid development times range from 23 days to two years; individual size and development time are positively correlated. The development time is strongly temperature and food-quality dependent; laboratory estimates probably are low. Mortality is high amongst immatures due to softer bodies and the rigors of molting. If adulthood is reached the individuals may live several years. Adult mortality probably is due to internal parasites and predation, primarily (Norton, 1985).

Whelan (1978) studied Acarine succession in pasture leys. Initial invasion of newly-established leys was by species which practise phoresy on insects, and predominantly by actinedids and Acaridids. Oribatei and Gamasids species tended to be later invaders, and were responsible for increases in total species numbers, while Actinedida and Acaridida spsecies remained unchanged. This suggests that the oribatids and gamasids have a more K-selective survival strategy (McArthur and Wilson, 1967) than have acaridids and actinedids. K-selective traits of the oribatids include high species diversity, low fecundity, increased instar length variability with development, high longevity with iteroparity (Norton, 1985), and low metabolic rates (Mitchell, 1979).

2.2.7 Collembola

Collembola are ubiquitous soil and litter dwellers; however they are most numerous in cold and temperate climates, are found in higher numbers in forest soils than in grasslands, and have low populations in dry soils. (They tend to be more r-selective than the Oribatei.) The very high populations sometimes found in grasslands and forests are dominated by very small species. Species diversity is low in deserts and arctic soils, however in the arctic the populations may be large (Petersen and Luxton, 1982).

Collembola are vertically distributed according to individual

size. Surface litter dwelling entomobryids may be several mm long, with a strong furca or "springtail" which they use to propel themselves quickly away from predators. Surface and near surface dwellers often have well developed eye clusters and bright pigmentation. Species found in the lower organic and upper mineral soil are small to very small (often less than .1mm long), non-pigmented, blind and relatively sedentary organisms. They may be found to depths of 60 cm in grasslands and savannas and to 30 cm in forests, while in tundra soils they tend to be limited to the top 3 cm (Petersen and Luxton, 1982).

Vertical migration of collembolans with precipitation is common. In desert ecosystems collembolans migrate to surface litter layers within hours of rainfall. Hassall et. al. (1986a) found that in an Albertan Populus tremuloides woodland, Onychiurus subtenuis inhabit the litter layer for a few days following rainfall, returning to the humus layer when the litter dries. This migration apparently is a response to the temporary availability of the more palatable, rapidly sporulating fungal species of the litter layer.

Like oribatids the collembolans show little species feeding specificity, although there is a tendency for the larger species to feed on fungi and the smaller on humus material. Again this is related to the vertical distribution of the organisms. Foodstuffs include detritus, fungi, bacteria, and algae. Decaying leaf tissue, pre-infested by fungi is a common preference. Considerable amounts of inorganic and other materials also are ingested; gut contents may

include mineral grains and parts of dipteran pupae, other Collembola, and decaying earthworms (Hale, 1967; Fjellberg, 1985).

The ability of collembolans to thrive in very cold climates is based on cold hardiness, and several overwintering strategies. While many species remain active at below freezing temperatures, most do not reproduce or develop under such conditions. The dangers of freezing include damage to tissues due to ice crystal formation, and oxygen deficit when trapped under ice. Some species move deeper into the soil to avoid freezing conditions, others overwinter in the snow. Aitchison found that most species in southern Manitoban soils overwinter in the same layer they are found in during frost-free months (1984). Many Collembola empty their guts of potential freezing nuclei, and can supercool to -15 or -25C. Some can enter and remain in an anaerobic, inanimate state when trapped in or under ice (Leinaas, 1983).

Collembolan life cycles in Southern Manitoba are two to ten months long, with one to five generations per year (Aitchison, 1984); however arctic species may not start to reproduce until after two years, and may live three to seven years (Fjellberg, 1985). Populations show significant seasonal variation, often peaking in autumn (Hale, 1967).

2.2.8 Enchytraeids

Enchytraeids are found in most temperate to cold climates, in mesic to wet soils. They are very sensitive to drought; in part this may be why they are more common in organic than mineral soil layers. High seasonal population fluctuations are related to moisture and temperature conditions. Enchytraeids may actively reproduce at freezing temperatures, and often are the dominant fauna in arctic soils. They survive well in moist r-selective environments (Zaccharíae, 1964; O'Connor, 1967; Petersen and Luxton, 1982).

Similar to their larger relatives, the earthworms, enchytraeids feed by ingesting the entire substrate and therefore their assimilation rates are relatively low. Some species preferentially feed on fungus, or avoid plant material or inorganic material (O'Connor, 1967). If the litter layer is moist enough for habitation the enchytraeids feed on microbial films on the leaf material. In lower layers they feed on arthropod and earthworm droppings (Zaccharíae, 1964).

Enchytraeid life cycles of 68 to 261 days have been observed under laboratory conditions. Asexual reproduction, in which fully grown worms break into three to eleven fragments, each developing into an adult, has also been observed (O'Connor, 1967).

2.3 Roles of Fauna in Soil

2.3.1 An Historical Introduction

The role of fauna in the soil has been discussed in a number of reviews in this century. McCollogh and Hayes discussed "The reciprocal relation of soil and insects" in an Ecology article in 1922. In a 1940 review of soil fauna Jacot emphasized the role of fauna in reducing the "carpet of dead and moldering leaves" of a forest floor "to a litter of minute faeces" which may be "mixed into the mineral soil by various animals". Kubiena championed the cause of the fauna as soil formers. Through his soil thin section studies, Kubiena became convinced that "aggregate formation in soils is to a great part caused by soil animals" (1955). The question of faunal influences on soil structure has been addressed frequently, most recently at a symposium at the University of Alberta in June 1984 (Quaestiones Entomologicae, Volume 21:4, 1985).

Probably the best review to date of the effects of animals on soil is that by F. D. Hole (1981). He listed and discussed twelve effects: mounding, mixing (faunal pedoturbation), forming voids, backfilling voids, forming and destroying peds, regulating soil erosion, regulating water and air movement, regulating plant litter, regulating animal litter, regulating nutrient cycling, regulating biota, and producing special constituents.

2.3.2 The Decomposition Pathway

The effects of fauna on soil can be considered from the

perspective of the decomposition pathway.

> The detritus decomposition pathway occurs on or within the soil after plant materials (litter, roots, sloughed cells and soluble compounds) become available through death, senescence or other pathways (Coleman, 1986).

Energy flows through this pathway in the form of organic carbon, cycled through the microbial and the faunal populations, and eventually returned to the atmosphere as CO_2 or stored in the soil in persistent forms. Mineral nutrients are recycled through the organisms and the active inorganic (solution and ion exchange) pool, and may be removed from the latter pool by plants, precipitation, translocation to lower horizons and leaching. Nutrient inputs into this open system are from dust and rainfall, from the mineral matrix, from the atmosphere (nitrogen), and from fertilizer inputs in managed systems. Losses are via erosion, volatilization (nitrogen and sulfur), leaching, and harvest in managed systems.

A plant-biased fertility perspective is concerned with efficiency of the nutrient cycling through the plant community, the removal of litter material, the development of stable soil organic materials, and the chemical and physical structural ability of the soil to maintain a healthy plant community. The development of a fertile soil from a mineral parent material can be understood as a system of feedbacks amongst members of the developing biologic community, and in hydrologic processes, within the given climatic and landscape constraints (Torrent and Nettleton, 1978).

2.3.3 A List of Faunal Roles.

The direct role of fauna in the decomposition pathway is minimal. About five percent of the total annual litter energy is utilized by the soil fauna; estimates vary from 0.8% in a spruce forest to 10% in a mesic deciduous mull (Petersen and Luxton, 1982). The remainder is oxidized by heterotrophic microorganisms. The oft-noted faunal population increases with sudden increases in soil litter (Petersen and Luxton, 1982) are a response to the microbial population. Soil faunal grazing of live macrofloral material usually is minimal, though some plant pathogenic nematodes and microfauna are soil dwellers[4].

Indirect roles in the detritus pathway include effects on the microbial population, on nutrient cycling, and on physical soil properties relevent to plant production, erosion and leaching loss rates. These effects are strongly interrelated; nutrient cycling and soil structural development affect the plant, microbial and faunal populations.

Comminution of organic litter material by the fauna improves the litter availability to microorganisms by increasing its surface area. Translocation of both foodstuffs and microbes increases contact between litter and microbial propagules. The fauna are reponsible for two microbial environments: the faunal gut is a favorable environment for some organisms, especially bacteria, and fecal pellets are dense yet finely porous, often heterogenous structures well suited to microbial habitation. Faunal roles in nutrient cycling, and more directly faunal

grazing of the microflora, affect microbial population dynamics.

Soil fauna also affect plant production indirectly by their role in soil structure development. Litter materials are reduced to humus material and may be mixed with mineral grains to form mull material. Dead root channels are converted to humus or mull aggrotubules. Fauna are implicated in soil aggregation and granular ped formation, which improve soil stability and moisture and cation exchange capacities.

2.3.4 Evidence of a Faunal Effect on Decomposition

The most direct evidence that fauna affect litter decomposition comes from fine mesh litter bag studies. Seastedt's survey of such studies shows an average 23% increase in the litter decay rate when mesofauna are present, compared to microbial decay alone. (After initial leaching effects, abiotic decay is essentially zero.) The effect of fauna varies between years and soil/litter types. There is some evidence that the faunal role increases with increasingly recalcitrant material (Seastedt, 1984). Webb noted that the faunal role is less significant in litter with a low C:N ratio, which decomposes rapidly (1977).

A number of researchers have considered the succession of soil fauna in litter decomposition (Van der Drift, 1965; Kevan, 1968; Anderson, 1975; Crossley Jr., 1977a; Seastedt, 1984). In the initial stages of decomposition, leaching and mechanical weathering are most

important, and the arthropod role is minimal (Crossley Jr., 1977a), though microbial attack may occur before senescent leaves have fallen. Microfauna and nematodes begin feeding on the microflora soon after leaf fall; microarthropod grazing begins later (Van der Drift, 1965). Direct attack of soft tissue material by fauna begins weeks or months later, by millipedes, isopods, dipterous larvae, and snails (Van der Drift, 1965), or acari and collembola (Kevan, 1968). As fecal material accumulates, the enchytraeid activity increases, reducing the pellets to amorphous fecal material. Finally the more resistant plant fragments as well as fecal pellets and mineral materials are consumed by the larger fauna, if present (Kevan, 1968).

2.3.5 Faunal/Microfloral Relationships

Microphytophagous fauna feed by a process of "microbial stripping" (Macfadyen, 1978). This is a process of repeated consumption of the substrate, digestion of the microbial protoplasm, and excretion of the structural materials of both the microbes and the substrate, to be reinfested by microbes. The fecal material often is chemically little different from the original substrate, and little mass of material has been removed (Raw, 1967; Macfadyen, 1978). Thirty to 60% of ingested bacteria may survive gut passage (Coleman et al., 1983).

Grazing increases microbial respiration, probably by preventing fungal matting (Norton, 1985) and the formation of an overpreponderance of aged fungal hyphae material and bacterial colonies. Overgrazing may

result in decreased respiration. Selective grazing of fungi by collembola, and greater survival of bacteria than fungal propagules in millipede and isopod gut passage may alter microbial populations in favor of bacteria (Anderson and Ineson, 1983). Leonard showed that fungal survival of overgrazing is dependent on the availability of protective microsites where the fungi cannot be reached by fauna (1983). Decaying plant tissues may provide such sites since microorganisms are more able to invade these than are the fauna (Anderson, 1977). Reduced predator populations may result in an increased saprophagous population, and increased decomposition rates (Petersen and Luxton, 1982) provided it does not lead to overgrazing.

This suggested relationship between faunal/microfloral interactions and decomposition rate is not well established, however. Hassall et. al. (1986b) found that

> although more than 1,000 Onychiurus subtenuis m^{-2} move rapidly into the L layer of this Populus tremuloides woodland whenever it is moistened by summer rains in order to graze on the micro-organisms there, and despite their carrying over 3,800 spores m^{-2} into it from over 100 species of fungi characteristic of the lower litter strata, the overall results of their inoculating, dispersing, and grazing activities do not have any significant effects on the rates at which this leaf litter is decomposed.

2.3.6 Nutrient Cycling

Fauna may affect the nutrient cycle by reducing erosion losses due to improved soil aggregation, reducing leaching losses due to improved water holding and cation exchange capacity of the soil aggregates, and by translocating less weathered mineral material to the upper soil from depth. More important are the effects of fauna on nutrient

mineralization and immobilization, directly (to a small degree) and indirectly affecting the microbial population.

In general, soil fauna mineralize nitrogen, since their own C:N ratio is about the same as that of their microbial food substrate, and they have a fairly low production efficiency (Coleman et al., 1983). Bacterial and fungal feeding nematodes and protozoa resulted in a "considerable facilitation of nutrient (nitrogen) return, leading to enhanced nutrient uptake and dry matter yield in test plants." (Coleman, 1986).

Other nutrients also are mineralized by faunal feeding. Leaching losses of nitrogen, phosphorus, potassium, magnesium (Seastedt, 1984), calcium and sodium (Anderson and Ineson, 1983) from litterbags are increased by faunal presence. With a healthy root and microbial population these released nutrients are quickly immobilized. A possible plant strategy for carbon exudation from growing root tips is described by Coleman et al (1983). Increased microbial activity near the root tip results in nutrient immobilization, and nutrient diffusion into the zone. As the growing tip moves on, exudation is decreased, carbon supplies are exhausted, and the microbial population peaks. Faunal grazing is increased in the zone. Nutrient mineralization occurs, and the net effect is an increased nutrient availability in the active root zone.

2.3.7 Fauna and Soil Structure

An average of 20 to 30% of the annual organic litter production in terrestrial ecosystems (Petersen and Luxton, 1982), and significant quantities of mineral material are processed by the soil fauna. Rusek (1985) listed three faunal processes of microstructure formation: the "disintegration of dead organic matter"; the "formation of a zoogenic microstructural soil matrix" in the upper soil; and "tunnelling and burrowing activities" in deeper layers. McGill and Spence (1985) emphasized a dynamic view of soil fabric, pointing out that fabric formation is a process of repeated cycles of generation, breakdown and reorganization, over long periods of time.

Kubiena's (1955; 1964) work showed the strong correlation between faunal activity and humus type. Where little faunal activity occurs, little humification is observed. Highly organized humusforms are found where microfaunal feces include both mineral and organic material. Soils dominated by small fauna have sharp horizon differentiation, especially between organic and mineral layers; the dominant formation processes are physical (especially gravitation) and abiotic chemical ones. Larger soil fauna break down horizon boundaries (Jacks, 1963).

The importance of fauna to the structure of organic layers is well established by soil thin section, faunal population, and fecal pellet studies. In the boreal forest zones, fresh leaf litter material is underlain by a zone of fragmented, partially decomposed plant material and associated microarthropod fecal pellets. The lower F layer is a

complex zone of decomposing plant fragments, discrete fecal pellets, and partially coalesced, often enchytraeid, fecal material. Plant fragments and fecal material are repeatedly ingested. The H layer is a partially coalesced matrix of aging fecal products, with few identifiable plant structures remaining (Bal, 1970; Rusek, 1985; Pawluk, 1985).

Fecal pellet morphology is well described by Rusek (1985). Oribatid pellets are compact, smooth, spherical to egg shaped structures without mineral grains, between 40 and 200 µm in diameter, and varying with age from light yellow to black in color. Collembolan pellets are rough surfaced, irregular shaped, small (20-100 µm), dark, amorphous structures, often containing mineral grains. Enchytraeid pellets are similar and not always distinguishable from collembolan; they often contain melanized plant material, mineral grains, and smaller fecal pellets, have extremely irregular shape, and coalesce with age. Diplopod, isopod, and dipteran droppings are larger, sometimes greater than 1 mm in diameter, with a random internal fabric. Diplopod and isopod feces contain plant fragments, smaller fecal material, and mineral matrix material; dipteran pellets are more often humic material without mineral grains. These larger pellets may be fragmented and partially reingested by smaller fauna (Foster, 1985; Rusek, 1985; Pawluk, 1985).

The role of earthworms (and occasionally diplopods and enchytraeids) in producing mull humusforms also is well documented.

Mull horizons are composed entirely of frequently reingested faunal fecal material; they have a spongy granular fabric of complexed, physically inseparable mineral and humified organic materials (Jacot, 1940; Kubiena, 1955; Kevan, 1968; Rusek, 1985).

2.3.8 Soil Aggregation

The broader role of fauna in soil aggregation is less certain. Soil population and micromorphology studies are limited by their descriptive nature; correlation of observations does not imply causation. From thin sections one can observe that events have occurred. "Pedogenesis leaves its marks and it is the duty of the micromorphologist to identify, evaluate and interpret these marks" (Eswaran, 1972). The details of the physical and chemical processes involved, however, must be learned from other methods (Brewer, 1972). To show faunal responsibility for a process in soil requires not only evidence that the fauna are capable of the role, but proof that the process cannot--or, more practically, does not--occur in their absence. Thus the assertions that "the mixing and binding activity (of fauna) cannot be replaced by any other agent in the soil" (Kubiena, 1955), and that "the columnar structure of a solonets (sic) can be explained on physico-chemical grounds; the granular structure of a chernozem cannot" (Jacks, 1963) are suspect. Biochemical substances, frost processes, and wetting and drying also may contribute to granulation. There is a "...general lack of clarity as to the importance of soil animals in

initiating and maintaining soil fabric rearrangement" (Pawluk, 1985).

The aggregation of soil particles occurs over a size range of several orders of magnitude with differing processes presumably responsible for aggregation at different size scales. Several classifications of aggregate size have been suggested (Lynch, 1984; Coleman, 1986); the most useful for discussion of the processes involved is a distinction between microaggregates (<250 um diameter) of flocculated clay size particles, and macroaggregates (>250 um, commonly 1-10 mm diameter) composed of microaggregates and other soil particles, including mineral grains and organic litter fragments (Oades, 1984). Microaggregation is primarily a result of charged colloid surface chemistry and organic polysaccharides. Fine roots, fungal hyphae, and climatic and fauna induced physical pressures are important in macroaggregate formation.

Many organic macromolecules and cellular structures, and microorganisms themselves are polyanions at soil pH, and are involved with inorganic colloids in dispersion and flocculation reactions. Polyvalent cation bridging occurs between organic and inorganic collordal materials. The disruption of aggregates by treatment of the soil with acid or with cation complexing agents is evidence of the occurrence of such bridging (Oades, 1984).

An array of organic acids is produced by roots and rhizosphere organisms. Biologically produced organic acids have varying ability to

chelate di- and trivalent cations. Soil fulvates are strong chelators; humates are relatively weak. Reduced pH and reduction of solution cation concentration as a result of organic acid production cause an increase in dispersible clays. This effect has been observed with corn seedlings. The observed correlation between increased fulvic acid to humic acid ratio and decreased aggregate stability with summerfallow also is predictable (Lynch, 1984; Oades, 1984).

The importance of polysaccharides in soil aggregation is now well established. Evidences include the correlation between aggregate stability and polysaccharides, the stabilisation of soil by the addition of polysaccharides, aggregate breakdown by selective oxidation of polysaccharides, and most convincing the in situ identification of clay-polysaccharide complexes using electron microscopy techniques (Cheshire, 1985; Oades, 1984). The compounds responsible are the insoluble mucilagenous compounds exuded by plant roots, fungal hyphae, and some bacteria. Bacterial cells, fungal hyphae, and fine root fragments may be completely coated and physically protected from degradation, by fine clay particles. Fungal hyphae and fine roots bind the silt size aggregates and mineral grains to form macroaggregates (Oades, 1984; Foster, 1985).

Bacterial and root mucilages do not diffuse through the soil (Oades, 1984); nor are soluble polysaccharides directly involved in aggregate formation (Monnier and Jeanson, 1965). Bacteria in the mineral soil are found in association with roots and localizations of

organic material (Brewer et al., 1983). This limits the polysaccharide role in microaggregation to the immediate vicinity of the soil organisms. Grassland systems with large annual turnovers of fine root material have strong aggregation; signs of aggregation appear as grasses invade raw parent material (Jacks, 1965). The benefit of growing grasses in a cropping rotation to improve soil stability is well established (Oades, 1984).

2.3.9 The Mull Epipedon

A mull epipedon is characterized by "the complete disintegration and humification of plant residues", an intimate complexing of humus and clay materials, and the reorganization of these materials into a friable, granular structure (Pawluk and Bal, 1985). The disintegration and humification processes are primarily (though not solely) microbial, catalyzed by a large and complex pedofaunal population. Mull humus fabric typically is formed by earthworm, enchytraeid or millipede ingestion of the soil material. These fauna have an important ability to pack the soil materials together to form very stable macrostructures. Jacks (1963) suggested the analogy of the fauna forming bricks from the microbially produced polysaccharide mortar. However Pawluk's (1985) observations of arctic tundra soils suggest that mull fabrics may arise from other processes, presumably freezing and thawing. Further, Ah horizons of parkland Black Chernozems have a 'proto' mull[5] fabric without any apparent faunal populations capable of

producing mull fabric by single ingestions of the soil matrix materials. The structure may be a result of repeated reworking and reconsumption of the soil material by macro- and mesofauna (Pawluk, 1985; McGill and Spence, 1985) and repeated penetration of the soil by fine roots, with their entourage of mucilages. The importance of freeze/thaw and wetting/drying processes to formation of platy and columnar structures respectively, has been established, however their role in the formation of the granular structure of Chernozemic Ah horizons is largely unknown.

2.4 Gray Luvisols

2.4.1 Some properties of Gray Luvisols

Gray Luvisolic soils are the dominant soils of the forested areas of the Interior Plains of Western Canada. They are characterized by a light colored, platy, eluvial A horizon and a blocky, illuvial B horizon. They do not have Solonetzic or Podzolic B horizons, and are not dominated by gleying, permafrost, a Chernozemic Ah, or organic horizons (Canada Soil Survey Committee, 1978).

The translocation, by water, of micaceous clays as well as low amounts of Al, Fe, and organic constituents from the A horizon to the Bt is the dominant pedogenic process in a Gray Luvisol (Howitt and Pawluk, 1985b). Annual carbon inputs are primarily to the soil surface, in the form of litterfall. Little mixing of the organic and mineral soil components occurs; a sequence of organic layers, from

fresh litter through various stages of decomposition to completely humified material, overlies the mineral soil.

These pedogenic processes lead to physical and chemical properties substantially altered from those of the (typically calcareous till) parent geologic material. Lessivage results in an upper mineral horizon with reduced clay content and slightly to strongly acidic reaction, and little or no buildup of organic matter. Ice lens formation during periods of freeze-thaw reinforces a weak platy structure in this Ae horizon. Water holding capacity, cation exchange capacity, and organic nutrient contents are low, compared with Chernozemic soils. To use Bal's (1982) terminology, Gray Luvisols have a low "buffer capacity". Illuvial organo-clay cutan deposition and freeze-thaw and wet-dry cycles result in a strong blocky structure and reduced permeability in the B horizon. These cause occasional temporary saturation of the upper solum (Arshad and St. Arnaud, 1980).

The surface organic horizons of a Gray Luvisol are critical to their native fertility. The LFH horizons regulate the movement of moisture into the mineral soil (Howitt and Pawluk, 1985b), and protect it from wind and water erosion. Organic matter decomposition and biological nutrient cycling processes occur primarily in the organic layers.

2.4.2 Properties of cultivated Gray Luvisols

Gray Luvisols are not well suited to arable agriculture. The growing season may be limiting, with a tendency towards drought in the early season, and excessive moisture at harvest time. The delicate ecostructure of these highly stratified soils is dramatically altered by clearing and cultivation. Removal of the organic layers and production of annual crops exposes the weakly structured upper mineral solum to the direct effects of snowmelt, rainfall and solar radiation (Bentley et. al., 1971).

Robertson and McGill (1983) listed tendency to crust, a susceptibility to pulverization, clodding or compaction due to tillage, low water holding capacity, low native fertility, and low pH buffer capacity as problematic characteristics of the cultivated A horizon. These result in reduced aeration and water infiltration, increased erosion, reduced water reserve, poor germination, seedling emergence, and plant development, and rapid soil acidification. The dense B horizon further impedes water transmission, aeration, and root development.

A rotation management system, alternating annual crop production with periods of forage production, has been found to increase soil organic matter content in the A horizon, and reduce some of the structure-related cultivation problems. This has been the recommended system for over fifty years (Robertson, 1979), and is the common practice today. The long term effects of such a management system have

been studied extensively at the Breton Plots.

The total carbon content of the upper solum of a Gray Luvisol is reduced by cultivation (Reinl, 1984); this reduction is due primarily to the partial removal of the litter layers during the clearing operations, and the rapid decomposition of the remainder after incorporation into the Ap. The carbon content of a cultivated Ap typically is greater than that of an adjacent native Ae horizon, and lower than that of the Aeh or Ahe horizon, (McGill et. al., 1986; Howitt and Pawluk, 1985a).

The effects of management systems on properties of Gray Luvisols vary with the system used. The carbon and nitrogen contents of an Ap horizon under a grain/forage rotation system were found to be greater than those under a grain/fallow rotation, after 50 years. Also a greater portion of the organic matter was in a biological form, and was biologically more active under a system with forages in the rotation (McGill et. al., 1986). Improved aggregation and tilth characteristics probably are due primarily to these factors (Robertson and McGill, 1983).

Tillage, rainfall impact, freeze-thaw and wet-dry cycles, and faunal activity are the main factors involved in fabric rearrangement, with the effects of tillage dominant. The weak, irregular shaped granic units formed by tillage are easily coalesced into a vughy porphyric fabric by direct rain impact. An increased granic and mull

component of the microfabric has been observed in soils with a litter cover, probably due to protection from rain impact, and to an improved microenvironment for faunal activity. Microarthropod populations have been observed to reflect these trends. More discrete and strongly developed granules were observed in fertilized plots, probably due to improved plant growth and therefore soil protection, as well as increased organic matter content and microbial and faunal activities (Pawluk, 1980; Berg and Pawluk, 1984).

2.5 Notes

1 Two titles do mention earthworms. Foster et al. (1985) suggested earthworm casting may be used as an indicator of soil fertility status in Western Nigeria, and Linden (1985) showed the effect of two worm species on water infiltration in tilled and untilled continuous corn. Also, one of the papers of the American Society of Agronomy suggested the use of an ant colony as a classroom illustration of faunal pedoturbation (Schuster et al., 1985).

2 Humusform "... is not confined to the so-called 'humus substances', nor even to the 'organic matter' of the soil since it comprises also the inorganic matter and the way in which the organic and inorganic constituents are mixed or combined with one another.... In terms of the usual profile nomenclature it comprises more or less the 'living' A horizon plus the L layer on its surface, although no humus form could be thought of without the connexion with the remaining parts of the soil and the interrelation between life and dynamics of both" (Kubiena, 1955).

3 Note that to Coleman, in practice, "soil" refers to the mineral layers only. This tendency for agronomists and agronomic ecologists to see the organic layers as "on" the soil adds to the misunderstanding with the zoologists, for whom the term "soil" is practically synonymous with "humusform".

4 This is strictly part of the primary, rather than the detritus food chain. Crossovers between the foodchains are common in soil, due to

faunal and microfloral species which may feed in both, and predators which feed on fauna from either. This is another example of ecosystem resistance to classification, probably the primary difficulty of ecology. (See Macfadyen, 1975.)

5 Pawluk (1985) described the fabric of the upper Ah of a parkland Chernozemic soil as a "proto" mull because of "the presence of diverse, discrete, poorly homogenized units of soil material (which) suggests an immature or 'proto' stage of mull development".

3. METHODS

3.1 Site Description

The site of the field research is several miles west of Winfield, Alberta (Sec. 8&9, Tp 46, R 4, W 5), on a ground moraine deposit (Sylvan Lake Till) with undulating topography, at an elevation of 900m (Smith and Gill, 1974). Average summer and winter temperatures for the region are approximately 13.8°C and -8.6°C, respectively. Average annual precipitation is about 440 mm, with 60% (265 mm) falling in the months of May through August, and 23% (100 mm) in the months of November through March (Lindsay et al., 1968).

The native forest vegetation in moderately well drained locations is dominated by Picea glauca, Populus tremuloides, and P. balsamifera. Some smaller Salix spp. and Betula papyrifera also are present. The understory is dominated by Rosa acicularis, Epilobium angustifolium, and Calamagrostis canadensis. In poorly drained areas Picea mariana, Larix laricina, and Salix spp. are the dominant tree species, with the lower stratum dominated by Calamagrostis canadensis and Epilobium angustifolium, or by Carex spp.

The western part of the study area is native forest (Figure 1). The remainder of the research area is divided into four agricultural fields, cleared 50 to 60 years ago.

The two southern fields, which belong to Mr. A. Bukkems, have been

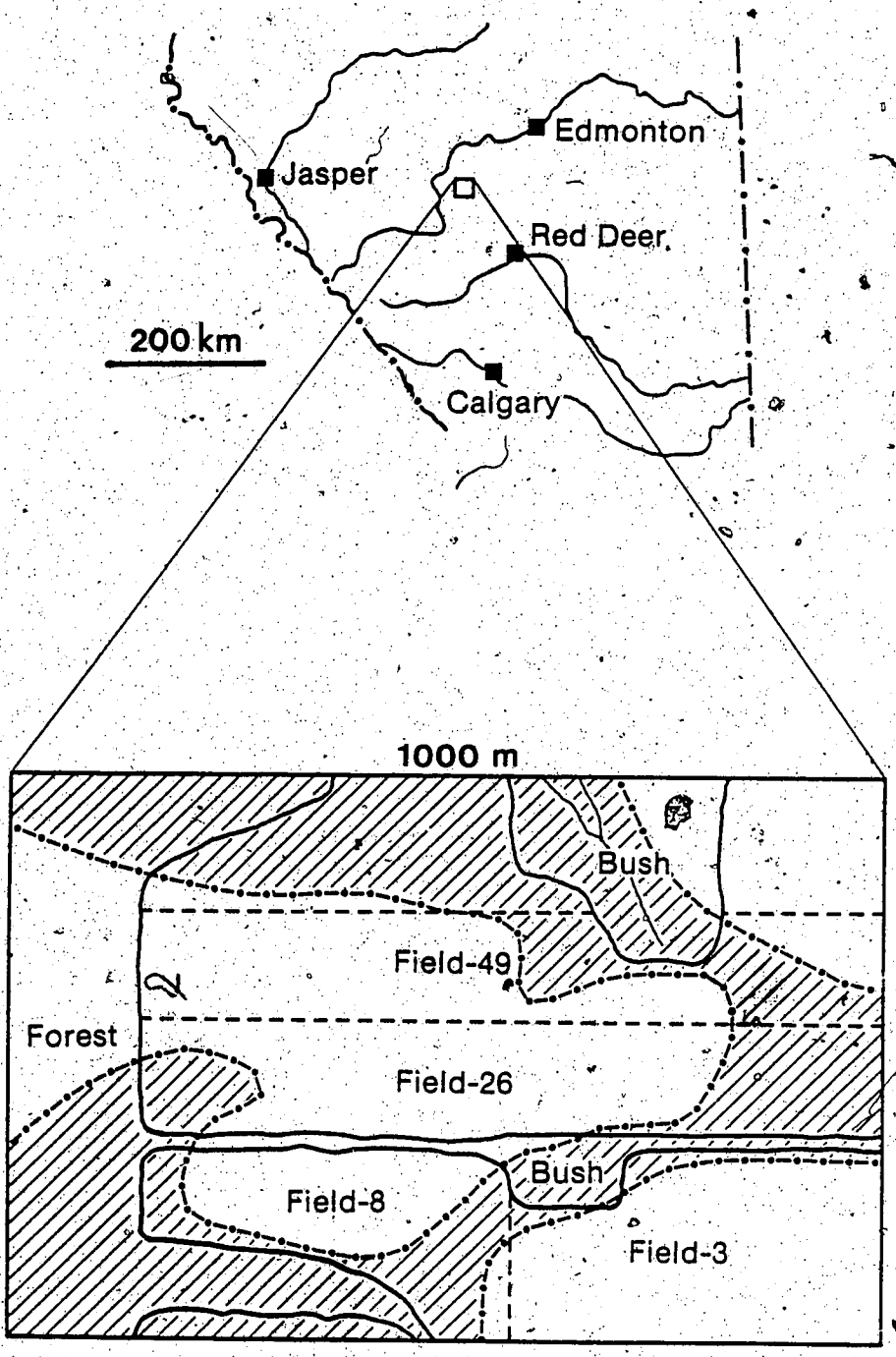

Figure 1. Location map of the study area. Gleyed areas are indicated by cross-hatching.

managed in a forage-grain rotation system typical of the agriculture of the region. At the time the field research began (fall 1982) these had been in hay crops for three and eight seasons, and are referred to in this paper as Field-3 and Field-8, respectively. Field-8 was plowed in the fall of 1983 and seeded to grain the following spring; Field-3 was plowed in the fall of 1984.

The forage crop on the Bukkems' fields was a mixture of Phleum pratense, Bromus inermis, Agropyron repens, Poa pratensis, Festuca rubra, and Calamagrostis canadensis grasses with Trifolium repens, T. pratense, and T. hybridum legumes. Weeds present included Taraxacum officinale, Fragaria virginiana, Carex spp., Arnica spp., and Equisetum spp.

The remaining two fields are a part of the Hendrigan farm.[1] These had been in continuous forage, without cultivation, for 26 and 49 years (Fields 26 and 49, respectively), at the time this research began. The dominant grasses in the Hendrigan fields are Poa pratensis and Festuca rubra, with a Phleum pratense component present. A significant population of Trifolium repens is maintained by annually broadcasting the seed at a rate of one kg ha^{-1}. Commonly found weeds include Taraxacum officianale, Achillea millefolium, Agropyron repens, Fragaria virginiana, and Equisetum spp. A few small poorly drained areas of these fields are dominated by Carex spp. with Phleum pratense and Juncus tenuis present.

3.2 Soil Description

The soils of the research area are Orthic Gray (Hubalta series) and Dark Gray Luvisols where drainage is moderately good. Imperfectly drained lower slope and local depressional areas (Figure 1) have Gleyed Luvisols and Orthic Luvic Gleysols (Raven series). The forest soils have 10 cm of moder type litter (Table 4), and may have an Ahe to 8 cm thick; often the Ahe is absent. Depth to carbonates varies from 42 to 91 cm.

3.3 Physical and Chemical Methods

3.3.1 Soil Sampling for Physical and Chemical Analyses

Preliminary soil sampling was carried out in October 1982. Three pits were dug to a depth of one metre in each of the Hendrigan fields, and one pit was dug in each of the Bukkems fields, and in the forest. Horizon designations and depths were noted, and soil samples from each horizon were air dried for use in total carbon, total nitrogen, and acidity analyses.

Soils were sampled again in the June 1983, using a hydraulic corer. Cores were 4.1 cm diameter, to a depth of 60 to 100 cm, depending on amount of compaction observed. Three sets of three cores were taken from each field and from the forest. Cores within a set were taken within 20 cm of one another. The first core in each set was used for horizon description and designation, and then sampled by

Table 4. Soil profile descriptions.

a. Description of a typical moderately well drained Orthic Gray Luvisol profile, from the research site, with notes on variability.

L	10 - 6 cm. Undecomposed and semi-decomposed poplar leaves and spruce needles; few to plentiful fine roots; slightly acid.
FH	6 - 0 cm. Black (10YR 2/1 m); decomposed leaves and needles, frequently interlayered with fungal mats, and fibrous to matted organic matter, with silt grains in lower horizon; abundant very fine and fine random, and plentiful medium random roots; clear smooth boundary; medium acid.
Ahe	0 - 4 cm. Dark grayish brown (10YR 4/2 d); loam; granular to weak platy; loose to friable; plentiful very fine and fine random and medium and coarse oblique roots; clear smooth boundary; 0 to 8 cm thick; strongly acid.
Ae	4 - 18 cm. Light gray (10YR 7/1 d); loam; moderate fine platy; very friable; few to plentiful very fine and fine random and horizontal, and few medium to coarse oblique roots; clear smooth boundary; 5 to 20 cm thick; strongly acid.
AB	18 - 25 cm. Dark brown (10YR 4/3 m), Yellowish brown (10YR 5/4 d); clay loam; weak platy to moderate fine subangular blocky; firm; few random roots; 5 to 13 cm thick or absent; very strongly acid.
Bt_1	25 - 41 cm. Dark brown (10YR 4/3 m); clay; strong fine to medium subangular blocky; firm; few fine to medium roots, between peds; dark gray (10YR 4/1 m) clay skins on ped faces; gradual smooth boundary; 11 to 26 cm thick; very strongly acid.
Bt_2	41 - 58 cm. Dark brown (10YR 4/3 m); clay; weak prismatic macrostructure breaking to strong medium subangular blocky mesostructure; firm; few medium roots; dark gray (10YR 4/1 m) clay skins along cleavage faces; gradual smooth boundary; 10 to 29 cm thick; strongly acid.
BC	58 - 65 cm. Dark brown (10YR 4/3 m); clay loam; weakly prismatic to amorphous; plastic; gradual smooth boundary; 5 to 24 cm thick; present only on deeper profiles; strongly acid to slightly acid with depth.
Ck	65+ cm. Dark brown (10YR 4/3 m); clay loam; amorphous; plastic; weak to moderate effervescence; depth to Ck varies from 42 to 91 cm; mildly alkaline.

Table 4, continued.

b. Description of the cultivated horizons of the Hendrigan fields (Field-26 and Field-49).

Turf 3 - 0 cm. Very densely woven fibrous mat of undecomposed and partially decomposed root material, with fecal and humic materials and some mineral grains between fibres, concentrated at lower depths. Small horizontal wedges of mineral soil occasionally found near the lower boundary. Abrupt smooth boundary; 2 to 4 cm thick; strongly acid.

Ap 0 - 11 cm. Light brownish gray (10YR 6/2 d) to gray (10YR 5/1 d); loam; fine granular to weak coarse platy; very friable to loose; abundant very fine to fine random roots, most abundant in upper horizon; abrupt smooth boundary; 8 to 15 cm thick; strongly acid.

Note: The remainder of the profile is similar to the forest profile, without the presence of medium and coarse roots.

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c. Description of the cultivated horizons of the Bukkems fields (Field-3 and Field-8).

Turf 1 - 0 cm. Densely woven fibrous mat of undecomposed and partly decomposed root material, with fecal and humic material and mineral grains incorporated. Intermittent in Field-8, not present in Field-3. Abrupt smooth boundary; strongly acid.

Ap 0 - 19 cm. Gray (10YR 5/1 d) to dark grayish brown (10YR 4/2 d), with pockets of light gray (10YR 7/1 d) Ae material; loam; fine granular; friable, loose; abundant very fine and fine random roots, and plentiful vertical medium roots; partially decomposed turf material occasionally found at 8 to 10 cm depth; abrupt smooth boundary; 15 to 21 cm thick; strongly acid.

Note: The remainder of the profile is similar to the forest profile, without the presence of coarse roots. The Ae horizon is typically absent due to depth of cultivation.

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horizon and air dried. The remaining two cores were sampled by horizon for bulk density assessment. Matching horizons from the three cores were bulked for total carbon, total nitrogen, and acidity analyses.

Incremental depth soil samples were taken in August 1983, to show the distribution of soil carbon in the organic and upper mineral layers. Samples were taken from four locations from each of the Hendrigan fields and from the forest. Three cores of mineral soil, 4.8 cm in diameter, were taken to a depth of 6.0 cm, subdivided into four 1.5 cm increments, and bulked by increment, at each of the sampling locations. Similarly, the organic layers were sampled using a 7.5 cm diameter sampler, three cores per sampling location. These samples were split into upper and lower halves and bulked by location. Total carbon analyses were done on these samples.

In October 1984, surface horizon samples were taken from Field-49, Field-3, and the forest, for determination of biomass. Samples of the Ap horizon were taken from ten locations from Field-3. Turf and Ap samples were taken from ten locations from Field-49, and 8 LF, FH, and surface mineral sample sets were taken from the forest. These samples were kept at 4^{o}C until fumigation could be carried out.

3.3.2 Bulk Density

Soil horizon bulk density was calculated as the mass of an oven dried core sample (measured to 0.1 g) divided by the product of the

sample's length (measured to 1 mm) and the area of the coring tube (1320 mm^2). Soil compaction during the sampling process introduces a positive error in this determination. This error was minimized by sampling when the soil was quite dry and less apt to compact, and by rejecting those cores with significant compaction.

3.3.3 Acidity

Mineral soil pH was measured in a 0.01M $CaCl_2$ suspension, using duplicate soil samples (ground to 2 mm) in a soil to solution ratio of 1:2.5 (McKeague, 1978). Organic samples, ground to 100 mesh in a Siebtechnik laboratory disk mill, were suspended in $CaCl_2$ solution in a 1:5 soil to solution ratio, also in duplicate. Potentiometric measurements were read from a Fisher Acumet Model 630 pH meter, standardized in buffer solutions at pH 4 and pH 7.

3.3.4 Particle Size Analysis

One profile from each of the four fields and one from the forest was chosen for particle size analysis of the mineral horizons. Single samples of approximately 40 g a.d. were suspended in 1000 ml of Calgon solution, as described in McKeague (1978). Readings were taken (using an ASTM Soil Hydrometer Model 152H, at 20°C) 30 seconds, 60 seconds and 8 hours after suspension, corresponding to particle diameters of approximately 75, 50 and 2 um, respectively.

3.3.5 Total Carbon

Samples for total carbon analysis were finely ground in a Siebtechnik Labor disk mill. The carbon analysis was by dry combustion, using a Leco Carbon Determinator, Model CR12. Carbon percentages were recorded to the nearest hundredth of a percent.

3.3.6 Total Nitrogen

Fine ground 0.5 g mineral samples and 0.1 g organic samples were analysed for total nitrogen using a Kjeldahl digest apparatus, with kelpak (K_2SO_4-$CuSO_4$) as the catalyst and oxidizing agent. The nitrogen present was complexed as ammonia-salicylate, and determined colorimetrically using a Technicon Autoanalyser (Technicon Industrial Method No. 376-75W/B).

3.3.7 Biomass by Fumigation Technique

Jenkinson and Powlson (1976) invented a technique to estimate soil biomass by chloroform fumigation. A modified version of this technique was used on the fall 1984 mineral soil samples. Four replicate 25 g sub-samples from each sample were incubated at field moisture content (approximately field capacity) for 12 days, two replicates having been fumigated prior to incubation. Carbon respired was collected in 0.25N NaOH solution; following incubation this was titrated with 0.10N HCl, using phenolphthalein indicator. Soil mineral nitrogen was extracted

from each sample in 2N KCl. Ammonium-salicylate complex was formed from the NH_4^+ and determined colorimetrically using a Technicon Autoanalyser (Technicon Industrial Method No. 334-74 W). Nitrate concentration also was determined by Autoanalyser (Technicon Industrial Method No. 487-77A). Carbon and nitrogen flush values were calculated as the differences between fumigated and non-fumigated sample values for respired carbon and mineral nitrogen.

3.4 Soil Animal Population Sampling Methods

3.4.1 Microarthropod sampling methods

Soil microarthropods were sampled at four times in the summer of 1983, between May 17 and August 23. Three to five soil cores (9.0 cm long by 4.8 cm in diameter) from each field and from the forest were divided into 3 cm segments and placed in a Macfadyen high gradient extractor for 5 days. Animals were collected in ethylene glycol and stored. Collembola were enumerated as Symphypleona and Arthropleona, and Acari were enumerated as Oribatids, Gamasida, Actinedida, and unidentified Acari. Other organisms (commonly Staphylinidae and Diptera larvae) were enumerated as a group.

3.4.2 Macrofauna Sampling Methods

Larger arthropods and annelids were sampled by hand from 0.125 m^2 soil samples, at three sampling times, in the summer of 1983. Two organic soil samples and one mineral sample to 20 cm depth were taken

from each stand and from the forest at each sampling time, except from Field-3, which had no organic layers. Two samples to a 5 cm depth and one from 5-20 cm depth were taken from this field at each sampling time. Specimens were stored in 70% ethanol, and identified. Some specimens suffered damage due to drying, and could not be identified.

3.4.3 Microscopy and Identification

Selected specimens of common microarthropod species were dehydrated using sequential ethanol washes of increasing concentration, were dried by critical point drying, and examined with a Cambridge Stereoscan S4 scanning electron microscope. Common gamasid, actinedid and acaridid specimens were mounted on microscope slides using Hoyer's Medium (Krantz, 1978), and sent to E. E. Lindquist, I. Smith and K. W. Wu respectively, of the Biosystematics Research Institute of Canada, for identification. Oribatei and Collembola specimens were identified in 70% alcohol by V. Behan-Pelletier of the Biosystematics Research Institute, and J. A. Addison, of Tofield, Alberta, respectively.

3.5 Micromorphological Methods

Soil thin sections (7.5 cm x 5 cm x 30 um) were prepared from each field and from the forest using Scotchcast epoxy resin for vacuum impregnation. Pairs of sections were prepared from 5 cm depth increments, to 15 cm depth. Three pairs were prepared from Field-3, three pairs from Field-49, two pairs from the forest, one pair from

Field-8, and one pair from Field-26. Thin section description was according to the terminology of Brewer (1964, 1979).

3. Common-Uniformity and Statistical Interpretation

A fundamental assumption of this study is that, before cultivation, the soils of the agricultural fields at the research site were similar to the current forest soil in those parameters being considered. There are two aspects to this assumption: first, that there is no significant spatially dependent variance across the research site, and second, that the forest soil has not changed significantly in the years since the adjacent fields were broken. The second is valid if one avoids those areas of forest which have been anthropogenically disturbed, and those parameters which may respond to any possible changes to the local groundwater system which may result from agricultural activity. The first aspect of the assumption requires more attention.

Soil parameters are spatially highly variable. This variation is observed between samples taken in close proximity; larger landscape-related variance trends also may be superimposed on the local variation. Slope position and aspect, microclimate, surficial geology, groundwater regimes, and past vegetation history are landscape characteristics which vary spatially, and affect soil parameters.

An agricultural field experiment designed to study differences

between treatments must be able to distinguish treatment variance from soil spatial variance. To do this, treatments must be replicated in a spatially random manner. Variance within a single treatment plot is a measure of local soil variability; variance between means of plots of like treatment is a measure of the landscape related variance. Analysis of variance is the statistical method most often used to distinguish these variances, and determine whether significant differences exist between treatments.

An unfortunate characteristic of the research site of this paper is that it was not originally designed as a research site. (In the 1930's Mr. Hendrigan was more concerned with economic survival than with statistical method!) While variance within a plot can be estimated for a given parameter, possible significant differences between plots due to landscape-related soil variance cannot be distinguished from treatment-induced differences, because of the lack of randomly distributed replicate plots. To make observations about treatment effects one must assume that spatially dependent variance across the research site does not interfere significantly with the treatment effects.

To minimize the effects of landscape related variance on the observations of this experiment, sampling within fields was limited as much as possible to upper and mid slope positions, with good to moderate drainage. At the same time the uncertainty remaining in the assumption of insignificant spatially dependent variance between fields

must be recognized.

Analysis of Variance[2] was used with Least Significant Difference or Student-Neuman-Keuls' tests when the F-value was significant, to determine significant differences between means, with 95% confidence. The SPSS[X] and SAS statistical packages were used for these analyses.

3.7 Notes

1. The late Lou Hendrigan's farming philosophy and system are described in an article by T. Hockaday, "Old ideas that still work", in Cattlemen, June 1981.

2. In this case variance is not being analysed, strictly speaking, since spatial variance between treatments is not distinguished from treatment effects. The alternative of doing multiple unpaired t-tests is no more valid statistically, since an unpaired t-test is mathematically identical to a one way analysis of variance with two treatments (Little and Hills, 1978, p.39). While either method will estimate whether means differ, neither can say why. Analysis of variance is easier to carry out, and less apt to result in type 1 errors, since fewer comparisons are permitted.

4. RESULTS AND DISCUSSION

4.1 Analytical Properties

4.1.1 Horizonation and Particle Size Analysis

4.1.1.1 Results

The soils of the research site have developed in morainal material of clay loam texture, with 34 to 39% sand, 26 to 28% silt and 33 to 38% clay in the C horizons (Table 5). Illuviation has resulted in Bt horizons with 38 to 45% clay; Ae clay content is 16 to 27%.

Particle size analysis data in Table 5 are from single cores, therefore statistical comparison of fields is not possible. The uniformity of the particle size distributions of similar horizons (in particular the C horizons) supports the assumption of uniformity of the research site previous to clearing and cultivation. The high clay content measured for the Forest Ahe horizon (40%), and the Field-26 Ae horizon sand (21%) and silt (63%) contents are anomalous, and may reflect a thin lacustrine veneer.

The forest organic horizons were of course absent from the cultivated sites. Field-3 had no turf horizon; in Field-8 a nearly continuous turf of varying thickness had developed. Field-26 and Field-49 had continuous, very tough, tightly woven turf horizons. The turf of Field-26 was an average of 2.4 cm thick; Field-49 had a significantly thicker 3.3 cm turf.

Table 3. Particle size analysis for mineral horizons. Results from five core samples.

Stand	Horizon	% sand	% silt	% clay
Forest	Ahe	32	28	40
	Ae	39	39	23
	AB	39	28	33
	Bt1	35	27	38
	Bt2	32	27	42
	C	35	28	36
Field-3	Ap1	38	42	20
	Ap2	40	39	21
	Ae	43	30	27
	AB	39	25	36
	Btgj	39	23	38
	Btg	37	24	39
	BC	35	26	39
	Ckg	36	27	37
Field-8	Ap	37	43	20
	AB	42	33	25
	Bt1	36	24	41
	Bt2	36	24	40
	Ck	36	26	37
	Cca	37	28	34
Field-26	Ap	32	49	19
	Ae	21	63	16
	AB	37	31	32
	Bt1	33	22	45
	Bt2	37	23	40
	BC	33	28	38
	Ck	34	28	38
Field-49	Ap	36	43	21
	Ae	44	36	20
	AB	40	27	32
	Bt1	31	24	45
	Bt2	33	26	42
	Ck	36	26	38
	Cca	39	28	33

Some forest profiles included an Ahe horizon as much as eight centimetres thick; often the Ahe was absent (Tables 4, 6). The Ae horizon was an average of nine centimetres thick; thicknesses of five to 20 cm were observed. The AB horizon was an average of 10 cm thick.

The Ap horizon thicknesses of Field-3 and Field-8 were 20 and 19 cm respectively (not significantly different) while the Ap horizons of Field-26 and Field-49 were significantly thinner (11 cm). The Field-26 and Field-49 Ap horizons were underlain by truncated Ae horizons, while the Ap horizons of Field-3 and Field-8 usually included all the original Ae, and were underlain by a truncated AB horizon. The lower boundaries of all Ap horizons were abrupt and smooth.

The Bt horizons had thicknesses which were variable and were not found to be statistically different among fields.

The differences in horizonation between sites cause a problem in the statistical interpretation of the soil chemistry data. In the analysis of the Fall 1982 and June 1983 data, the Ap horizons were compared with the forest Ahe samples, although they include material from the Ae and AB horizons as well. Forest mineral soil samples taken in October of 1984 included both Ahe and Ae material, while the forage stand samples were from the total Ap horizons. However, the deeper Ap horizons included a greater percentage of Ae and AB horizon material than did the shallow Ap horizons.

Table 6. Horizon thicknesses (cm) measured in the October 1982 and June 1983 profile samples. Mean (x), standard deviation (sd), and number of samples (n) are reported by field and horizon.

Horizon	Forest			Field-3			Field-8			Field-26			Field-49		
	x	sd	n	x	sd	n	x	sd	n	x	sd	n	x	sd	n
LFH / turf	10.5	1.9	4	na	na	na	1.	0.	3	2.4	0.8	5	3.3	0.4	5
Ahe / Ap	7.	2.	3	20.	1.	4	19.	2.	4	11.5	2.1	5	11.	3.	5
Ae	9.	3.	4	na	na	na	na	na.	na	5.	2.	4	8.	2.	4
AB	10.	7.	4	7.	2.	4	8.	2.	4	8.	2.	4	9.	7.	4
Bt	16.	4.	4	14.	2.	4	18.	6.	4	18.	5.	5	15.	3.	5
Bt_2	20.	10.	3	17.	4.	4	16.	6.	4	14.	5.	4	13.	3.	4

4.1.1.2 Discussion

In recent years, with heavier machinery, Mr. Bukkems has tended to cultivate the soil to a greater depth than was practical in the first half of this century. The effects of this, and to a lesser extent the effects of compaction with time under a forage stand, were seen in the differences of depth of Ap horizons between the Bukkems and Hendrigan fields.

In a survey of changes in soil organic carbon due to agriculture in Alberta, Reinl (1984) found a mean Ap horizon thickness in cultivated Gray Luvisols (from seven sites) of 16.7±2.7 cm. Adjacent native soil LFH and Ahe horizon depth was 10.2±6.3 cm, in the Reinl (1984) study.

The original organic horizons developed under forest vegetation were destroyed by clearing and initial cultivation of the field sites. Organic residues not burned in the clearing process presumably have been oxidized or humified in the interim. Frequent cultivation has prevented the buildup of an organic horizon in Field-3; turf horizons previously formed in Field-8 also were destroyed by cultivation during grain production cycles.

It is not expected that cultivation and surface vegetation differences would significantly affect the thicknesses of the Bt horizons within 50 years; if differences had been observed they would

make highly suspect the assumption of initial similarity between sites. (That differences were not found does not validate the assumption, nor were enough samples taken to show differences in mean thicknesses which may exist, given the variances observed.)

4.1.2 Bulk Density

4.1.2.1 Results

Density measurements of the turf horizons were highly variable (Table 7), because of incorporated mineral materials and, in Field-8, difficulty in making volume measurements due to varying thickness within individual samples. The estimated density of 0.38 Mg m^{-3} for this turf probably was inaccurate. The thicker turfs were similar in density to the forest organic horizons (Figure 2; densities of L, F, and H horizons were not measured separately).

The mean density of the forest Ahe horizon was 1.13 Mg m^{-3}, the Ae was 1.48 Mg m^{-3}. The Ap horizons had mean densities of 1.18, 1.29, 1.37, and 1.22 Mg m^{-3} from fields 3, 8, 26 and 49 respectively. The density of the Ap horizon of Field-26 was significantly greater than those from Field-3 and Field-49, and than the forest Ahe horizon.

The typical undisturbed forest profile had continually increasing soil density with depth, to a density of about 1.7 Mg m^{-3} in the Bt_2 and C horizons. The cultivated profiles had a minor density peak in the horizons immediately below the Ap horizon.

Table 7. Horizon bulk density ($Mg\ m^{-3}$) calculated for the October 1982 and June 1983 profile samples. Mean (x), standard deviation (sd), and number of samples (n) are reported by field and horizon.

Horizon	Forest			Field-3			Field-8			Field-26			Field-49		
	x	sd	n	x	sd	n	x	sd	n	x	sd	n	x	sd	n
LFH / turf	0.17	0.02	3	na	na	na	0.38	0.11	3	0.15	0.03	3	0.18	0.08	3
Ahe / Ap	1.13	----	2	1.18	0.02	3	1.29	0.06	3	1.37	0.03	3	1.22	0.06	3
Ae	1.48	0.15	3	na	na	na	na	na	na	1.61	0.13	3	1.56	0.11	3
AB	1.58	0.05	3	1.69	0.17	3	1.64	0.02	3	1.54	----	2	1.48	----	2
Bt	1.61	0.03	3	1.60	0.07	3	1.57	0.04	3	1.58	0.06	3	1.57	0.04	3
Bt_1	1.70	----	2	1.66	0.02	3	1.71	0.04	3	1.70	0.04	3	1.62	0.03	3
C_2	1.68	0.04	3	1.73	0.02	3	1.74	----	2	1.68	----	1	1.69	----	1

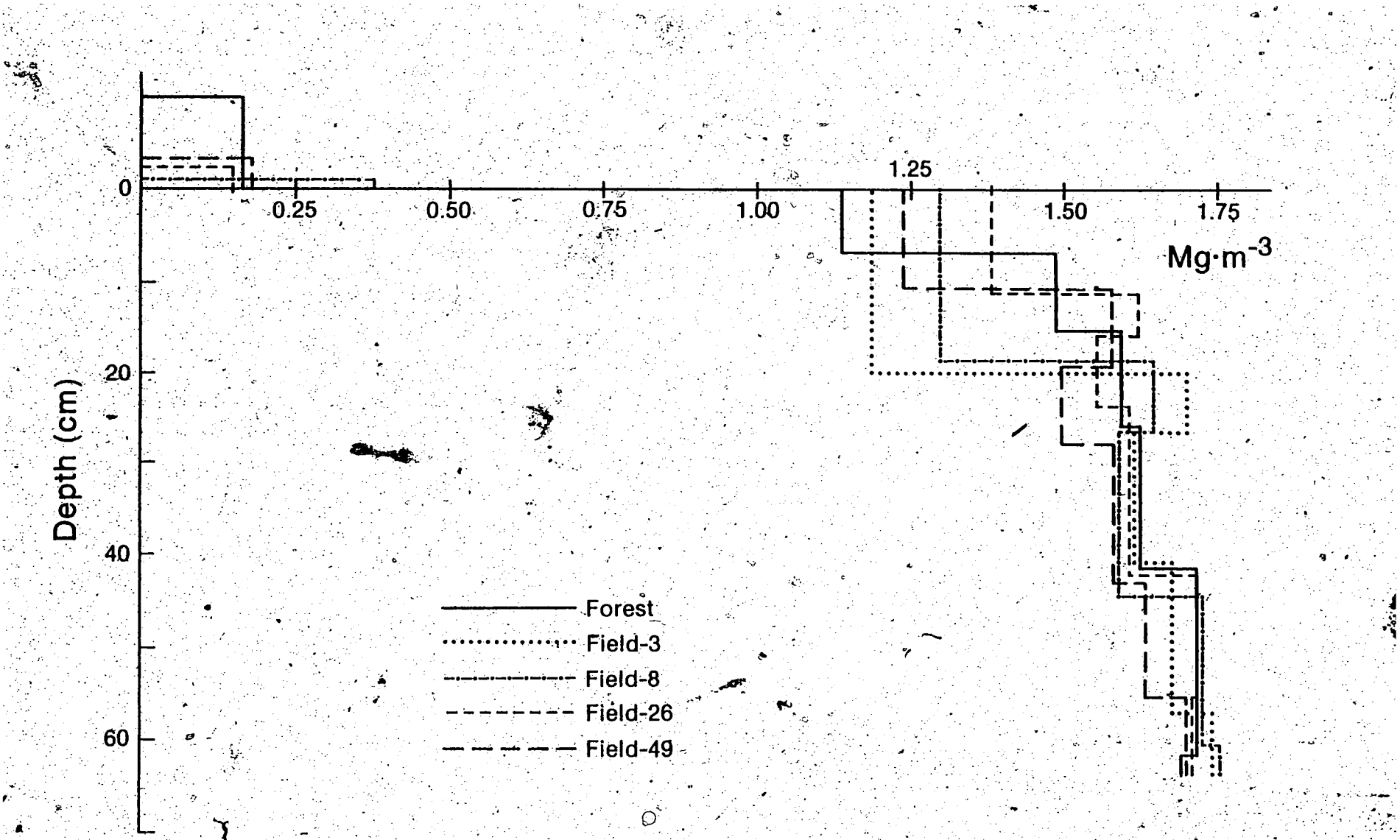

Figure 2. Mean soil bulk density by depth, for each stand.

4.1.2.2 Discussion

The Ap horizon densities reported above compare well with others in the literature. Reinl (1984) found a mean Ap horizon density of 1.3 ± 0.1 Mg m^{-3} from Gray Luvisolic sites. The mean densities of the Breton plot Ap horizons (on Gray Luvisols after more than 50 years under a 5 year hay/grain or a 2 year wheat/fallow rotation) ranged from 1.30 to 1.37 Mg m^{-3} (McGill et al., 1986).

A number of factors may affect the density of a soil. Cultivation, root development, faunal pedoturbation, and increased organic matter content may decrease soil density; traffic, grazing and weathering processes may increase density. A thick turf horizon might reduce the compacting effects of the latter factors.

An apparent trend of increasing density of the Ap horizons with stand age, from Field-3 to Field-26 may be due to compaction from traffic, grazing and weathering. This trend may peak some time between 8 and 49 years since cultivation, after which time the developed turf may protect the soil from further compaction, and the effects of biological processes which reduce soil density, may become evident.

The high densities immediately below the Ap horizons probably were a "plow pan" effect. In the two older stands this also may have been due to traffic and grazing compaction forces not adequately

counteracted at this depth by the loosening effects of root growth. Or this peak may be an artifact of core compaction during sampling; this possibility is supported by the relatively high standard deviations of the densities of the Field-3 AB horizon, and the Ae horizons from Field-26 and Field-49.

4.1.3 Soil pH

4.1.3.1 Results

Soil pH was measured in $CaCl_2$ solution, so that the values recorded in Table 8 (Figure 3) are about one pH unit lower than those which might be expected in distilled H_2O. The three turf horizons were significantly more acidic (pH 4.6 to 4.7) than the forest organic horizon (5.4). The Ae horizons of Field-26 and Field-49 also had a significantly lower pH (4.6) than the forest Ae (4.8), however these values were similar enough that their differences probably are not important to understanding the system. Other values were not statistically different between sites. The Ap mean pH values were 4.7 to 4.8, and Bt horizon pH values were 4.3 to 5.2. The C horizon samples were neutral to basic because of the presence of carbonates.

4.1.3.2 Discussion

The low soil pH values are typical of Gray Luvisols in the area. The virgin forest site at the Brazon plots had an LFH pH of 5.5, an Ae pH of 4.8-5.1, and a Bt pH of 4.7-4.9, measured in $CaCl_2$. Ap horizon

Table 8. Horizon H activity (pH) measured in the October 1982 and June 1983 profile samples. Mean pH, standard deviation (sd), and number of samples (n) are reported by field and horizon.

Horizon	Forest			Field-3			Field-8			Field-26			Field-49		
	pH	sd	n	pH	sd	n	pH	sd	n	pH	sd	n	pH	sd	n
LFH / turf	5.4	0.2	4	na	na	na	4.6	0.2	3	4.7	0.2	5	4.6	0.1	5
Ahe / Ap	4.9	0.2	3	4.8	0.2	4	4.8	0.1	4	4.7	0.1	5	4.8	0.4	5
Ae	4.8	0.2	4	na	na	na	na	na	na	4.6	0.1	4	4.6	0.1	4
AB	4.8	0.4	4	4.6	0.1	4	4.4	0.2	4	4.4	0.1	4	4.6	0.9	4
Bf	4.8	0.7	4	4.5	0.1	4	4.3	0.2	4	4.4	0.2	5	5.2	1.3	5
Bt 1	5.1	1.2	3	4.9	0.2	4	4.5	0.7	4	4.7	0.6	5	4.7	0.9	4
C 2	7.1	0.4	4	6.3	0.8	4	7.3	0.3	3	7.5	0.1	3	7.5	0.1	3

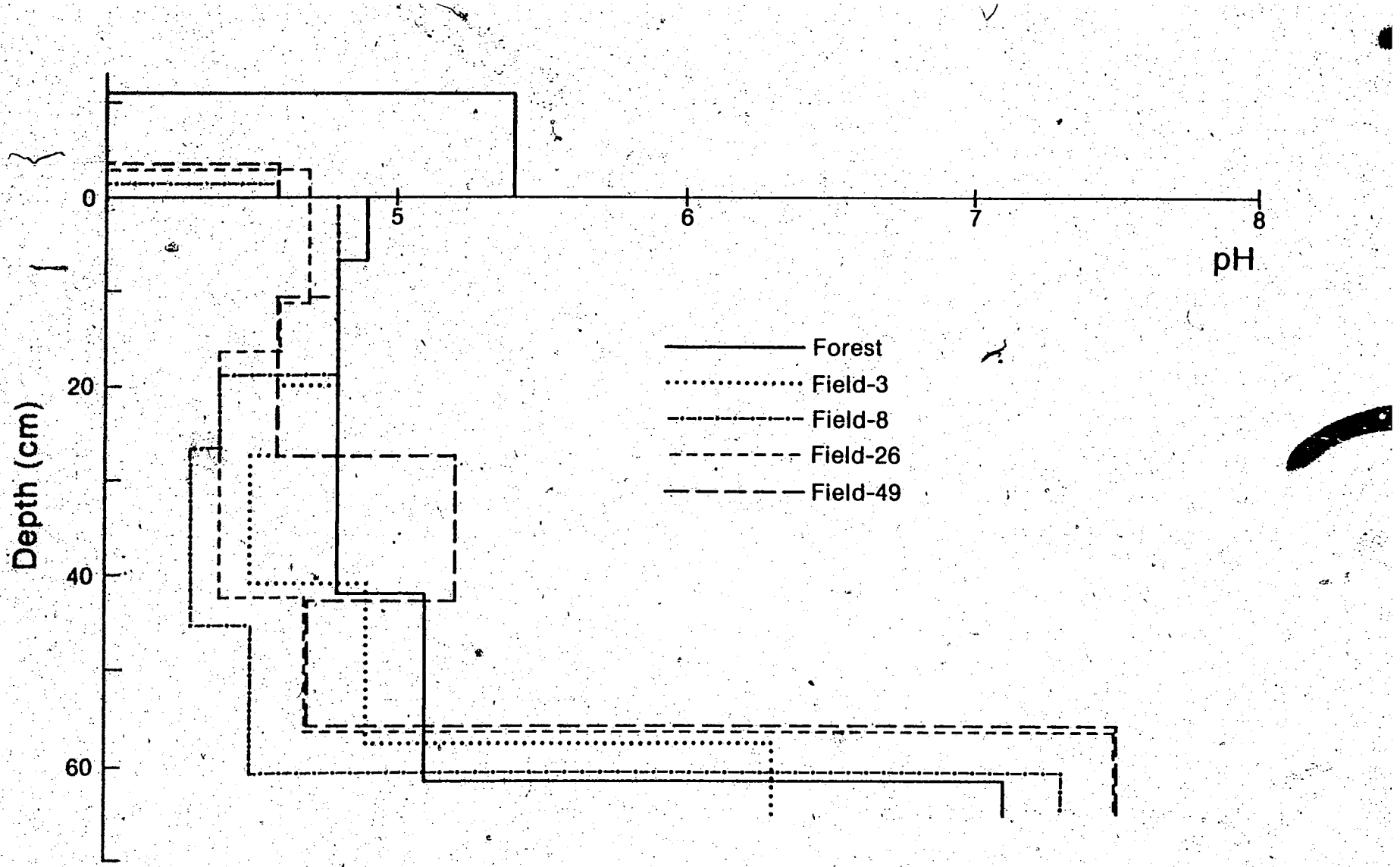

Figure 3. Mean soil activity (pH) by depth, for each stand.

pH values were 4.7-6.1 at the Breton plots (Cannon et al., 1984). What is surprising (and unexplained) is the consistently lower pH of the turf horizons compared with the forest organic horizons.

Canopy drip pH from the forest site at Breton was near neutral, which indicates "that acidic soil pH values were the result of mineral hydrolysis and/or biological processes, rather than external factors" (Howitt and Pawluk, 1985b). Presumably the acidic products of decomposition reactions and/or the release of acidic components from plant fragments during decomposition may have been greater in the turf horizons than the forest organic horizons.

4.1.4 Total Carbon

4.1.4.1 Results

Percent total carbon (mass basis) was measured from all soil samples taken for chemical analyses. Results from the total profile samples taken in October 1982 and June 1983 were compared statistically. The August 1983 incremental samples and the October 1984 biomass samples provide more data from the surface horizons.

Mean carbon contents of the organic horizons (29%, 24%, 31% and 34% from the forest and fields 8, 26, and 49 respectively; Table 9; Figure 4) from the October 1982 and June 1983 samples were not significantly different.

Table 9. Carbon content (%, mass basis) measured in the October 1982 and June 1983 profile samples. Mean (x), standard deviation (sd), and number of samples (n) are reported by field and horizon.

Horizon	Forest			Field-3			Field-8			Field-26			Field-49		
	x	sd	n	x	sd	n	x	sd	n	x	sd	n	x	sd	n
LFH / turf	29.3	4.2	4	na	na	na	24.0	3.0	3	30.9	10.1	5	33.8	3.3	5
Ahe / Ap	5.21	3.42	3	3.21	0.62	4	2.11	0.45	4	2.06	0.18	5	2.81	0.54	5
Ae	0.72	0.24	4	na	na	na	na	na	na	0.43	0.06	4	0.54	0.22	4
AB	0.50	0.10	4	0.40	0.05	3	0.48	0.10	4	0.49	0.07	4	0.48	0.06	4
Bt$_1$	0.51	0.05	3	0.49	0.06	4	0.54	0.03	3	0.51	0.02	5	0.54	0.08	5
Bt$_2$	0.53	----	2	0.54	----	1	0.52	----	1	0.44	----	2	0.51	0.05	3
C	0.62	----	1	0.44	----	1	0.45	----	1	0.72	----	1	0.74	----	1

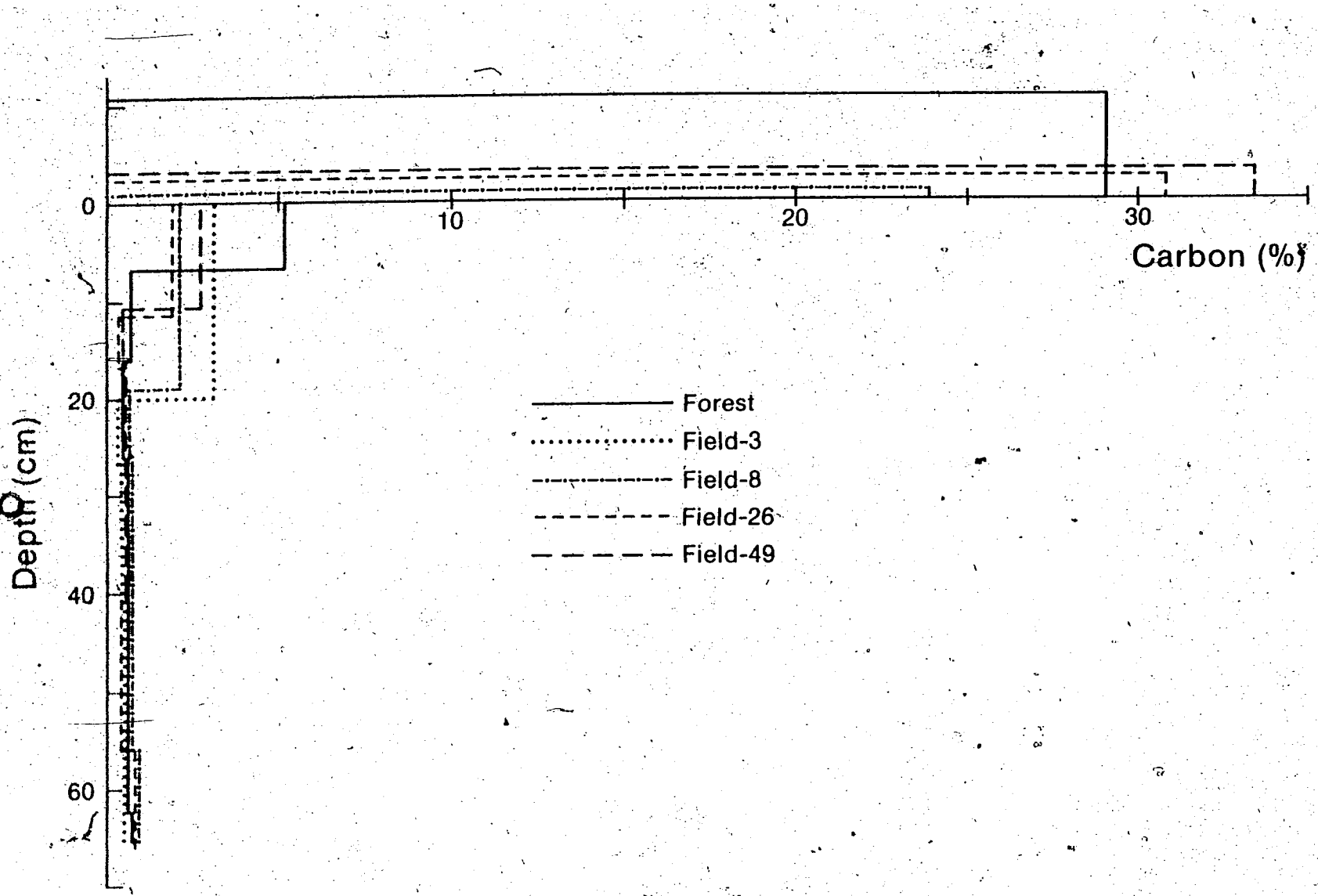

Figure 4. Mean total soil carbon (mass basis) by depth, for each stand.

The organic horizon samples from the August 1983 sample set, from Field-26 and Field-49 and from the forest were divided into upper and lower depth increments. The mean total carbon contents of the upper increments were 43%, 43%, and 44% for the forest, Field-26 and Field-49 samples, respectively (Table 11, not statistically different). The lower increments had respective carbon contents of 23%, 32%, and 33%, with the value for the forest sample significantly lower than those of the turf horizons.

In the October 1984 sampling for fumigation, the forest organic horizons were divided into two depths. The upper (LF) horizon had a measured mean total carbon content of 47% (Table 10), significantly higher than the underlying (FH) horizon (36%) and the turf horizon from Field-49 (39%).

The mean carbon contents of the Ap horizons (3.2%, 2.1%, 2.1%, and 2.8% from the October 1982 and June 1983 samples from fields 3, 8, 26, and 49 respectively; Table 9) do not differ statistically; all were significantly less than the forest Ahe horizon mean of 5.2%. Mean total carbon contents of the mineral samples from the October 1984 sampling (Table 10) were: 3.5% for the Field-49 Ap horizon, 2.4% for the Field-3 Ap horizon, and 1.4% for the forest A horizons (Ahe and Ae) to 10 cm depth. These were significantly different from one another.

Mineral soil samples of the August 1982 sample set were taken at four 1.5 cm depth increments (Table 11; Figure 5). Total carbon values

Table 10. Mean total carbon and nitrogen contents of surface soil samples from the October 1984 sampling for biomass determination. Standard deviations are in parentheses.

Stand	Layer	n	Carbon % mass basis	Nitrogen (mg/g)	C to N ratio
Forest	[illegible]	8	47.3 (1.9)	19.9 (0.9)	23.8 (1.9)
	FH	8	35.9 (7.9)	19.0 (3.2)	18.7 (1.4)
	A	8	1.4 (0.8)	1.2 (0.6)	11.9 (1)
Field-3	Ap	10	2.4 (0.5)	1.7 (0.3)	13.8 (1)
Field-49	Turf	9	39.1 (2.5)	22.7 (2.0)	17.3 (1.5)
	Ap	9	3.5 (0.9)	2.5 (0.8)	14.4 (1)

Table 11. Mean total carbon content (%, mass basis) of the August 1983 incremental surface samples. Standard deviations are in parentheses. n=4.

Layer (mm depth)	Forest		Field-26		Field-49	
upper organic	43	(2)	43	(2)	44	(1)
lower organic	23	(4)	32	(4)	33	(6)
mineral (0-15)	11.0	(7.2)	2.9	(0.3)	3.7	(0.5)
mineral (15-30)	6.8	(4.0)	2.2	(0.2)	2.8	(0.5)
mineral (30-45)	2.9	(0.8)	2.0	(0.2)	2.7	(0.5)
mineral (45-60)	2.4	(0.8)	2.0	(0.2)	2.6	(0.6)

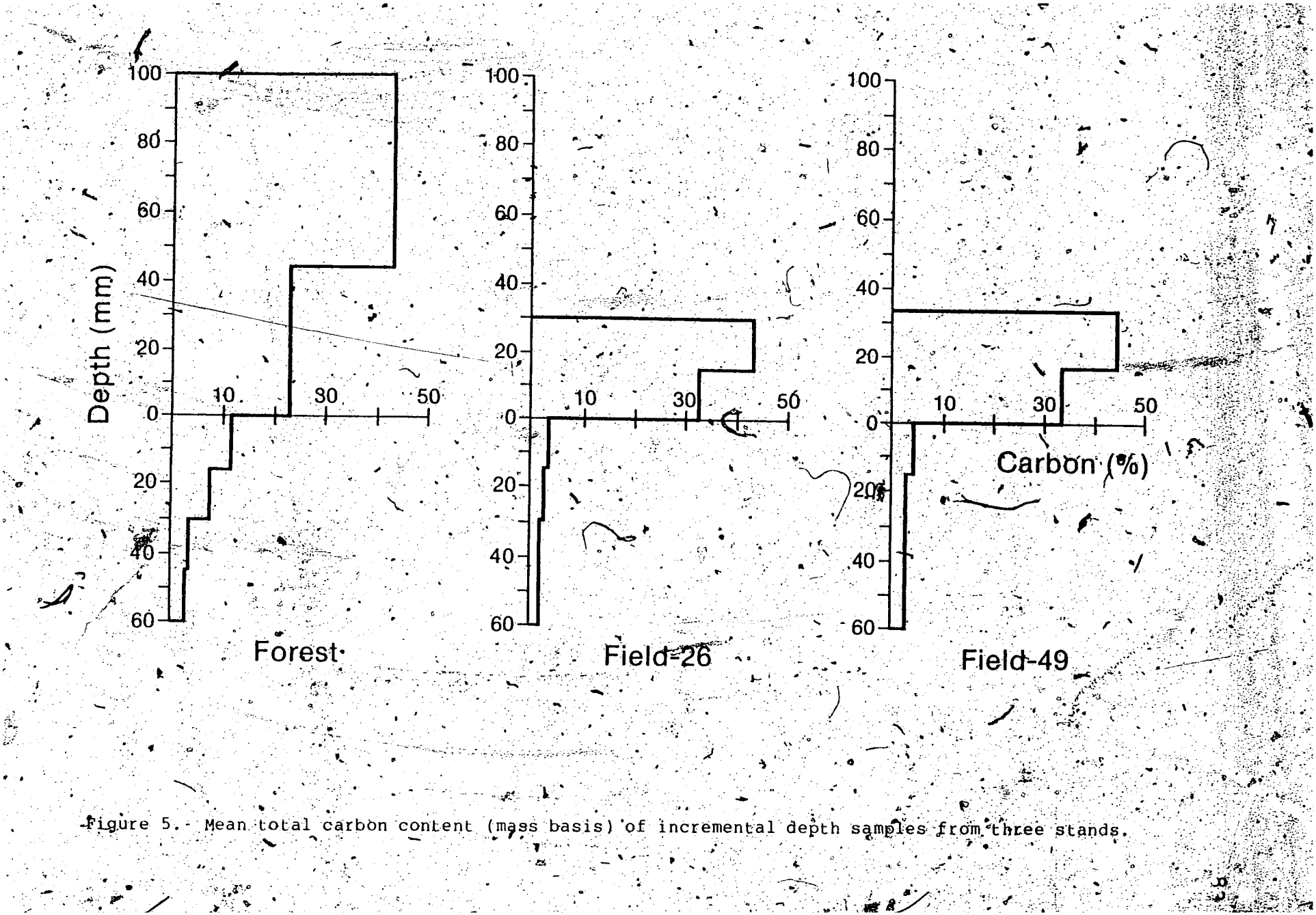

Figure 5.- Mean total carbon content (mass basis) of incremental depth samples from three stands.

from Field-26 from the four depths were not statistically different from those of Field-49, although the numerical means were each 0.6 to 0.8% lower. Carbon content decreases with depth in each field, from 2.9 to 2.0% in Field-26, and from 3.7 to 2.6% in Field-49, over the four increments (six centimetres depth). The carbon contents of the four forest soil incremental depth samples were 11.0, 6.8, 2.9 and 2.4%; the carbon contents of the upper two increments (0-3 cm) were significantly greater than the same increments from the forage fields. This observation was similar to the observed difference (noted above) between the forest Ahe and the cultivated Ap horizons.

Mean carbon contents of Ae horizons varied from .72% in the forest to .43% and .54% in Field-26 and Field-49 respectively and were not significantly different (Table 9). Mean carbon contents of AB horizons were .48% to .50%, while Bt horizon contents were between .44% and .94%. Larger total carbon percentages in the C horizons were from the presence of free carbonates.

4.1.4.2 Discussion

Reinl (1984) found 1.6-3.0% organic carbon in the Ap horizons of Gray Luvisol sites surveyed; Breton plot organic carbon contents average 1.16-1.75% (McGill et al., 1986).

The data from the Ap horizons were ambiguous concerning the change in carbon content with time under a forage stand. The first data set

did not have an adequate number of samples to show statistical differences. The second set showed a greater carbon content (mass basis) under a 49 year old forage stand than under a three year old stand from a hay/grain rotation management sytem. Both had a greater concentration of carbon than had the same depth of mineral soil from the undisturbed forest.

Reinl (1984) found a decrease in organic carbon content due to cultivation of Gray Luvisols. In that study, however, the forest organic horizons were not separated from the A horizons. The changes in soil organic matter dynamics brought about by imposed agricultural systems do not involve only gains or losses, but also significant redistributions.

The incremental depth samples suggest that the carbon content of the virgin forest soil may not decrease in abrupt increments, from the litter layer to the Ae horizon; rather there may be a relatively continuous decrease in carbon concentration from the fresh litter through the fermentation and humus layers, and into the mineral soil. (Incremental depth sampling with narrower depth increments would be required to test this.) Ecologically, the upper solum, from the litter layer to the Ae horizon, may be a near-continuum of finely stratified, vertically overlapping, horizontal microhabitats. (Thin sections permit a microscopic assessment of this hypothesis.)

In Fields 26 and 49, however, the carbon concentration was greater

in the lower turf than in the forest FH increment. (The lower turf horizon was less humified than the forest F_2 and H horizons.) The forest Ahe horizons had a higher carbon content than had the upper Ap horizons under turf. The carbon content decrease from the organic to the mineral horizon was less abrupt in the forest profiles than in Fields 26 and 49.

Clearing and cultivation of a Gray Luvisolic soil causes a rapid oxidation of much of the original LFH horizon material, and partially homogenizes the soil within the plow depth, resulting in a relatively uniform carbon distribution throughout the plow depth. Under the long term forage stands, a forest-like carbon distribution had partially redeveloped. Significant turf horizons had formed on the surface, and incremental decreases in carbon content with depth, in both the organic and mineral horizons, were evident, although the organic-to-mineral soil boundary was more abrupt, in terms of change in carbon content.

4.1.5 Total Carbon, Volume Basis

4.1.5.1 Results

The calculation of the mass of carbon per unit volume of soil permits comparison of profiles on the basis of total carbon content to a given depth. The volume-basis carbon contents of the organic horizons were not significantly different, despite the large differences in the estimated means of 46, 92, 56 and 63 mg cm^{-3} from the forest and fields eight, 26, and 49 respectively (Table 12; Figure

Table 12. Carbon content, soil volume basis ($mg\ cm^{-3}$) calculated for the October 1982 and June 1983 profile samples. Mean (x), standard deviation (sd), and number of samples (n) are reported by field and horizon.

Horizon	Forest			Field-3			Field-8			Field-26			Field-49		
	x	sd	n	x	sd	n	x	sd	n	x	sd	n	x	sd	n
LFH / turf	46.	7.	3	na	na	na	92.	28.	3	56.	11.	3	63.	21.	3
Ahe / Ap	37.	---	2	40.	5.	3	27.	6.	3	27.1	2.2	3	31.6	1.3	3
Ae	10.8	3.5	3	na	na	na	na	na	na	7.1	0.4	3	9.8	1.8	3
AB	7.7	1.6	3	6.8	0.9	3	7.7	1.8	3	7.6	---	2	7.8	---	2
Bt_1	8.2	0.9	3	7.5	0.8	3	8.5	0.2	3	7.9	0.7	3	8.0	1.6	3
Bt_2	9.1	---	2	8.8	---	1	9.1	---	1	7.7	---	1	8.2	---	2
C	10.6	---	1	7.5	---	1	7.9	---	1	---	---	-	---	---	-

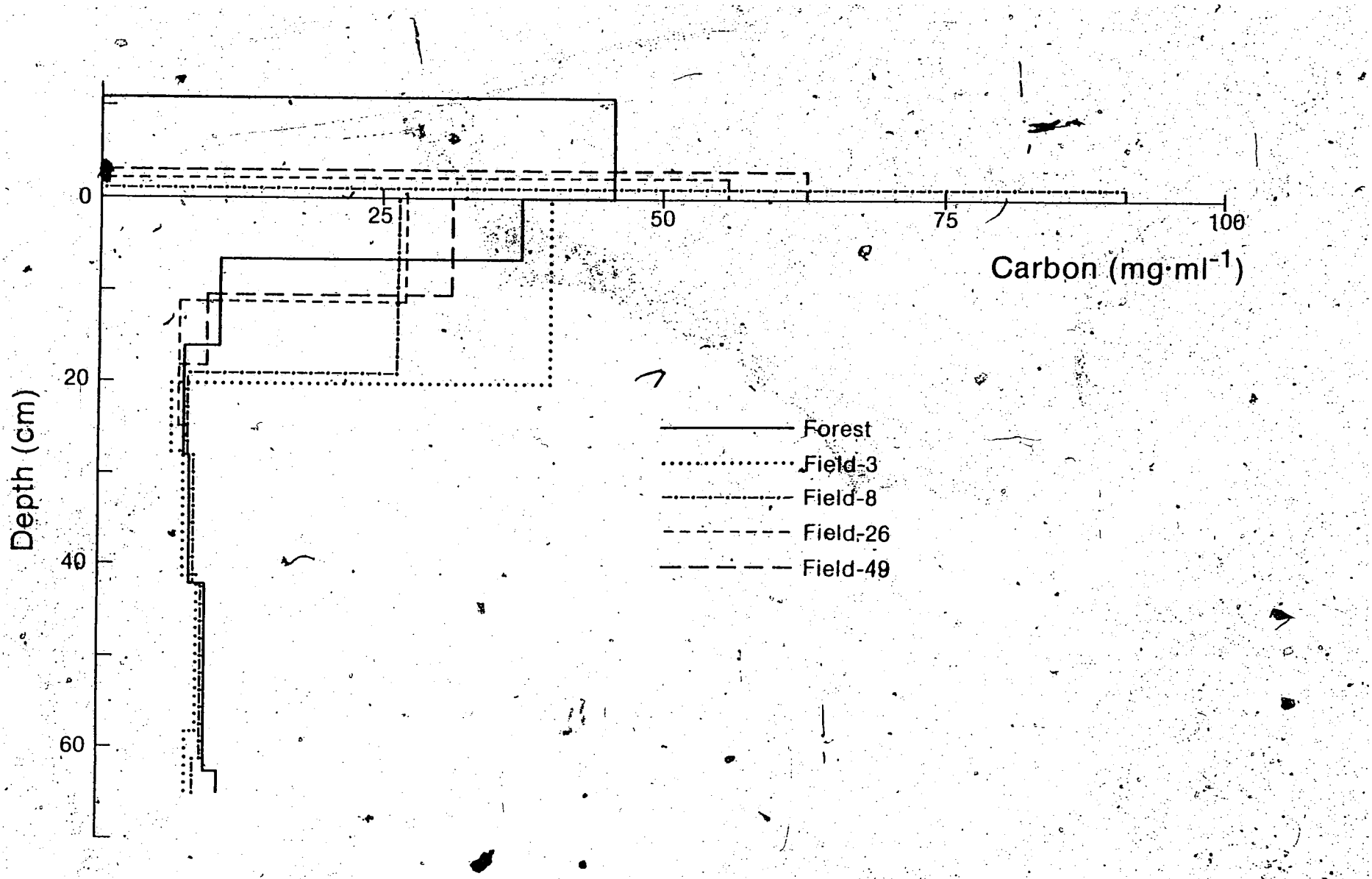

Figure 6. Mean total soil carbon (soil volume basis) by depth, for each stand.

6). The corresponding ratios of (standard deviation/mean) were 0.14, 0.31, 0.20, and 0.21 respectively. If these are compared with the corresponding ratios from the bulk density values (0.12, 0.29, 0.20, and 0.44) and the %C values from the June 83 samples (0.14, 0.11, 0.10, and 0.10) it appears the large variance in the volume-basis carbon content estimates for the turf horizons was from the variance in the bulk density estimates. Further, it appears the variance in the density values is due to inaccurate sample thickness measurement more than to the presence of varying amounts of mineral material in the samples, because the %C measurements, which also would be susceptible to varying mineral content, do not show as great a variance as do the bulk density measurements.

Volume-basis mean carbon contents by horizon (Table 12; Figure 6) were 37, 40, 27, 27, and 32 mg cm^{-3} from the forest Ahe and the Ap horizons of fields 3, 8, 26 and 49, respectively. These did not differ significantly between sites. The previously noted significantly greater bulk density of the Field-26 Ap horizon and mass basis carbon content of the forest Ahe were negated by relatively low mass basis carbon content and low bulk density, respectively.

The total carbon content of the organic horizons, per cm^2, calculated from the October 1982 [illegible] June 1983 data, was significantly greater in the forest (Table 13; [illegible] mg) than in the turf horizons of the forage fields (91, 142 and 201 mg from fields 8, 26 and 49, respectively). This was a result of the significantly greater

Table 13. Mean total carbon and nitrogen contents of the profile samples, ($Mg\ cm^{-2}$) calculated for the October 1982 and June 1983 profile samples. Mean ($\bar{x}$) and standard deviation (sd) are reported for the total organic layers, total mineral layers to 35cm depth, and total profile to 35cm depth; n=4.

Sample	Element	Forest		Field-3		Field-8		Field-26		Field-49	
		$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd
Organic layers	C	500	171	na	na	91	28	142	37	201	52
	N	27.5	10.4	na	na	5.7	2.3	8.7	2.6	13.1	4.9
Mineral layers	C	451	218	930	123	610	66	480	34	512	31
	N	42.3	24.0	71.9	9.9	46.2	7.7	38.5	1.8	39.7	3.6
Total profile	C	951	349	930	123	700	94	622	25	714	77
	N	69.9	32.1	71.9	9.9	51.9	9.8	47.2	1.3	52.8	7.9

thickness of the forest horizon. Field-3 had not developed a turf.

Total profile carbon contents to a depth of 35 cm, from the same data set, were not significantly different among sites (Table 13; 622 to 951 mg per cm^2); however Field-3 had significantly more carbon in the mineral soil than had the other sites (930 mg compared with 450 to 610 mg).

Bulk density was not measured for the October 1984 sample set. If the October 1984 %C data are used with the mean bulk density and horizon depth data from the earlier data set to calculate total profile carbon contents, the mineral soil carbon contents per cm^2 to 35 cm depth are 356, 683, and 617 mg, and total profile contents are 856, 683 and 819 mg from the forest, Field-3, and Field-49, respectively. These are lower estimates for Field-3. The forest mineral soil content is significantly less than the carbon content of the mineral soil of fields 3 and 49, while total profile values are not significantly different among sites.

4.1.5.2 Discussion

Reinl (1984) found mean total profile (to the bottom of the Bt horizon) carbon contents of 1080 mg $cm^{-2} \cdot depth^{-1}$ in virgin forest sites, and 660 mg $cm^{-2} \cdot depth^{-1}$ in adjacent cultivated Gray Luvisols. Organic horizon plus A horizon carbon contents were 690 and 500 mg $cm^{-2} \cdot depth^{-1}$ from the forest and cultivated sites respectively. The

total profile mass of organic carbon decreased an average of 19% (6% to -16%) due to cultivation. The total profile decreases of 2 (0.35% observed in this study fall in the range observed by Reinl.

Again, the carbon data were ambiguous concerning the effect of age of forage stand on soil carbon content. The 1983 data suggest a greater decrease in total profile carbon under forage stands than under a system of frequent cultivation, while the 1984 data (based on a larger number of samples) show the opposite effect.

The organic horizons were an increasingly important portion of the total profile carbon, with increasing age of forage stand. In the forest profile, 52% of the total organic carbon was in the organic horizons, but none was found in organic horizons in the frequently cultivated Field-3. The organic horizons represent 13, 23, and 28% of the total profile carbon under forage stands 8, 26 and 49 years old, respectively.

The total carbon content of the mineral soil was dominated by the content of the Ap horizon. The three factors in the carbon content function are horizon carbon concentration, horizon bulk density, and horizon thickness. The first varies by a factor of 1.6, the second by 1.16, and the third by 1.8 among the Ap horizons of the four stands, from the 1983 data. It appears the total carbon content of the mineral soil was as much a product of depth of cultivation as of carbon concentration.

4.1.6 Total Nitrogen and C:N Ratio

4.1.6.1 Soil Nitrogen

Total nitrogen content, mass basis, of the organic horizons, sampled in October 1982 and June 1983, were 16.0, 14.9, 19.7, and 22.1 mg g^{-1} of soil, from the forest and fields 8, 26 and 49, respectively (Table 14; Figure 7). The value from Field-49 was significantly greater than those from the forest and Field-3; thus there was the suggestion of an increasing N content with age of turf. The LF horizon sampled in October 1984 had a nitrogen content of 19.9 mg g^{-1}, the FH horizon content was 19.0 mg, and the turf from Field-49 had a significantly greater N content of 22.7 mg g^{-1} of soil (Table 10). Again the Field-49 turf had a greater nitrogen concentration than the forest organic horizons had.

Volume basis estimates of total nitrogen content in the organic horizons from the October 1982 and June 1983 samples were not significantly different, ranging from 2.5 mg cm^{-3} in the forest to 5.8 mg cm^{-3} in Field-8 (Table 15; Figure 8). The variances were high for the turf samples because of variance in the bulk density estimates, and the Field-8 estimate probably was too high due to a high bulk density estimate.

The nitrogen content of the forest Ahe horizon (mass basis) was significantly greater than were the Ap horizon contents, from the

Table 14. Nitrogen content (mg/g) measured in the October 1982 and June 1983 profile samples. Mean (x), standard deviation (sd), and number of samples (n) are reported by field and horizon.

Horizon	Forest			Field-3			Field-8			Field-26			Field-49		
	x	sd	n	x	sd	n	x	sd	n	x	sd	n	x	sd	n
LFH / Turf	16.0	2.6	4	na	na	na	14.9	3.4	3	19.7	4.8	5	22.1	1.4	5
Ahe / Ap	4.51	2.91	3	2.41	0.44	4	1.54	0.46	4	1.48	0.15	5	1.98	0.49	5
Ae	0.68	0.24	4	na	na	na	na	na	na	0.41	0.04	4	0.49	0.16	4
AB	0.44	0.10	4	0.41	0.05	3	0.43	0.11	4	0.48	0.08	4	0.47	0.04	4
Bt 1	0.47	0.04	3	0.47	0.03	4	0.50	0.03	3	0.51	0.04	5	0.48	0.03	5
Bt 2	0.47	----	2	0.40	----	1	0.42	----	1	0.44	----	2	0.46	0.04	3
C	0.40	----	1	0.32	----	1	0.38	----	1	0.37	----	1	0.38	----	1

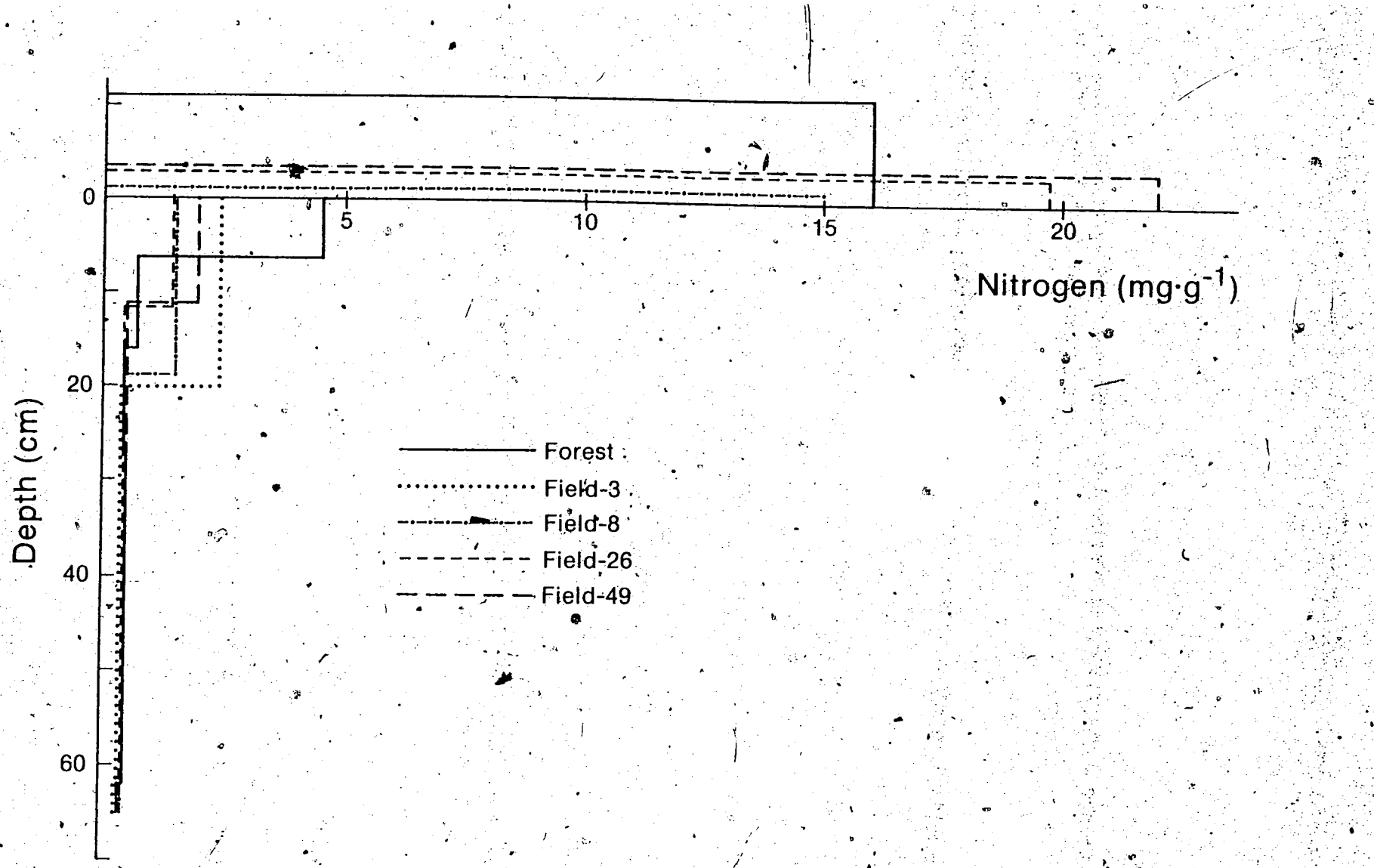

Figure 7. Mean total soil nitrogen (mass basis) by depth, for each stand.

Table 15. Nitrogen content, soil volume basis (mg/ml) calculated for the October 1982 and June 1983 profile samples. Mean (x), standard deviation (sd), and number of samples (n) are reported by field and horizon.

Horizon	Forest			Field-3			Field-8			Field-26			Field-49		
	x	sd	n	x	sd	n	x	sd	n	x	sd	n	x	sd	n
LFH / Hurt	2.5	0.5	3	na	na	na	5.8	2.3	3	3.4	0.7	3	4.2	1.8	3
Ahe / Ap	3.51	----	2	3.01	0.43	3	1.95	0.61	3	1.92	0.12	3	2.12	0.28	3
Ae	1.05	0.34	3	na	na	na	na	na	na	0.66	0.04	3	0.87	0.10	3
AB	0.67	0.16	3	0.69	0.03	3	0.67	0.20	3	0.74	----	2	0.73	----	2
Bt 1	0.75	0.07	3	0.74	0.05	3	0.78	0.05	3	0.76	0.07	3	0.74	0.08	3
Bt 2	0.81	----	2	0.65	----	1	0.73	----	1	0.77	----	1	0.73	----	2
C	0.68	----	1	0.55	----	1	0.67	----	1	----	----	-	----	----	-

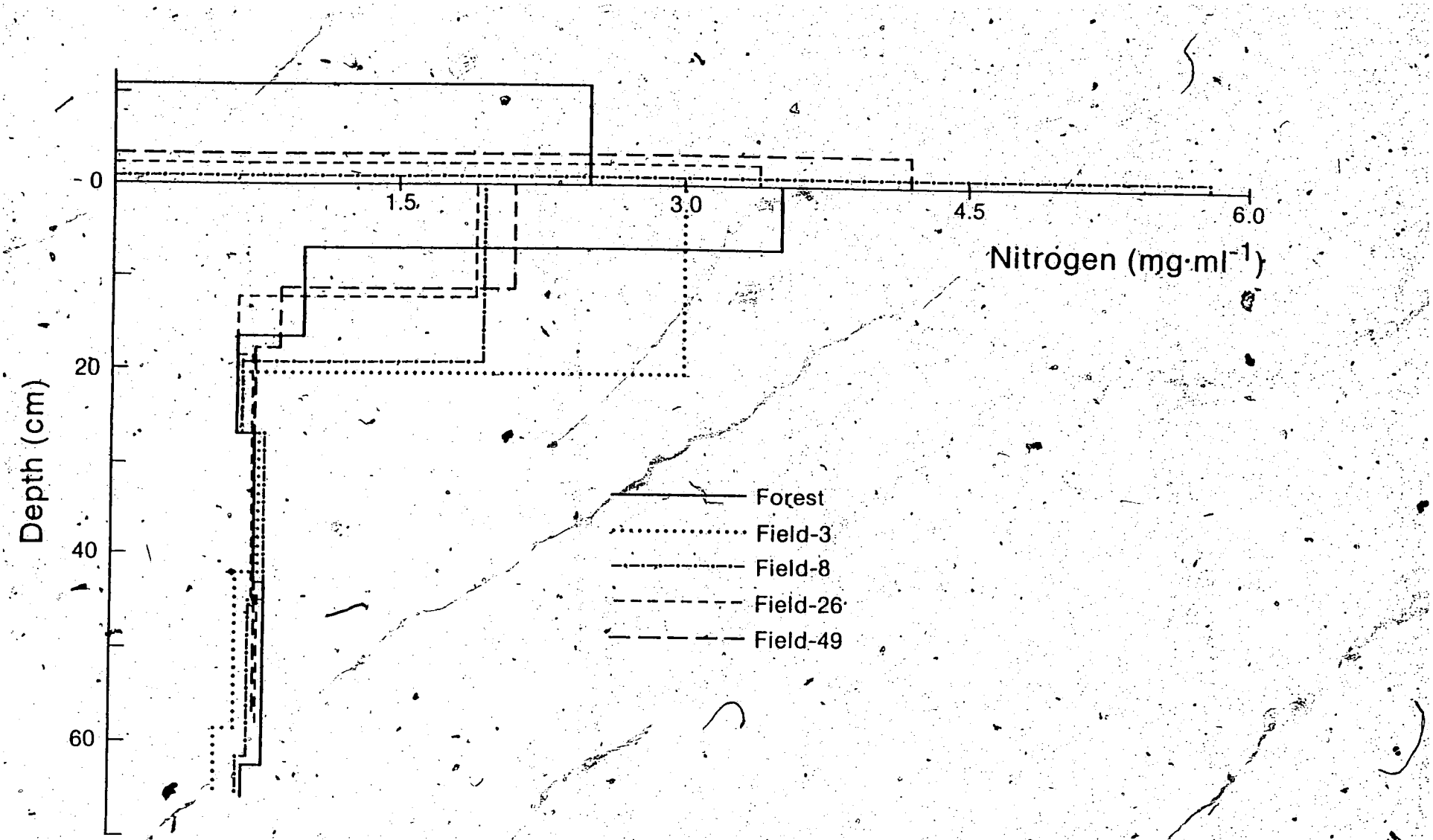

Figure 8. Mean total soil nitrogen (soil volume basis) by depth, for each stand.

October 1982 and June 1983 samples (Table 14; 4.51 mg compared with 2.41, 1.54, 1.48 and 1.98 mg from fields three, eight, 26 and 49 respectively). If the Ap horizons are considered alone, the Field-3 value was significantly greater than were the Field-8 and Field-26 values. On a volume basis the nitrogen contents of the Ahe and Ap horizon samples were found to be not significantly different, ranging from 1.92 to 3.51 mg cm^{-3} of soil (Table 15). Deeper horizon nitrogen contents were not found to differ among sites, on a mass or volume basis.

The October 1984 samples showed a significantly higher nitrogen content of the upper mineral soil (Ap horizon) in Field-49 (Table 10; 2.5 mg g^{-1}) compared to the forest (1.2 mg). The Field-3 Ap horizon value was between these two (1.7 mg) and not shown to differ significantly from either. On a volume basis, using mean bulk density estimates, these values were 1.4, 2.0 and 3.0 mg cm^{-3}, for the forest, Field-3 and Field-49, respectively.

Total nitrogen content to 35 cm depth follows the same trends as those observed for total carbon for the October 1982 and June 1983 samples (Table 13). The mineral soil total was significantly greater in Field-3 than in the other sites (71.9 mg compared with 43.3, 46.2, 38.5, and 39.7 mg from the forest and fields eight, 26, and 49 respectively) and the forest had a significantly greater organic horizon total nitrogen content (27.5 mg compared with 5.7, 8.7, and 13.1 mg from fields eight, 26, and 49 respectively), largely because of

the thicknesses of the Field-3 Ap and the forest organic horizon, respectively. The profile totals (69.9, 71.9, 51.9, 47.2, and 52.8 mg from the forest and fields 3, 8, 26, and 49 respectively) do not differ significantly.

4.1.6.2 C:N Ratio

Mean carbon to nitrogen ratios from the October 1982 and June 1983 data were significantly different among sites only in the organic horizons; the forest ratio of 18.4 was greater than the turf ratios of 16.4, 15.5 and 15.3 from fields 8, 26, and 49, respectively (Table 16). A trend toward decreasing C:N with increasing age of turf was suggested by these values as well. The October 1984 LF horizon sample C:N ratio of 23.8 (Table 10) was significantly greater than the FH horizon (18.7) and Field-49 turf horizon (17.3) C:N ratios.

The forest Ahe horizon C:N ratio from the October 1982 and June 1983 samples (Table 16) was 12.2; the Ae horizon ratio was 10.7. The Ap horizon ratios were 13.3, 13.9, 14.0, and 14.4, from fields 3, 8, 26, and 49 respectively. These values suggest a trend of increasing C:N ratio with age of forage stand. From the October 1984 samples, the Field-3 and Field-49 Ap horizon mean C:N ratios were 13.8 and 14.4 respectively, and the forest mineral soil C:N ratio was significantly less (11.9).

Table 16. - Carbon to nitrogen ratios, calculated for the October 1982 and June 1983 profile samples. Mean (x), standard deviation (sd), and number of samples (n) are reported by field and horizon.

Horizon	Forest			Field-3			Field-8			Field-26			Field-49		
	x	sd	n	x	sd	n	x	sd	n	x	sd	n	x	sd	n
LFH / turf	18.4	0.8	4	na	na	na	16.4	2.1	3	15.5	1.6	5	15.3	1.3	5
Ahe / Ap	12.2	2.5	3	13.3	0.4	4	13.9	1.0	4	14.0	1.0	5	14.4	1.3	5
Ae	10.7	0.3	4	na	na	na	na	na	na	10.4	1.0	4	10.9	1.2	4
AB	11.5	0.7	4	9.9	1.0	3	11.4	0.9	4	10.2	1.0	4	10.0	0.7	4
Bt 1	11.0	0.3	3	10.4	0.7	4	10.9	0.9	3	9.9	0.9	5	11.2	1.3	5
Bt 2	11.3	---	2	13.5	---	1	12.3	---	1	10.0	---	2	11.0	0.2	3
C	15.4	---	1	13.8	---	1	11.8	---	1	20.	---	1	20.	---	1

4.1.6.3 Discussion

Mean nitrogen contents of the Ap horizons of the Breton Plots were 1.0-1.6 mg g^{-1} and C:N ratios were 10.9-11.7 (Cannon et al., 1984). The Field-3 nitrogen content estimate from the 1984 samples (1.7 mg g^{-1}) was similar, while the value from the October 1982 and June 1983 sample set (2.4 mg) was greater. Also the Ap horizon C:N ratios (13.3-14.4) were greater than those observed at the Breton Plots.

The oxidation of carbon and the recycling of nitrogen during decomposition of organic materials result in a lower soil C:N ratio. The C:N ratio of the soil is therefore a function of the initial C:N ratio of materials added to the soil and the degree to which the materials have been decomposed. The decreasing C:N ratio with depth, from the LF to the Ae horizons in the forest, reflects increasing humification of the organic material. Similarly, the apparently decreasing C:N ratio of the turf horizons with age may reflect a greater content of humified components in the older turf horizons. The Ap horizons showed the opposite trend with age of forage stand. Assuming similar initial C:N ratios of the added materials, and similar nitrogen use efficiencies by the decomposing organisms, the rate of decomposition relative to the rate of additions must be less under the older stands..

4.2 Biomass Carbon and Nitrogen

4.2.1 Results

Carbon released during incubation was 88 $\mu g\ g^{-1}$ greater for the fumigated than the non-fumigated forest A horizon sample (Table 17). The carbon flush from the Field-3 Ap horizon was 111 $\mu g\ g^{-1}$ and from Field-49 was 203 $\mu g\ g^{-1}$. The Field-49 value was significantly greater than the other two. Mean nitrogen flushes after fumigation from the same samples were 9.3, 20.5, and 23.1 $\mu g\ g^{-1}$, from the forest, Field-3 and Field-49, respectively. The values from the two Ap horizons were significantly greater than the forest value. Together the carbon and nitrogen data suggest the biomass was largest in the Ap horizon from Field-49, intermediate in the Field-3 Ap horizon, and least in the forest upper mineral (Ahe and Ae) material.

The flushed carbon to flushed nitrogen ratios, 10.2, 5.2, and 8.8 from the forest, Field-3 and Field-49 respectively, differ significantly from one another (Table 17). Assuming a K_c value of 0.41 (McGill *et al.*, 1986), the biomass C to flushed N ratios were 24.9, 12.7, and 21.5.

The carbon flush represents 0.44 to 0.60% of the total carbon, from the three sample sets (Table 18; not statistically different). Given total carbon contents of 1.4, 2.4, and 3.5% for these soil samples, and assuming a K_c value of 0.41, biomass carbon was 1.4, 1.1, and 1.4% of the total carbon from the forest, Field-3, and Field-49 samples, respectively. The values for nitrogen flush as percentage of

Table 17. Mean total respired carbon and mineralized nitrogen (ug/ml soil), after fumigation of the mineral samples. Standard deviations are in parentheses.

Stand	Layer	n	Carbon (ug/ml)	Nitrogen (ug/ml)	C to N ratio
Forest	A	8	88 (62)	9.3 (7.3)	10.2 (1.9)
Field-3	Ap	10	111 (62)	20.5 (6.9)	5.2 (1.6)
Field-49	Ap	9	203 (60)	23.1 (4.8)	8.8 (2.2)

Table 18. Mean ratios (%) of mineralized carbon and nitrogen of fumigated samples to total carbon and nitrogen, respectively, and ratio of mineralized C:N to total C:N. Standard deviations are included in parentheses.

Stand	Layer	n	Mineralized Carbon %	Mineralized Nitrogen %	Mineral C:N / total C:N
Forest	A	8	0.60 (0.23)	0.75 (0.39)	0.87 (0.20)
Field-3	Ap	10	0.44 (0.20)	1.17 (0.29)	0.38 (0.11)
Field-49	Ap	9	0.60 (0.21)	1.02 (0.34)	0.62 (0.17)

total nitrogen from the Ap horizons (1.1% and 1.02%) were significantly greater than the forest value of 0.75%.

4.2.2 Discussion

The values for biomass carbon as a percent of total carbon were somewhat lower than those found by McGill et al. (1986) at the Breton Plots (2.4-3.1%); however they were not outside the observed range. The Breton Plot mean nitrogen flush was found to be 2.3% of total N. The method used by McGill et al. (1986) to calculate carbon and nitrogen flushes differed slightly from the method used in this study. They compared quantities evolved from fumigated soils during the first 10 days of incubation with those evolved from non-fumigated soils during incubation days 10-20.

The biomass C to flushed N ratios were within range of the Breton Plot Ap average of 14.4 (McGill et al., 1986). The flushed carbon to flushed N correlation coefficient was 0.80, similar to values of 0.73-0.94 found in other studies (Cannon et al., 1984).

There is a trend for greater biomass in the Ap horizons than in the forest Ahe and Ae horizon, and under a continuous forage sward compared to a forage/grain rotation management system. This trend parallels those for total carbon and nitrogen.

Because of the broad range of C:N ratios of soil microorganisms

(often 3-5 for bacteria and 10-12 for fungal hyphae), the K_n value varies greatly (Jenkinson and Ladd, 1981). The high flushed C:N ratio may suggest a large fungal component in the biomass of the forest A horizons, while the low ratio from Field-3 may suggest a greater bacterial component.

4.3 Soil Fauna

4.3.1. The Macrofauna

The mean macrofaunal population per sample of the forest soil (Table 19; 86 individuals) was significantly larger than that found in any of the fields. The Field-26 population (34 individuals) was greater than that in Field-3 (5 individuals), Field-8 (10 individuals) and Field-49 (13 individuals). Macrofauna were limited to the turf horizons and the turf/mineral soil contact in fields 8, 26, and 49. In Field-3 they were found in the upper few centimetres of mineral soil, often immediately beneath moss layers or plant litter.

The taxonomic levels to which fauna were identified were chosen subjectively, based on my ability to identify the specimens. The numbers of taxa showed a more heterogenous and complex forest population; the Field-3 population was the least complex. The latter was composed of large Diptera and Lepidoptera larvae and Araneae, and occasional predaceous Coleoptera (Staphylinidae). Field-8 had a similar population, with Staphylinidae somewhat more common. Enchytraeids were not found in Field-3 and Field-8; in Field-26 and

Table 19. Mean numbers of macrofauna and of taxonomic groups found in hand sorted samples. Animals were found in the organic layers, or in the upper 50mm of mineral soil where organic layers were absent. Standard deviations are in parentheses.

Stand	n	individuals per sample ($0.125m^2$)	taxa per sample ($0.125m^2$)	Major taxonomic groups observed
Forest	3	86 (13)	18 (1)	Enchytraeids, Diptera larvae (Tipulidae, others), Coleoptera (Carabidae, Staphylinidae, others), Lepidoptera larvae, Hymenoptera, Homoptera (Cicadellidae), Hemiptera, Araneae, Thysanoptera, Gastropoda.
Field-3	5	5 (5)	3 (2)	Diptera and Hymenoptera larvae, Coleoptera (Carabidae, Staphylinidae), Chilopoda, Lepidoptera larvae.
Field-8	6	10 (12)	6 (5)	Coleoptera (Staphylinidae, Curculionidae, Scarabaeidae, Cucujidae), Diptera larvae, Hymenoptera (Formicidae, others), Homoptera, Hemiptera, Lepidoptera, Araneae.
Field-26	5	34 (22)	8 (4)	Coleoptera (Staphylinidae, Curculionidae, Scarabaeidae, Cucujidae), Diptera larvae (Sciaridae, Brachycera), Enchytraeids, Hymenoptera (Formicidae, others), Homoptera (Cicadellidae), Lepidoptera, Araneae.
Field-49	5	13 (5)	8 (2)	Coleoptera (Staphylinidae, Curculionidae, Scarabaeidae, Cucujidae), Diptera larvae (Sciaridae, Brachycera), Enchytraeids, Hymenoptera (Formicidae, others), Homoptera (Cicadellidae), Lepidoptera, Araneae.

Field-49 they were found in the lower turf. The Coleopteran population was more diverse in Field-26, including Carabidae and Cucujidae as well as Staphylinidae; the Field-26 fauna also included large numbers of a small Dipteran larvae of the family Sciaridae, probably a Plastosciara species. The Field-49 population was similar to that of Field-26, with lower numbers overall. This may be a sampling error introduced by the difficulty involved in picking apart the densely woven Field-49 turf horizon. The forest population included large numbers of Enchytraeidae and Staphylinidae, as well as other Coleoptera, various Dipteran larvae, and Gastropoda. The forest fauna were generally limited to the organic horizons, although Coleoptera were observed in the mineral soil. Enchytraeids were found only in the lower organic horizons, and Gastropoda near the surface, whereas Coleoptera were distributed throughout the organic soil.

Earthworms were not found in the forest soil, or in any of the fields studied. Their absence is not simply due to a characteristic absence from the region, since they were present in nearby garden soils, and in the soil under an adjacent, well-manured, treed knoll where cattle like to stay overnight. One would assume earthworms have had access to the soils of the research site, but, for whatever reason, have not established a significant population.

4.3.2 Microarthropods

4.3.2.1 Sampling and Identification

Three significant characteristics of the sampling and identification methods must be noted in the discussion of the microarthropod data.

First, the three sampling depth increments were each 30 mm thick from the arable fields, however from the forest site it was not possible to take samples with the corer used unless the corer was pushed part way into the mineral soil. The result was the compaction of the forest organic layers to a thickness of about 70-80 mm, with approximately 10-20 mm of mineral soil at the bottom of the third increment. The effects of this are that the reference to the depth increments as 0-30 mm, 30-60 mm and 60-90 mm is not accurate for the forest samples, and an unknown number of specimens may have been crushed in the sampling process, decreasing the forest population estimate.

Secondly, I was not able to identify to which subgroup some of the acari belonged. This difficulty was most pronounced with the first (May 17) set of samples, when the population included a large number of immatures and my classification skills were more limited. The May 17 data set therefore included a large number of "unidentified" Acari, most of which probably were immature Oribatei.

Thirdly, the Collembola were subdivided into the taxonomic suborders Arthropleona and Symphypleona, according to body shape.

However, this subdivision is primarily taxonomic rather than ecologic (since members of both groups inhabit similar niches) and the Symphopleona were rare in these samples. Distinguishing surface dwellers from deep dwelling species would have been more useful.

4.3.2.2 The Microarthropod Population

The mean number of microarthropods extracted per core (1800 mm^2 by 90mm deep) from the forest was 143 (Table 20; Figure 8), significantly more than the 66 found from Field-3, and 71 from Field-8. The means from Field-26 and Field-49 (93 and 108, respectively) did not differ statistically from the others. The microarthropod population in each site was dominated by the Acari. Most of the Acari were of the suborder Oribatei; Gamasida were common, Actinedida were less so; rare Acaridida were observed but not counted separately. The great majority of the Collembola were Arthropleona. (Table 21 is a list of the common Acari and Collembola species identified; scanning electron micrographs of some specimens are shown in Plate 1.) Other organisms extracted included Dipteran larvae, Coleopteran larvae especially Staphylinidae and Carabidae, Homopteran and Hemipteran nymphs, enchytraeids, and rarely arachnids and Diplopoda.

The mean number of acari per core (Table 20) from the forest (110) was significantly greater than the numbers found in Field-3 (41) and Field-8 (62); the number from Field-49 (95) was significantly greater than the 41 from Field-3; the mean of 74 found from Field-26 was not

Table 20. Mean numbers of microarthropods per core (1800mm² · 90mm depth), by group and field. Superscripts indicate significances across columns, by M.S.D., p=0.05.

Group	Forest	Field-3	Field-8	Field-26	Field-49
Acari	110[a]	41[c]	62[bc]	74[abc]	95[ab]
Oribatei	84[a]	33[b]	48[b]	53[b]	64[ab]
Gamasida	10	5	8	5	6
Actinedida	4	1	1	1	1
unidentified	13	3	4	15	24
Collembola	28	22	8	16	11
Arthropleona	28	21	8	15	8
Symphypleona	0	1	0	2	2
Other[1]	5	3	1	3	2
Total	143[a]	66[b]	71[b]	93[ab]	108[ab]

[1] This group included Diptera larvae of several species, Coleoptera larvae especially Staphylinidae and Carabidae, Homoptera and Hemiptera nymphs, Enchytraeids, and, rarely, Arachnids and Diplopoda.

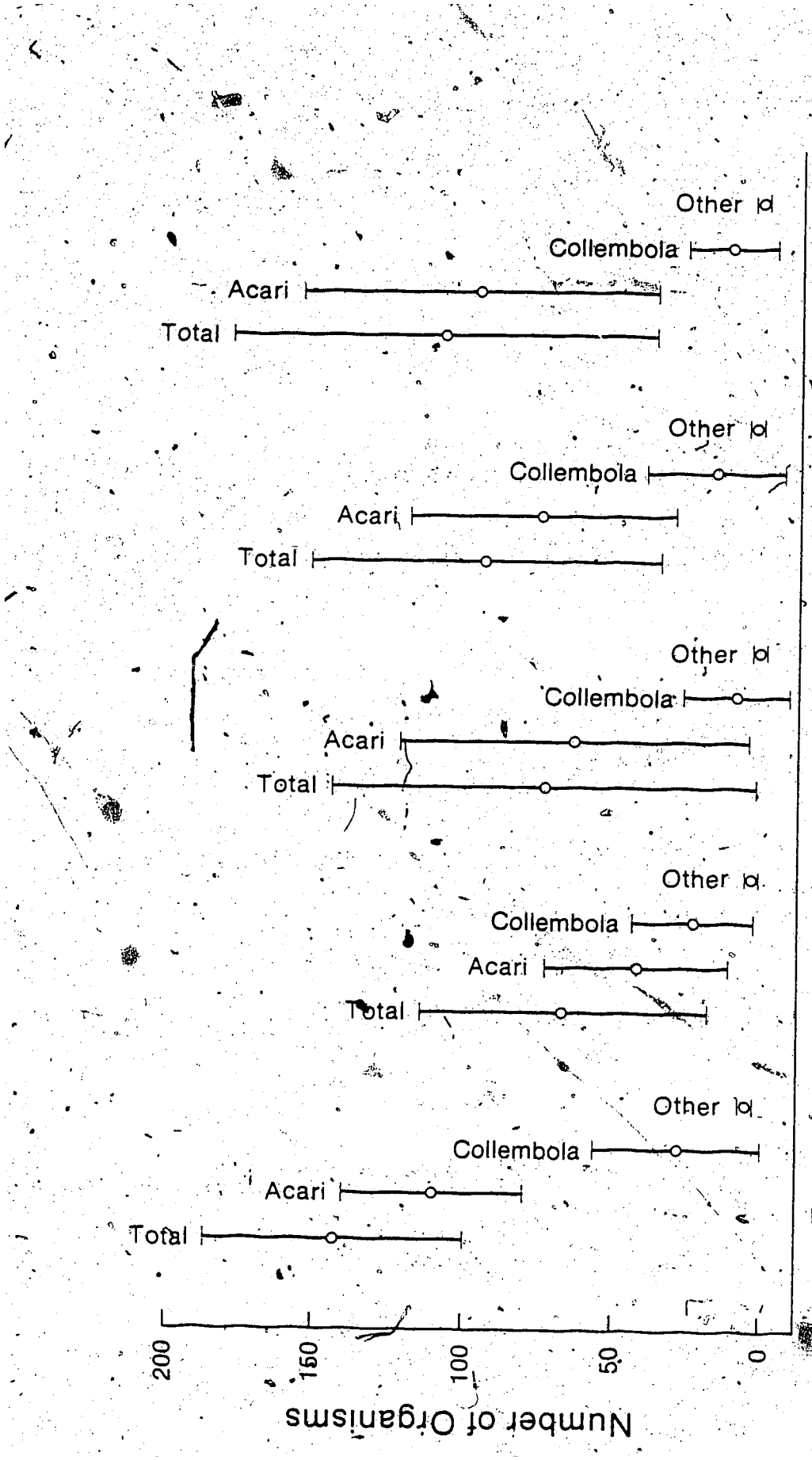

Figure 9. Mean soil microarthropod numbers per core, by order, for each stand. Vertical bars show standard deviations.

Table 21. List of the microarthropod species observed.

Acari:	Oribatei:	Ceratoppia bipilis (Hermann)
		Ceratozetes gracilis (Michael)
		Fuscozetes nr. fuscipes (C. L. Koch)
		Heminothrus (Platynothrus) nr. yamasakii (Aoki)
		Oppiella nova (Oudemans)
		Oribatodes nr. miribilis (Banks)
		Tectocepheus velatus (Michael)
		Trhypochthonius tectorum (Berlese)
		Phthiracarus sp.
		Trichoribates sp.
		Achipteriidae: gen. et sp. undetermined
	Gamasida:	Amblyseius putmani (Chant)
		Cheiroseius near borealis (Berlese)
		Gamasellus vibrissatus Emberson
		Hypoaspis near angusta Karg
		Hypoaspis nolli Karg
		Macrocheles near insignitus Berlese
		Ololaelaps sellnicki Bregetova & Koroleva
		Parazercon radiatus (Berlese)
		Zygoseius furciger Berlese
		Seius sp.
		Trachytes sp.
		Zercon sp.
		Uropodidae: gen. et sp. undetermined
	Actinedida:	Charadacarus delirescens Newell
		Eupodes acuminatus Willman
		Eupodes alaskanensis Strandtmann
		Robustocheles (s.s.) mucronata (Willman)
		Stigmaeus comatus Summers
		Abrolophus spp. (2)
		Alycus sp.
		Cocceupodes sp.
		Ereynetes sp.
		Eustigmaeus sp.
		Microtrombidium sp.
		Tydeus sp.
	Acaridida:	Tyrophagus longior (Gervais, 1844)
		Rhizoglyphus sp.
Collembola:	Anurida (Micranurida) pygmaea (Borner)	
	Arrhopalites sp. prob. benitus (Folsom)	
	Folsomia sp. prob. elongata (MacGillivray)	
	Folsomia nivalis (Packard)	
	Hypogastrura essa Christiansen	
	Isotoma notabilis Schaffer	
	Isotoma viridis Bourlet	
	Lepidocyrtus sp. cinereus ? Folsom	
	Sminthurinus elegans (Fitch)	
	Tomocerus flavescens Tullberg (species complex)	

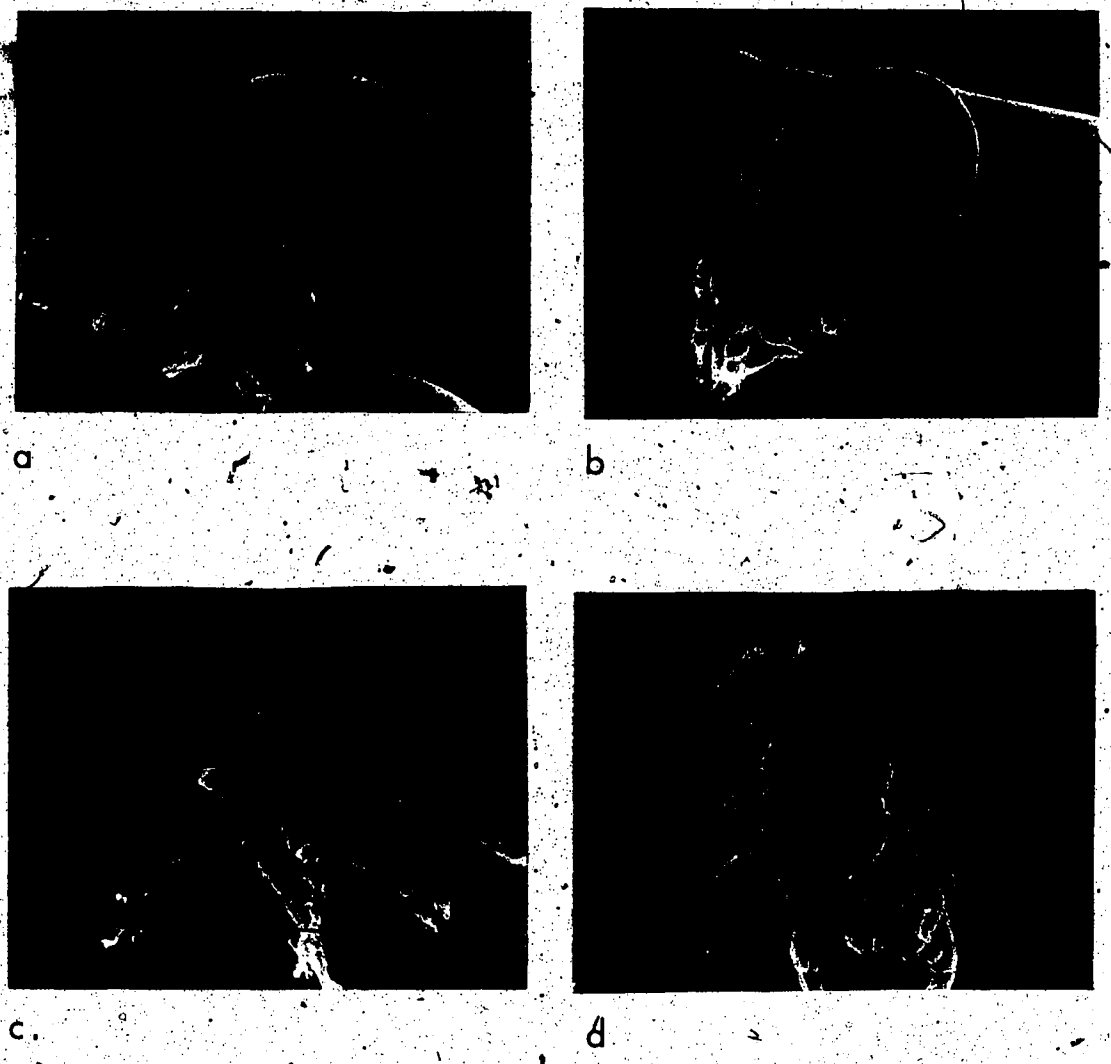

Plate 1. Scanning electron micrographs of some microarthropods from the research site. a. Acarina, Oribatei, probably Ceratozetes gracilis; b. Acarina, Oribatei, probably Oppiella nova; c. Acarina, Gamasida, unidentified; d. Collembola, unidentified.

significantly different from the others. The mean collembolan numbers per sample (28, 22, 8, 16 and 11 from the forest and fields 3, 8, 26, and 49, respectively) did not differ significantly among the five sites. The Collembola were a significantly greater portion of the total microarthropod population in Field-3 (28%; Table 22)-than in the other sites (8 to 18%). The acari were 66 to 89% of the total microarthropods found, with the Field-49 percentage significantly greater than that of Field-3.

4.3.2.3 The Acari Population

Oribatei means were 53 to 67% of the total microarthropod numbers (Table 22); these percentages did not differ significantly among fields, although the mean number of oribatei per core (Table 20, Figure 10) from the forest (84) was greater than the mean numbers from Field-3 (33), Field-8 (48), and Field-26 (53). The Field-49 population (64) was not statistically different from the others. The Gamasida population was a significantly greater percentage of the total in Field-8 (14%) than in the forest (7%), Field-26 (6%) and Field-49 (7%), while the mean numbers per core (5 to 10; Table 20, Figure 10) did not differ significantly.

Eighty-three to 90% of the identified acari were Oribatei (Table 23). The Field-3 and Field-8 numbers of 85 and 83% respectively were significantly less than the Field-26 and Field-49 values of 90%; the forest Oribatei were 86% of the identified acari, not statistically

Table 22. Microarthropod groups as a percentage of total microarthropods, by field. Superscripts indicate significances across columns by L.S.D., p=0.05.

Group	Forest	Field-3	Field-8	Field-26	Field-49
Acari	78^{ab}	66^{b}	80^{ab}	81^{ab}	89^{a}
Oribatei	60	53	67	62	66
Gamasida	7^{b}	9^{ab}	14^{a}	6^{b}	7^{b}
Collembola	18^{b}	28^{a}	9^{b}	15^{b}	8^{b}

Table 23. Acari by suborder, as a percent of total identified Acari. Superscripts indicate significances across columns by L.S.D., p=0.05.

Suborder	Forest	Field-3	Field-8	Field-26	Field-49
Oribatei	85.9^{ab}	85.0^{a}	83.2^{a}	90.2^{b}	89.5^{b}
Gamasida	10.4^{bc}	12.9^{ab}	14.6^{a}	8.5^{c}	9.1^{bc}
Actinedida	3.7	2.1	2.1	1.3	1.4

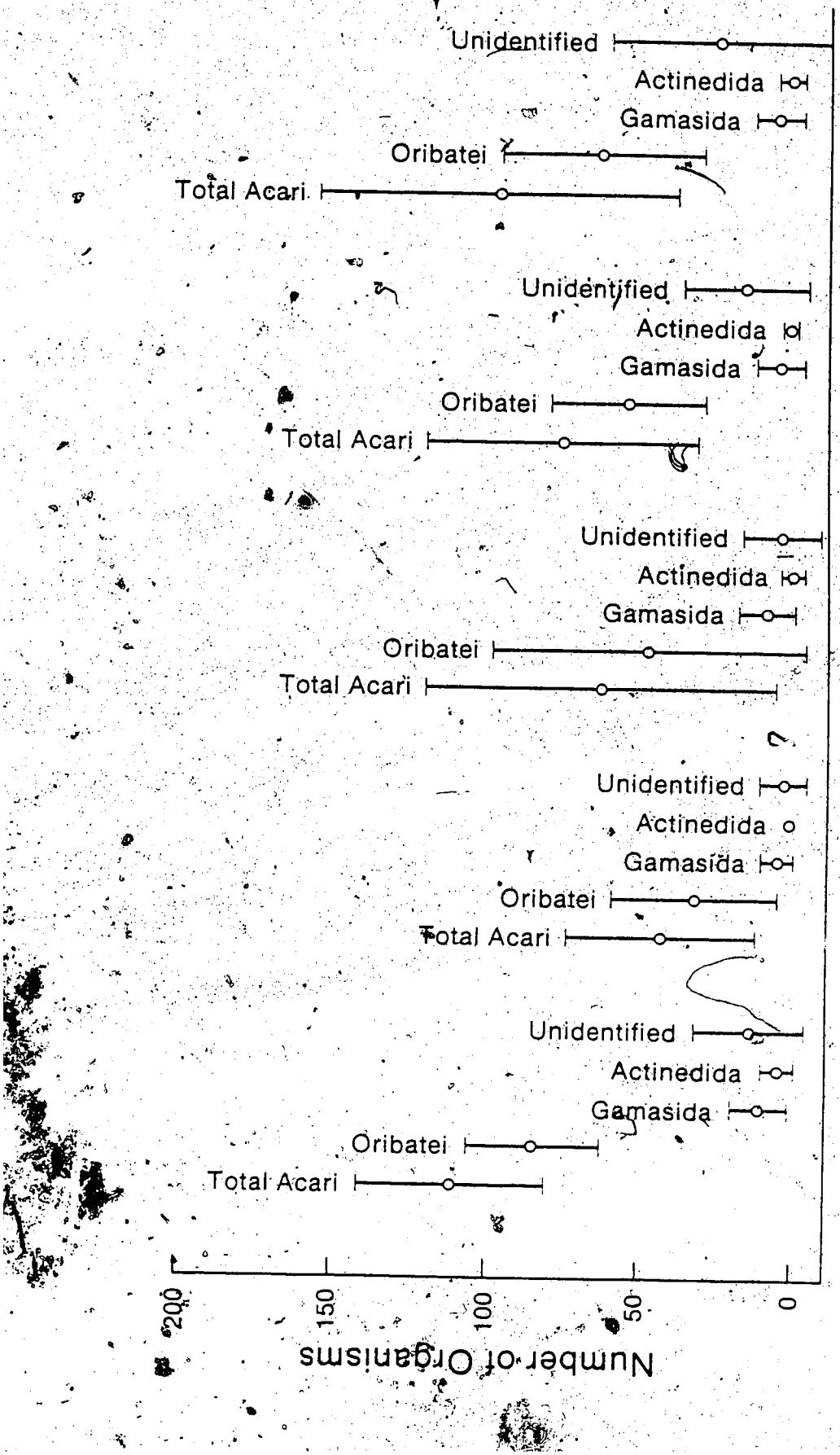

Figure 10. Mean soil Acari numbers per core, by suborder, for each stand. Vertical bars show standard deviations.

different from the other percentages. (If unidentified acari are assumed to be Oribatei, the adjusted Oribatei numbers were 84 to 93% of the total acari, and followed the same statistical trends as the total acari numbers; Table 20). The Gamasida were a significantly larger percentage of identified acari in Field-8 (16%) than in Field-26 (9%) and Field-49 (9%) and in the forest (10%). The Field-3 value (13%) also was greater than that of Field-26. The Actinedida were 1-4% of the identified acari; although these means did not differ significantly, a possible trend of greatest numbers in the forest, and least in the old forage stands, was suggested.

4.3.2.4 Field, Date and Depth Effects

The analysis of the variance of the total microarthropod numbers per core sample (Table 24a) showed significant field, date and depth effects, as well as significant two-way interaction effects; the three way interaction effect was not significant. Neither the three-way nor the field-by-sampling date interactions varied significantly in the acari data (Table 24b). In the collembolan data set, field, date, depth, and field-by-depth were the significant sources of variance (Table 24c).

The mean number of microarthropods per core was significantly greater from the May 17 sampling (140 individuals) than from the three later dates (74, 90, and 81 individuals from May 26, July 12 and August 23, respectively; Table 25a, Figure 11). Within sampling dates, only

Table 24a. Analysis of variance of the total microarthropod populations by field, sampling date and sample depth.

Source	df	sum of squares	F value	Probability
Field	4	16570	6.02	0.0002
Date	3	14580	7.06	0.0002
Field x Date	12	16570	2.01	0.0272
Depth	2	303800	220.71	0.0001
Field x Depth	8	19170	3.48	0.0010
Date x Depth	6	24040	5.82	0.0001
Field x Date x Depth	24	19400	1.17	0.2743

Table 24b. Analysis of variance of the acari populations by field, sampling date and sample depth.

Source	df	Sum of squares	F value	Probability
Field	4	12290	6.09	0.0001
Date	3	9341	6.17	0.0006
Field x Date	12	10300	1.70	0.0716
Depth	2	213400	211.55	0.0001
Field x Depth	8	14530	3.60	0.0007
Date x Depth	6	18540	6.13	0.0001
Field x Date x Depth	24	15030	1.24	0.2154

Table 24c. Analysis of variance of the collembolan populations by field, sampling date and sample depth.

Source	df	Sum of Squares	F value	Probability
Field	4	1200	2.98	0.0211
Date	3	887	2.94	0.0348
Field x Date	12	1637	1.35	0.1941
Depth	2	5777	28.69	0.0001
Field x Depth	8	1831	2.27	0.0253
Date x Depth	6	700	1.16	0.3314
Field x Date x Depth	24	2186	0.90	0.5993

Table 25a. Mean microarthropod totals per sample (1800mm^2 90mm depth), by sampling date and field. Superscripts indicate significances across columns, and down the final column, by L.S.D., p=0.05.

Sampling Date	Forest	Field-3	Field-8	Field-26	Field-49	Mean
May 17	134	130	65	148	184	140^a
May 26	164^a	42^b	34^b	51^b	67^b	74^b
July 12	122	68	114	70	77	90^b
August 23	161	37	61	79	74	81^b

Table 25b. Mean acari totals per sample (1800mm^2 90mm depth), by sampling date and field. Superscripts indicate significances across columns, and down the final column, by L.S.D., p=0.05.

Sampling Date	Forest	Field-3	Field-8	Field-26	Field-49	Mean
May 17	104	83	55	119	157	112^a
May 26	139^a	30^b	31^b	45^b	57^b	63^b
July 12	101	44	93	61	75	75^b
August 23	100	18	59	52	66	59^b

Table 25c. Mean collembolan totals per sample (1800mm^2 90mm depth), by sampling date and field. Superscripts indicate significances across columns, and down the final column, by L.S.D., p=0.05.

Sampling Date	Forest	Field-3	Field-8	Field-26	Field-49	Mean
May 17	26	44	10	26	25	25^a
May 26	22^a	10^b	1^b	6^b	8^b	10^b
July 12	16	20	20	6	2	13^{ab}
August 23	52	18	4	22	4	18^{ab}

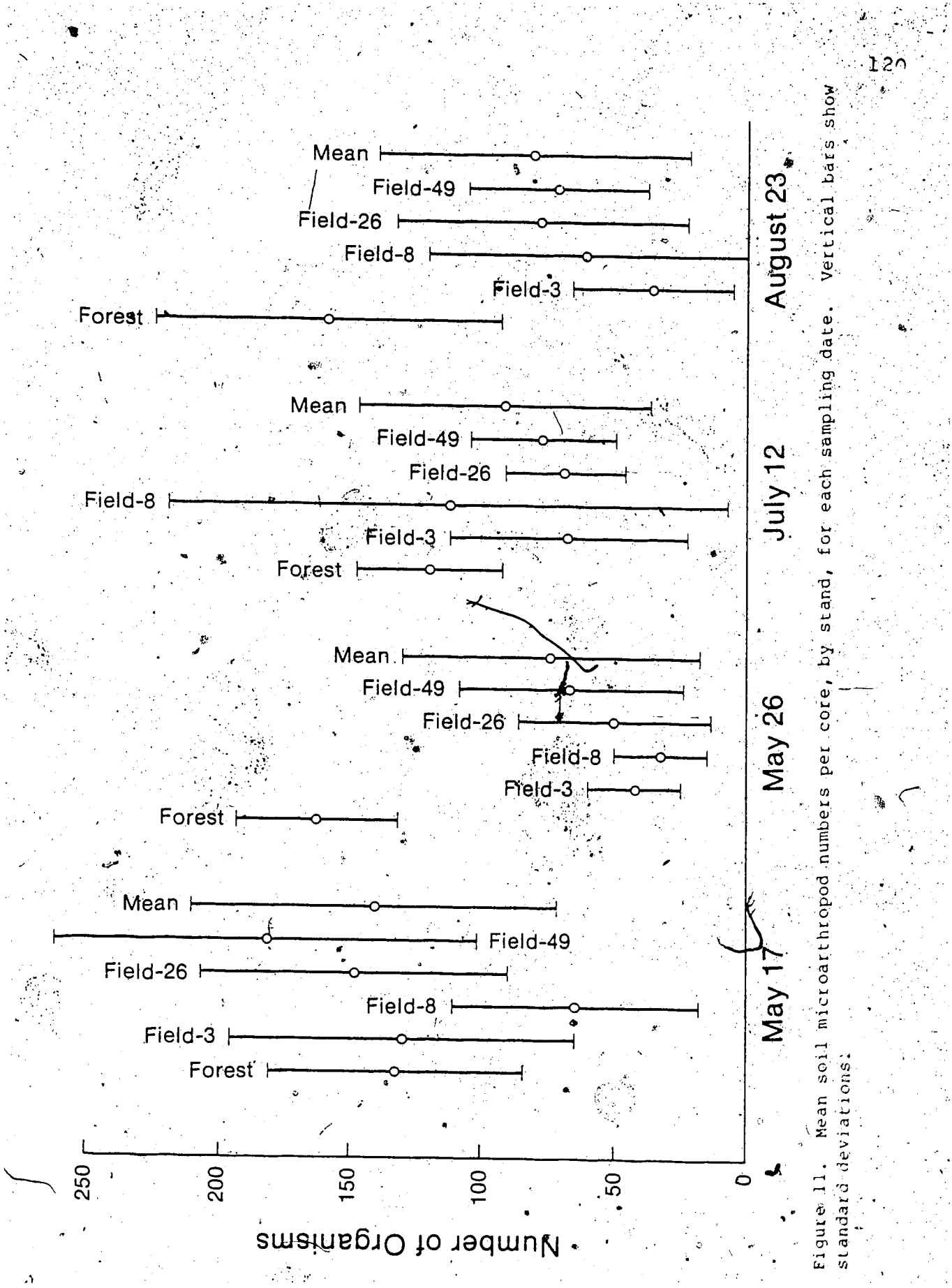

Figure 11. Mean soil microarthropod numbers per core, by stand, for each sampling date. Vertical bars show standard deviations.

the May 26 sampling data set showed a significant differance in macroarthropod numbers between sites; the forest mean of 164 individuals was significantly greater than the values from the arable fields (42, 34, 51, and 67 individuals from fields 3, 8, 26, and 49 respectively).

Total acari numbers by sampling date (Table 25b) followed the same statistical trends as the total microarthropod populations, with the mean population from the first sampling date (112) significantly greater than the following three dates (63, 75 and 59 respectively), and the forest acari population (139) significantly greater than the arable field populations (30 to 57) in the May 26 sample set. The mean number of Collembola (25 individuals; Table 25c) from the May 17 sample set was significantly greater than the May 26 sample population (10); the July 12 (13) and August 23 (18) sets did not differ from the others. The May 26 sample set had significantly more Collembola in the forest samples (22) than in the field samples (1 to 10).

Eighty-nine percent of the total microarthropods were found in the 0-30mm sampling depth. The Collembola were more common at depth than the acari, on a percent basis, with 78% in the 0-30mm depth, compared with 91% of the acari.

The percentage of the total microarthropods per core found in the 0-30 mm depth increment (Table 26a) was greater in Field-8 (92%), Field-26 (96%), and Field-49 (94%) than in Field-3 (80%) or the forest

Table 26a. Microarthropods by depth increments, as a percentage of totals to 90mm depth, by field, across all sampling dates. Superscripts indicate significances across columns by L.S.D., p=0.05.

Depth	Forest	Field-3	Field-8	Field-26	Field-49
0 - 30mm	80^{a}	80^{a}	92^{b}	96^{b}	94^{b}
30 - 60mm	15^{a}	11^{b}	4^{c}	3^{c}	3^{c}
60 - 90mm	5^{ab}	8^{a}	4^{ab}	1^{b}	4^{b}

Table 26b. Acari by depth increments, as a percentage of totals to 90mm depth, by field, across all sampling dates. Superscripts indicate significances across columns by L.S.D., p=0.05.

Depth	Forest	Field-3	Field-8	Field-26	Field-49
0 - 30mm	78^{a}	90^{b}	97^{b}	97^{b}	95^{b}
30 - 60mm	16^{a}	3^{b}	1^{b}	3^{b}	2^{b}
60 - 90mm	5^{ab}	7^{a}	1^{ab}	0^{b}	3^{ab}

Table 26c. Collembola by depth increments, as a percentage of totals to 90mm depth, by field, across all sampling dates. Superscripts indicate significances across columns by L.S.D., p=0.05.

Depth	Forest	Field-3	Field-8	Field-26	Field-49
0 - 30mm	84^{ab}	64^{a}	55^{ab}	94^{b}	82^{ab}
30 - 60mm	11^{ab}	23^{a}	27^{ab}	6^{b}	4^{b}
60 - 90mm	5^{a}	14^{a}	18^{a}	0^{a}	13^{a}

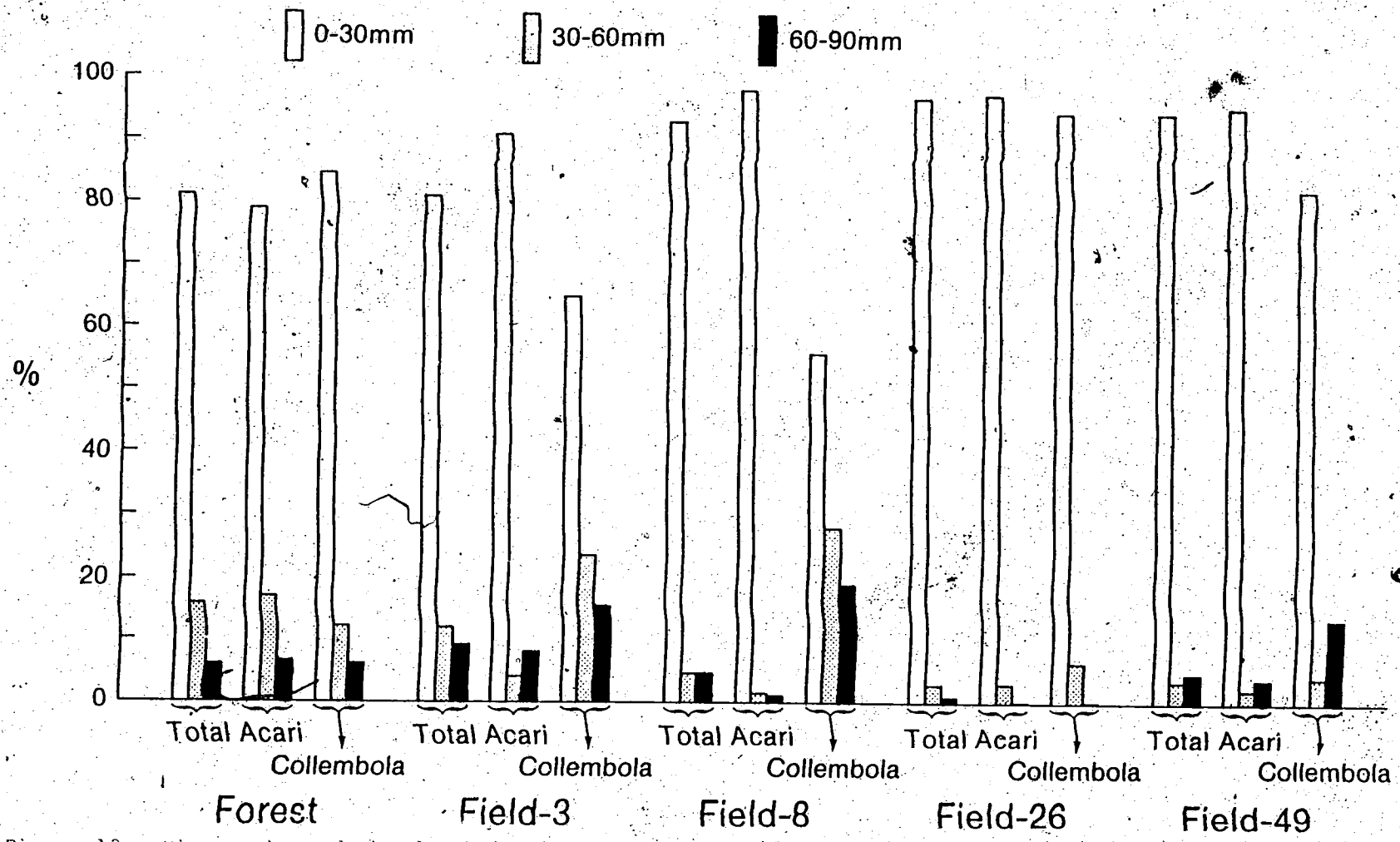

Figure 12. Microarthropods by depth increments as a percentage of total microarthropods to 90mm depth.

(80%). Fifteen percent of the forest microarthropods were in the samples from the 30-60 mm increment, significantly more than the 11% in the same increment of Field-3; both were greater than the 3 to 4% found in fields 8, 26 and 49. A significantly greater percentage of the core total was found in the 60-90 mm increment in Field-3 (8%) than the same increment of Field-26 (1%) and Field-49 (4%); the Field-8 (4%) and forest (5%) values were not statistically different from the others.

The percentage of the total acari per core found in the 0-30 mm depth increment (Table 26b) was significantly greater in the arable fields (90 to 97%) than in the forest (78%). The 30-60 mm increment reflects these percentages, with a significantly greater 16% in the forest compared with 1-3% in the arable fields. The 60-90 mm depth had a significantly greater percentage in Field-3 (7%) than Field-26 (0%); the remaining means of 1-5% did not statistically differ from the others.

The total collembolan percentages found in the 0-30 mm depth increment were 84, 64, 55, 94, and 82% from the forest and fields 3, 8, 26, and 49 respectively, with the Field-3 value significantly less than the value from Field-26 (Table 26c). The 30-60 mm depth data followed these, with 11, 23, 27, 6, and 4% in the same respective order; again the Field-3 and Field-26 values were significantly different. The percentages found at 60-90 mm depth (0-18%) did not differ significantly. At that depth, collembolan populations appeared to be highly aggregated, with most samples containing no Collembola; the

occasional sample with Collembola commonly had tens of specimens.

4.3.2.5 Microarthropods and Soil Moisture Content

Linear regression of the microarthropod numbers in the 0-30 mm depth increments by soil moisture content of adjacent 0-30 mm cores resulted in an r^2 value of 0.28. The r^2 from the regression of acari by moisture content was 0.26, and the collembola by moisture content regression r^2 was 0.06.. All were statistically significant.

4.3.3 Discussion

Mean numbers of soil Acari and Collembola per square metre were in the low range of the numbers expected from a temperate forest biome (Table 2); the dominance of the Acari and especially the Oribatei in the mesofauna was typical.

Of the forest soil macrofauna, the Coleoptera, Araneae, and Diptera numbers were not unusual, however the enchytraeid numbers found were two orders of magnitude lower than expected. The hand sampling of the macrofauna was intended to be relatively quantitative; this probably was not achieved for the enchytraeid populations. An extraction method would have been more appropriate for the sampling of the enchytraeid population.

Berg and Pawluk (1984) found 13 000 to 49 000 microarthropods m^{-2}

in a fallow cultivated Gray Luvisol at the Breton Plots, and 24 000 to 122 000 in cultivated soil under various litter and vegetation covers, with an overall mean of 48 000 microarthropods m^{-2}. These numbers, equivalent to 24 to 89, 43 to 221, and 87 individuals per core, were similar to the numbers reported here.

Much larger microarthropod populations than those in the Luvisolic Ap horizons of this study have been recorded from Black Chernozemic soils. Pawluk (1986) found numbers of microarthropods in a Black Chernozemic soil under several vegetation and management regimes to be two orders of magnitude greater than those reported here for Luvisolic Ap horizons. The sampling and extraction methods were similar, however Pawluk's sampling was done in the Fall. What portion of the difference was due to seasonal variability cannot be stated without full year population studies of each site, however Petersen and Luxton's (1982) review suggested seasonal variability greater than 4-20 times was not expected.

Organic soil is a more suitable habitat for Acari than for Collembola, while the collembolan population in frequently cultivated Ap horizons may approach or exceed the Acari population. Under most litters and vegetation covers at the Breton Plots (Berg and Pawluk, 1984) the Acari-to-Collembola ratio was less than one; under grass litter and under a fescue stand the ratio was 2:1 to 3:1, similar to the Field-3 ratio of this study. The Acari-to-Collembola ratio of the forest (4:1) was typical of boreal forests (Table 2). The ratios from

Field-8 (8:1), Field-26 (8:1) and Field-49 (9:1) also were in this range.

Collembola in Pawluk's (1986) Black Chernozemic study commonly were in greater number in the 30-60 and 60-90 mm depths than in the surface increment; Acari populations tended to be greatest near the surface, but less skewed than the populations reported in this study. Berg and Pawluk (1984) found Collembolan and Acari numbers generally greater in the 0-30 mm increment than in lower increments, however the distribution was less skewed toward the surface; in some cases the Collembolan populations approached an even distribution with depth. Apparently frequent cultivation encouraged an even distribution of the microarthropod population in the upper mineral soil, while cessation of cultivation and the development of organic layers both encouraged a population skewed toward the surface. The Acari (with their thick integument, their inability to consume mineral soil material, and the preference of many species for invasion of relatively intact plant litter) had a population oriented more toward the surface and the organic layers, than had the Collembola.

The forest macrofaunal population appeared most complex, with many phyla, classes, and families represented. Frequent cultivation limited the population of Field-3 to large Insecta larvae, with Araneae as the dominant predator. The population under the older forage stands had regained some of its complexity, with predaceous Coleoptera, smaller Diptera larvae and Enchytraeidae present.

Continuous forage stands have not encouraged the development of a Chernozem-like faunal population. The population of Field-3 was similar to that of other arable Gray Luvisolic soils, and substantially altered (in size, composition, complexity and distribution) from that of the undisturbed forest. Under a continuous forage stand, the population characteristics again approached those of the original forest.

4.4 Micromorphology

4.4.1 Related Distribution

The forest LFH horizons had granic to granoidic fabrics (Table 27; Plates 2, 4a-c). Granic units were dominantly plant fragments (in general these were increasingly fragmented and humified with depth), faunal fecal material, and, in the lower layers, charcoal fragments and silt-size mineral grains. Coalesced fecal pellets and (in the lower organic horizons) humified organic matter, charcoal fragments, and fine plant fragments formed a granoidic fabric. A significant mull component also was present in the H horizon.

The granic sequence formed the dominant related fabric sequence of the Ahe horizons, (Plate 4c) although a significant fragmoidic porphyric component was present as well. Fine granic and granoidic (probably fecal) materials similar to those in the lower organic layers were found throughout the Ahe, in channels and voids between granoidic

Table 27. Micromorphological descriptions from thin sections of the surface soil layers.

Forest Site Profile

L. 8-6cm. Humi-phytogranic.
Undecomposed and partially decomposed Populus leaf and Picea needle fragments.
Irregular, coalesced (humigranoidic) 0.05-0.1mm fecal pellets within large phytogranic fragments, and free 0.2-0.7mm normal pellets are common.
Generally isotropic.
Yellow orange and orange color.

F. 6-3cm. Humigranoidic / humi-phytogranic.
Partially decomposed Populus leaf and Picea needle fragments, and few 0.5-2mm roots.
Many irregular 0.05-0.1mm discrete and coalesced fecal pellets, commonly within plant fragments. Common 0.5-0.8mm irregular to spheroidal pellets also present.
Generally isotropic.
Reddish brown to dark reddish brown color.

H. 3-0cm. Mull-phyto-humigranic.
A complex fabric of coalesced and discrete fecal material, partially decomposed and decomposed plant fragments, charcoal fragments, and a few zones of mullgranic to granoidic components.
Fecal pellets (0.05-0.1mm) commonly are coalesced into highly porous weakly banded 1-3mm fragmoidic units.
Quartz silt grains are throughout the zone.
Some roots are present.

Ahe. 0-2cm. Granic to granoidic // banded fragmoidic porphyric to vughy porphyric.
Partially coalesced 0.05-0.1mm irregular fecal pellets are common in channels and grouped into porous weakly banded fragmoidic units.
Charcoal fragments are common.
Frequent reddish brown and dark reddish brown to black, normal and irregular 0.5-2mm nodules are found, often as discrete subspheroidal units.
Matrix units have a silasepic plasma fabric.

Ae. 2-6cm. Isobanded vughy porphyric.
Frequent orange to reddish brown and dark reddish brown to black normal 0.5-2mm nodules, with inundulic to skelmosepic fabrics.
Partially coalesced 0.05mm fecal pellets are rare, and limited to small aggrotubules.
Roots are common.
The matrix material has a silasepic plasma fabric.

Table 27, continued.

Field Three

Ap. 0-14cm Granic to granoidic // fragmoidic to vughy porphyric.
A fragmoidic to vughy porphyric fabric of large moderately to well accommodated units.
Numerous craze planes and channels and subhorizontal to horizontal joint planes, with fine humi-matrigranic and metafragmoidic material.
Common charcoal fragments.
Common roots.
Common partially decomposed plant fragments.
Aggrotubules of 0.03-0.1mm irregular fecal pellets.
Many reddish brown and dark reddish brown to black 0.3-2mm normal nodules.
Generally dark brown in color.
Silasepic to weak skelsepic plasma fabric.

Also present are zones and nodules (1 to 4mm) of a light gray colored porphyric and fragmoidic porphyric material.
Few, small normal nodules (0.15-0.8mm).
Craze planes and large channels (1-4mm) are present.
Fine fecal material limited to a few channels.
Silasepic plasma fabric.

Field Eight

I Turf. 1-0cm. Mull-humi-phytogranic.
Undecomposed and partially decomposed plant fragments, with many discrete and partially coalesced 0.05mm and few 0.3mm fecal pellets.

II Ap. 0-7cm. Matrigranic-matrigranoidic / weakly banded granoidic porphyric.
Subparallel to parallel joint planes, with weak banding at the 2-4cm depth.
Many fine (0.05-0.1mm) discrete and partially coalesced fecal pellets, usually clustered, in channels and voids.
Few large (5x20mm) and frequent smaller aggrotubules of fine fecal material, and large (2-5mm diameter) channels with frequent longitudinal root transects and common fine irregular fecal pellets.
Many reddish brown to black 0.3-2mm normal nodules and common charcoal fragments throughout.
Silasepic, brown color.

Table 27, continued.

III Ap. 7-10cm. Granoidic porphyric to vughy porphyric.
Frequent craze planes and subhorizontal to horizontal joint planes with some fine matrigranic material in channels and planes.
Fecal material is rare.
Many reddish brown to black 0.3-2mm normal nodules and common charcoal fragments throughout.
Large (2-8mm) orange brown nodules common, especially near the lower boundary.
Orange brown to light brown color.

IV Ap. [illegible]13cm. Weakly banded vughy porphyric.
Vughy porphyric material with subhorizontal irregular joint planes.
Few fine (0.05mm) discrete and partially coalesced fecal pellets, usually clustered, are found in channels and voids.
Many reddish brown to black 0.3-2mm normal nodules, and charcoal fragments are present throughout the zone.
(2-4mm) orange brown nodules also are present.
lor.

Field 26.

I Turf. 2.5-0cm. Humi-phytogranic.
A complex of undecomposed and partially decomposed plant fragments, and irregular and normal partially coalesced and discrete 0.01-0.1mm and discrete irregular 0.2-0.5mm fecal pellets, with a weak mull component.
Large (3x10mm) phenoclasts of matrogranoidic material may be present.
Undecomposed plant fragments are anisotropic.
The turf to Ap boundary is abrupt, with 1-2mm of granic to matrigranoidic porphyric gradation, and very little mull formation.

II Ap. 0-11.5cm. Weakly banded vughy porphyric / vughy porphyric.
An increasingly dense fabric with depth, with skew planes and subhorizontal to horizontal joint planes and numerous metavughs and channels.
Fine roots are common, with narrow (0.1-0.2mm) voids between the root and the matrix material.
Few undecomposed and partially decomposed plant fragments.
Fecal material is fine, irregular, coalesced, containing silt material, and is uncommon, limited to a few fairly small (1-5mm) channels.
Many charcoal fragments.
Many orange, reddish brown, and dark reddish brown to black irregular to normal 0.15-1mm nodules.
Silasepic to weak skelsepic fabric.
Generally light brown color.

Table 27, continued.

Field 49.

Turf: 2-0cm. Humi-phytogranic.
A complex of undecomposed and partially decomposed plant fragments, and irregular and normal partially coalesced and discrete fecal pellets (0.01-0.1mm) and discrete irregular fecal pellets (0.2-0.5mm), and a weak mull component.
The undecomposed plant fragments are anisotropic.

Ap. 0-1cm. Humi-mull-phyto-matrigranic // matrigranoidic // matrigranoidic porphyric.
A complex zone grading from granic to matrigranoidic porphyric with depth, with a thin upper zone of gradation to the fabric of the turf above.
Many oblique roots.
Many aggrotubules of fine fecal material.

Ap. 1-11cm. Weakly banded vughy porphyric // vughy porphyric.
An increasingly dense fabric with depth.
Subhorizontal to horizontal joint and craze planes and numerous metavughs and channels.
Fine roots and oblique sections are common, with narrow (0.1-0.2mm) voids between the root and matrix material.
Fecal material is rare, fine, irregular, coalesced, containing silt material, and is limited to a few fairly small (1-5mm) channels.
Many charcoal fragments.
Few undecomposed and partially decomposed plant fragments.
Many orange, reddish brown, and dark reddish brown to black irregular to normal 0.15-1mm nodules.
Silasepic to weak skelsepic fabric.
Generally light brown color.

Ae. 11-12cm. Weakly banded fragmoidic porphyric // vughy porphyric.
Small zones of fine matrigranoidic material in subhorizontal and horizontal joint planes and channels.
Small (0.15mm) to medium (0.6mm) reddish brown to dark reddish brown nodules are common.
Silasepic plasma fabric.
Generally lighter color than the Ap above.

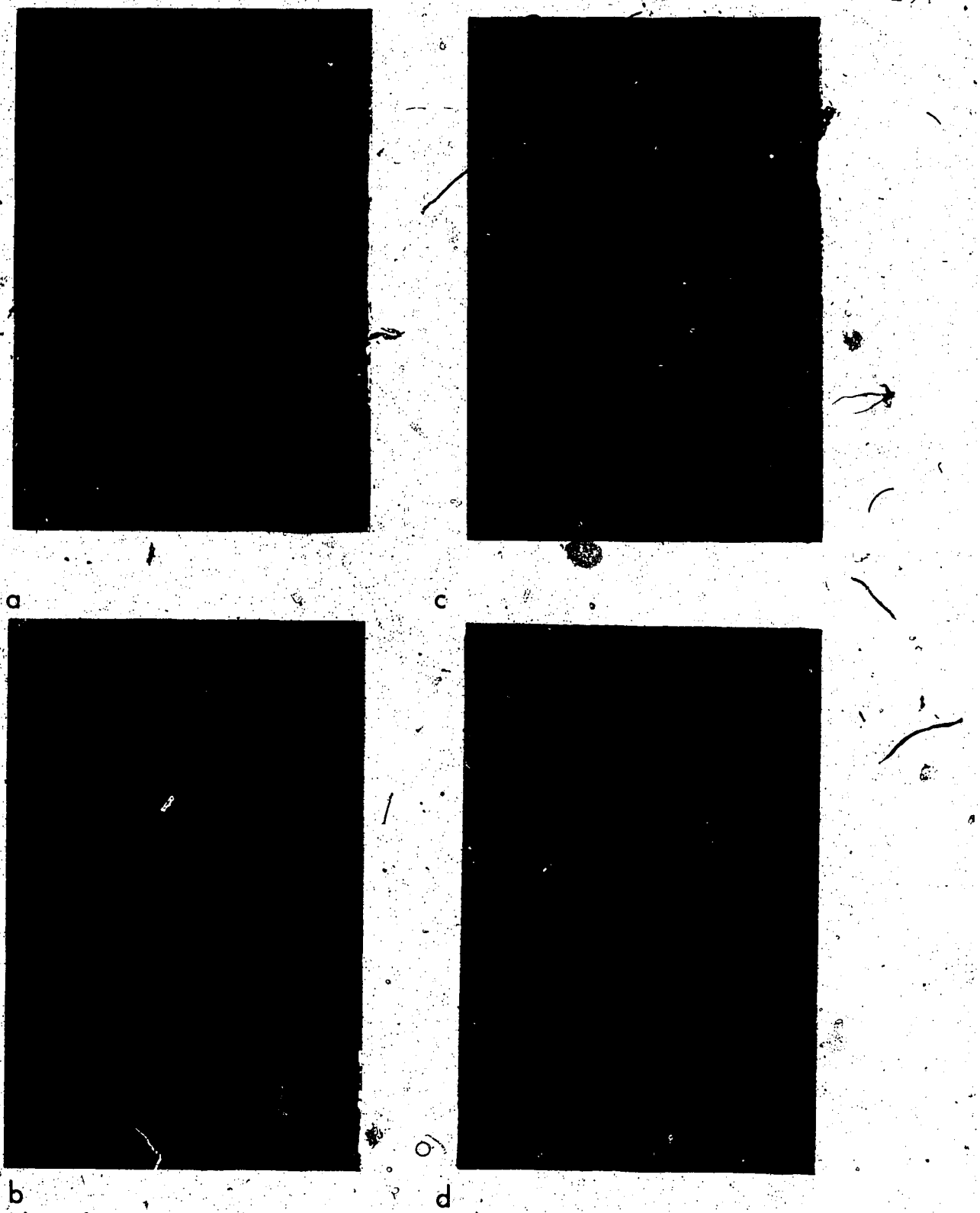

Plate 2. - Thin sections of surface horizons from two forest profiles. **a.** Profile V-1, 0-7 cm; **b.** profile V-1, 7-14 cm; **c.** profile V-3, 0-7 cm; **d.** profile V-3, 7-14 cm.

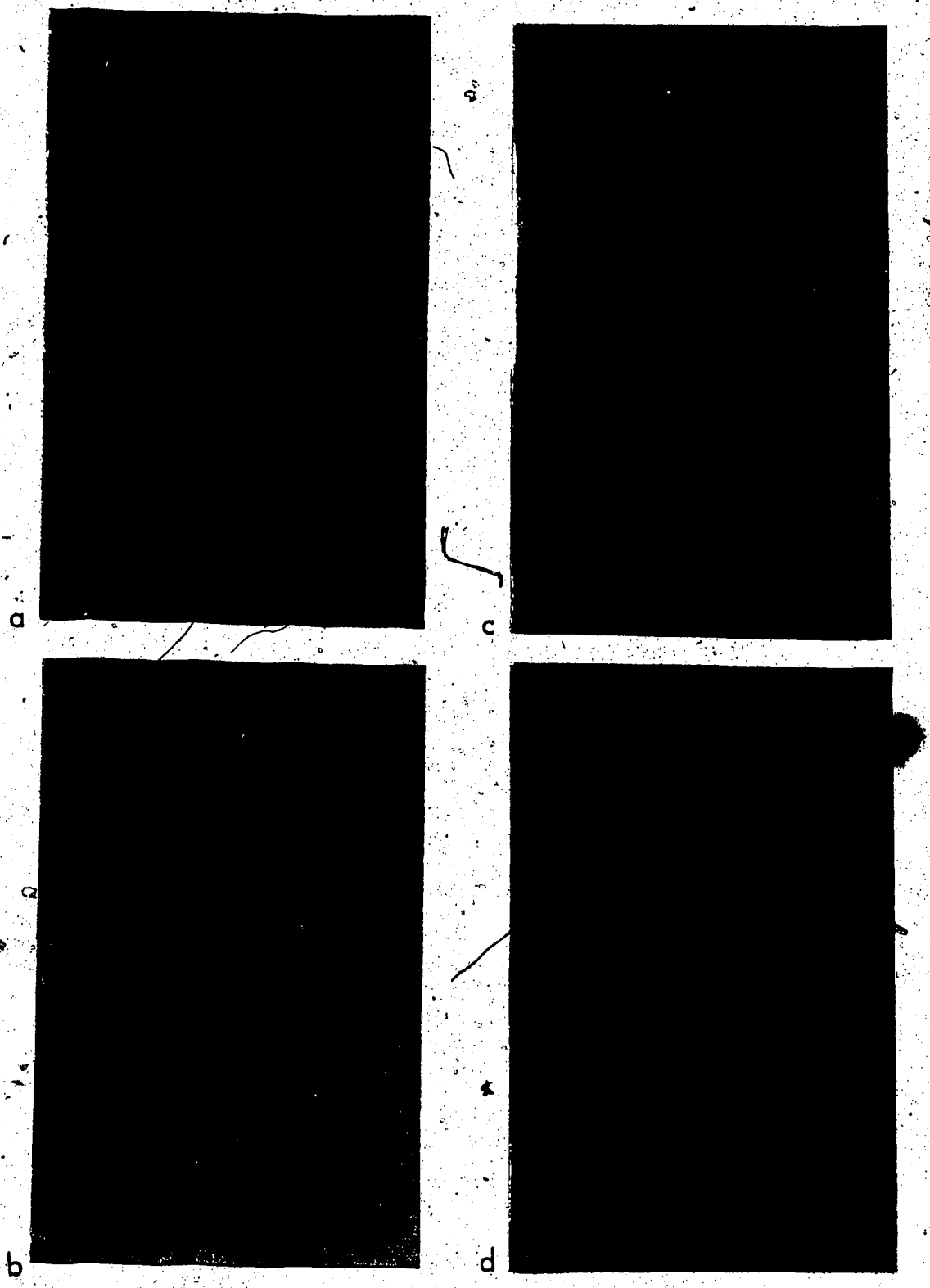

Plate 3. Thin sections of soil surface horizons under forage grasses. a. Field-3, 0-7 cm; b. Field-3, 7-14 cm; c. Field-49, 0-7 cm; d. Field-49, 7-14 cm.

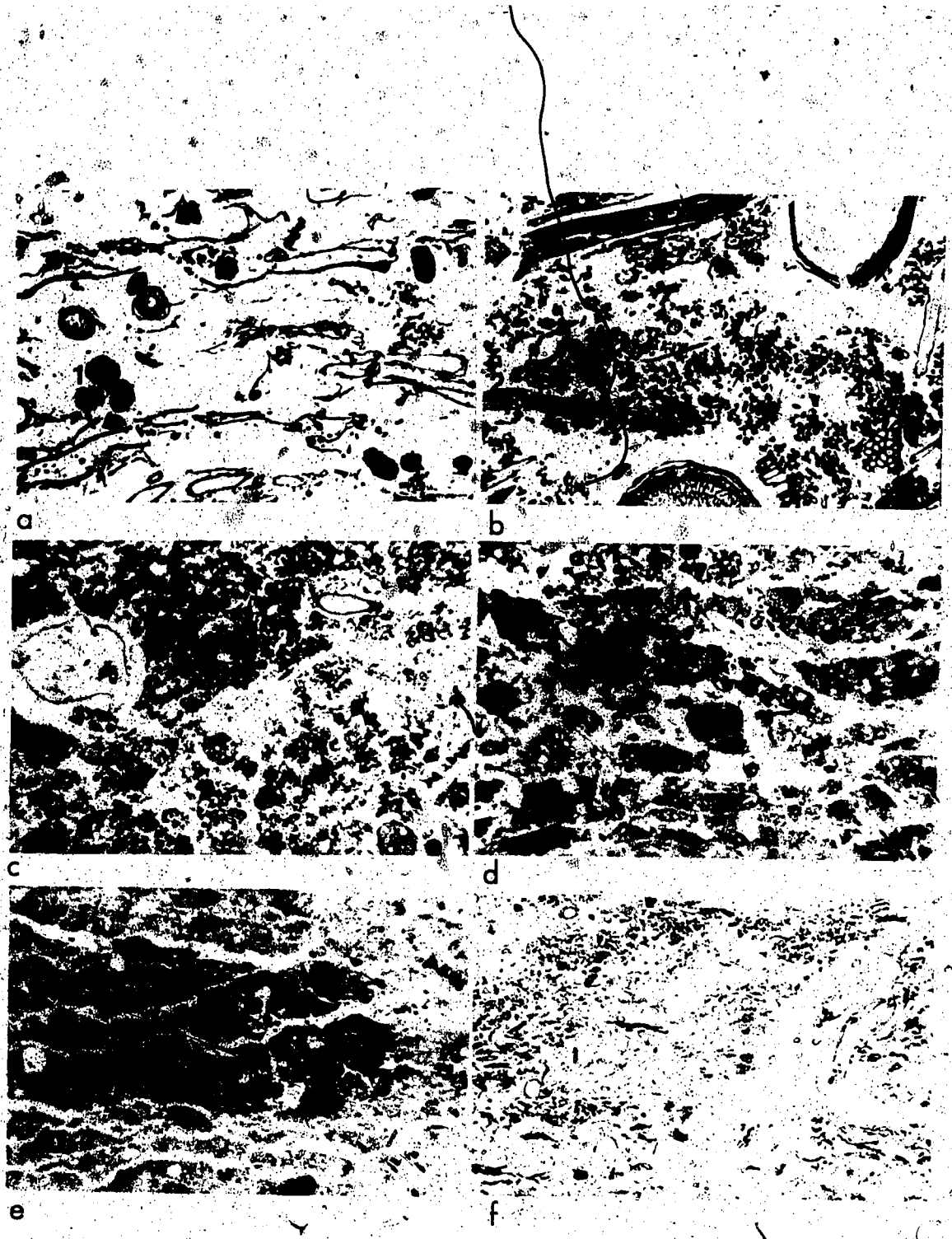

Plate 4. Soil microfabric features of the organic layers and the undisturbed forest A horizons (actual scene widths 15 mm unless noted otherwise; see text for descriptions). a. Forest soil upper F layer; b. lower F layer; c. H layer and Ahe horizon contact; d. Upper Ae horizon (scene width 12 mm); e. Ae horizon, with large (11 mm x 5 mm) pedorelict; f. turf layer under the 49 year old grass stand. Labels indicate pellets of 1 insect larvae, 2 Acari, 3 Collembola, and 4 Enchytraeids.

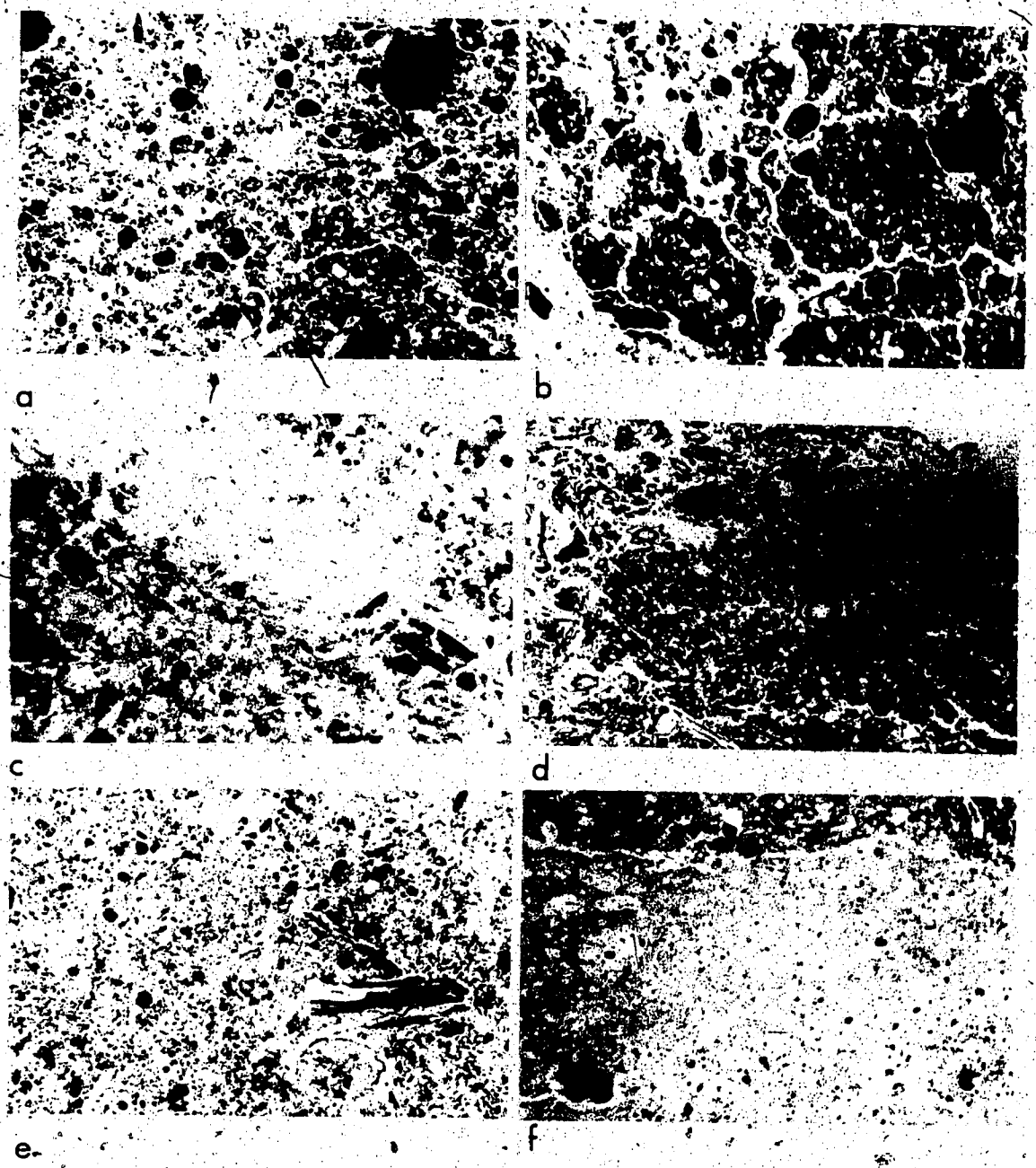

Plate 5. Soil microfabric features of Ap horizons under 3 year old and 49 year old forage stands (actual scene width 15 mm unless noted otherwise; see text for descriptions). a. Field-3 Ap at 10-20 mm depth; b. Field-3 Ap showing craze planes and lighter incorporated AB material, lower left; c. large organic pocket and channel in Field-3 Ap (scene width 19 mm); d. upper 10mm of Ap horizon under 49 year old forage stand (scene width 23 mm); e. Field-49 Ap, at 20-30mm depth; f. Field-49 Ae with Ap contact near top of scene.

porphyric, fragmoidic porphyric and vughy porphyric units. Most of the large matrix units did not appear to be of faunal origin. The Ae horizon had a strongly isobanded vughy porphyric fabric (Plate 4e), with a minor fine granic to granoidic component in channels and voids, especially near the upper boundary of the horizon (Plate 4d).

The turf layers of the agricultural soils were composed of plant roots and fragments, partially decomposed plant matter, and fecal material (Plate 4f). Some coalescence of the fecal material had occurred near the mineral soil contact.

The [redacted]nic sequence characterized the cultivated mineral soils (Plates 3[redacted]5). Most of the material was matrigranoidic porphyric to vughy porphyric, with granic and granoidic components limited to the upper few centimetres of the cultivated soil and to aggrotubules. Mixed complex matrigranic-vughy porphyric fabric occurred in the upper 10mm of the Ap horizons of Field-26 and Field-49 (Plate 5d). The remainder of the horizon was dominated by a dense vughy porphyric fabric (Plate 5e,f). Some large fragmoidic units were present in the Field-3 Ap (Plate 5a-c). Planes and aggrotubules were larger and more frequent in the Field-3 and Field-8 soils. Weak banding was found in all Ap horizons.

4.4.2 Voids

Simple packing voids were dominant in the organic layers. Channels and chambers, often partially filled with fine fecal material, were present within plant fragments (Plate 4b). The H horizon of the forest also contained compound packing voids and channels. Weak craze planes were found between, but also interconnected vughs within humi-fragmoidic units in this layer.

The Ahe horizons (Plate 4c) contained compound packing voids, root channels, craze planes and subhorizontal joint planes between units, and interconnected vughs and vughs within humigranoidic and porphyric units. Plant fragments and root transects often were partially reworked by fauna.

The voids of the Ae horizon from the forest (Plate 4d,e) were subhorizontal (0.1-0.5 mm thick) joint planes, vughs, and root channels. Compound packing voids were limited to occasional aggrotubules. The joint planes were much less common in the Ae horizon of Field-49 than in the forest Ae.

The Ap horizons of Field-3 and Field-8 contained many craze and skew planes and large root channels (Plate 5a-c). Channels were numerous in the upper soil. Much of the upper soil, and root channels at lower depths, contained compound packing voids. Interconnected vughs and vughs were common throughout the matrix material.

The Ap horizons of Field-26 and Field-49 had a thin zone of compound packing voids and channels at the upper surface (Plate 5d), and fine root channels, fine skew planes, subhorizontal joint planes, interconnected vughs, and vughs throughout the horizon. Very fine root channels were common throughout the Field-26 and Field-49 Ap horizons, however compound packing voids in the lower Ap horizon were limited to a few channels. Root channels were finer in the Field-26 and Field-49 Ap horizons (Plate 5d,e) than in those of Field-3 and Field-8 (Plate 5b).

4.4.3 Fecal Pellets

Fecal pellets were present in all horizons from which thin sections were prepared, however they were limited to channels and voids in the mineral horizons, whereas they formed a large portion of the matrix of the lower F and H horizons of the forest soil.

Fecal pellets found in the forest organic layers included:

1. small (30-50 µm and 80-100 µm) compact, spherical, smooth surfaced, brown to dark brown pellets, within (and the same color as) plant material, or in clusters free in the soil, throughout the organic layers; of oribatid origin (Plate 4b);
2. similar sized spheroidal, irregular surfaced, and often coalesced dark brown pellets of humic material, occasionally containing silt grains, scattered throughout the organic layers;

mainly of collembolan origin (Plate 4b);

3. slightly larger (100-200 µm), similar to the collembolan pellets, found in the lower F and H horizons; probably of enchytraeid origin (Plate 4b,c); and

4. large (0.6-1.6 mm) usually spheroidal, smooth or irregular surfaced, containing plant fragments and/or smaller fecal pellets and occasionally silt grains, alone or in clusters of 2-5, throughout the organic horizons; probably of insect larval origin (Plate 4a).

Pellets of the turf layers were similar, with fewer of the large size (Plate 4f). They were most common in the lower half of the turf, and frequently were found grouped in (often partially coalesced) bands or zones.

Fecal pellets found in the mineral horizons were small (50-200 µm), clustered in aggrotubules and channels (apparently of collembolan origin; Rusek, 1985), or within decomposing plant material (apparently of oribatid origin). Pellets were common throughout the craze planes and channels of the forest Ahe (Plate 4c,d) and the upper portion of the Field-3 and Field-8 Ap horizons. Aggrotubules were larger and more common in these horizons than in the Ap horizons of Field-26 and Field-49. Except in the upper 10 mm, fecal pellets were rare in the latter two horizons.

4.4.4 Other Pedological Features

Orange brown to dark brown or black nodules were common throughout the mineral horizons. Similar nodules in A horizons of Gray Luvisols and Luvic Gleysols have been shown (Arshad and St. Arnaud, 1980) to be iron-manganese concentrations, caused by restricted drainage and resultant frequent saturation of the upper solum.

Aggrotubules were found in all mineral horizons, and were most common in the forest Ahe and in the Ap horizons of fields three and eight. Aggrotubules in the Ap horizons of Field-26 and Field-49 were smaller than those in Field-3 and Field-8. The tubules contained fecal pellets of mull material or granic matrix units of unknown origin.

Three types of pedorelicts present were:

1. wedges (horizontal, to 5 mm thick) of Ap material in the turf layers of Field-26 and Field-49,
2. Ae or AB material in the Ap horizon of Field-3 and Field-8, probably due to recent deeper plowing (Plate 5b) and
3. a horizontal rectangular (5 mm x 10 mm) zone of dark (presumably Ahe) material in the Ae of one of the forest profiles (Plate 4e). This most likely was an old aggrotubule from a root channel, since compressed and banded by the forces responsible for the strong banding of the Ae.

4.4.5 Discussion

The microstructure of the upper solum of the forest soil was similar to that of Gray Luvisols described by Howitt and Pawluk (1985a) and Santos et. al. (1985). Strongly banded Ae horizons with iron-manganese concretions were observed in each study. Santos et. al. (1985) did not observe fecal material in the L horizon (whereas some large, probably insect larval pellets were observed in the L horizon in this study) but did describe "very dark brown to black organic bodies similar to those called 'melanon' by Bal (1973)", in the lower organic layers, and concentrated at the bottom of the H horizon.

Signs of a highly active faunal population in the LFH horizons, and low activity in the Ae, similar to those observed in this study, were commented on by Santos et. al (1985), as a challenge to the assumption that abrupt horizon boundaries imply little faunal activity. The fauna observed here are not able to mix the mineral soil to a significant degree, but are very instrumental in the structural development of the organic layers. The vertical stratification of the organic layers and their faunal community is the result of a feedback relationship between them, and with the microfloral community, and is driven by various environmental factors, including gradients of moisture, temperature and age of substrate.

The microstructure of the upper solum of Field-3 is similar to that observed in the grain/forage rotation plots at Breton (Pawluk, 1980). Granic structural units formed by cultivation are weak; with

time they coalesce to form a granoidic to vughy porphyric fabric. The incorporation of manure and plant material with cultivation was evident from the frequent pockets of organic material, and small, dark pigmented zones. Some of the frequent large channels present probably remained from cultivation, while others containing large grass and legume roots may have been formed by the plants. Some mull formation was evident in channels and tubules, especially near the soil surface, and where organic materials were evident.

Zones of much lighter colored matrix material in the Ap of Field-3 may have been incorporated from the AB horizon by cultivation. These zones have remained discrete from the darker Ap matrix. In the absence of faunal ingestion of the matrix material, cultivation is the main soil mixing factor. That these zones remain discrete from the darker Ap matrix suggests a recent deeper cultivation.

With time under a continuous forage stand, buried organic materials decompose and the voids they occupied, and the channels created by cultivation narrow and close. Blevins et. al. (1984) reported that macroporosity decreased under a no-till management system, and microporosity increased; the net effect was a total reduction in porosity and an increase in bulk density.

All Ap horizons had subhorizontal joint planes; in the older stands these were the dominant form of large void. Whether these were from compaction, freeze-thaw action and ice lens formation, or both was

not evident. Similar joint planes have been observed in Ap horizons at the Breton Plots (Berg and Pawluk, 1984).

Signs of faunal activity under the older stands were localized in the turf layer and the upper 10-20 mm of mineral soil. Mull formation was minimal, and at the mineral surface. Fecal pellets were most abundant in the lower turf; this probably is because of both localization of the faunal community (enchytraeids were found only in the lower turf) and translocation by water.

The matrix material of the Ap horizons of Field-26 and Field-49 was lighter colored and more homogenous, with a bleached look in thin section, compared with that of Field-3 and Field-8. This may be evidence of continued lessivage under the forage system. There were no signs of development of a Chernozem-like mull fabric (Pawluk, 1986), or even of a well channeled and dark colored granic fabric like that found in the forest Ahe horizon.

4.5 A Synthesis

The observed micromorphology and signs of faunal activity from the thin sections correspond well with the faunal population data. Large pellets, typical of insect larvae and Gastropoda were especially common in the L and F horizons, collembolan and acarine pellets were found throughout the organic layers, and enchytraeid pellets were in the H and lower turf layers. Fecal pellets were much less common in

the mineral layers. The faunal population trends followed the same pattern. Also the clustered nature of collembolan populations at depth is predicted by the pockets and aggrotubules of organic material found in thin sections of the Ap horizons, and the localization of fecal material to these zones.

Earthworm pellets were not observed in any of the thin sections, nor were earthworms found in the faunal sampling. No reason for their absence was evident, although it may have had to do with the pH of the soil, relatively low organic matter levels, or possibly the presence of obnoxious vegetation types. Their absence may be relevant to the observed lack of faunal pedoturbation and mull development.

A qualitative correlation was observed between faunal population complexity, in terms of number of taxa observed, and microhabitat complexity. The stratified organic horizons of the forest soil were the most complex microhabitat systems, and had the largest variety and number of fauna. With clearing and cultivation, the habitat complexity was greatly decreased, and limited to a few channels and voids in the mineral soil matrix. The faunal population of Field-3 was the least complex. The development of a turf layer in Field-8 introduced a new habitat; a more complex macrofaunal population was observed. With thickening of the turf in Field-26 and Field-49 this habitat showed stratification and a habitat for enchytraeids was developed. Enchytraeids are highly sensitive to moisture stress, and feed on microarthropod fecal materials (O'Connor, 1967). The only appropriate

environments in the study site were the lower organic layers of the forest soils and the older forage stands, where fecal pellets had accumulated; this is where the enchytraeids were found.

An increase in organic matter content in the cultivated Ap horizons over the forest Ae was evident in the color of the matrix material, and in an increase in mull material in the upper few centimetres of the horizon. The forest Ahe had higher organic matter content, a darker color in thin section, and more humic and mull material than the cultivated horizons. The increase in organic matter from Field-3 to Field-49 was not evident in thin-section, however. Nor did fauna appear to have taken advantage of any increased grazing potential in the greater biomass present in the Field-49 Ap over that in Field-3.

The absence of a significant invasion of the Ap horizons by soil fauna, with time under a continuous forage system, is not easily explained from the data gathered. The apparent decrease in macropores, observed in the thin sections, and possibly reflected in the increase in bulk density from Field-3 to Field-26, may have discouraged non-burrowing fauna from invading the mineral layers. Carbon and biomass contents of the Ap horizons remained lower than those of Black Chernozemic Ah or Ap horizons (Tarnay, 1980; Peinl, 1984), and may not have reached a level which provides adequate foodstuffs for the microarthropods. Without the comminuting and mull forming effects of earthworms, the development of a microhabitat suitable to

microarthropods may be a very slow process of hundreds of years of high annual root turnover, for which the fine, perennial, turf-forming grasses of the continuous forage stands may not be well suited.

5. CONCLUSIONS

The biological reserves of a Gray Luvisol under virgin forest are localized in the highly stratified, microstructurally complex organic horizons. Fifty-three percent of the carbon and 39% of the nitrogen supplies of the soil to 35cm depth were found in these horizons. The macrofauna and microarthropod populations were located there as well. Under a long-term continuous forage stand, this biostructure was substantially altered. The organic horizons were replaced by a thinner, and less heterogenous turf layer, with a reduced and less diverse faunal population. Only one-quarter of the carbon and one-fifth of the nitrogen of the profile to 35cm depth was found in the turf. Carbon and nitrogen concentrations, and biomass activity were significantly higher in the Ap horizon under the continuous forage stands compared with the forest A (Ahe plus Ae) horizons.

The effects of some long-term processes which are interrupted by cultivation, were observed by comparing soils under forage stands of different ages. While the data were somewhat ambiguous, carbon and nitrogen concentrations appeared greater in the Ap horizon under the 49 year old forage stand than under the 3 year old stand. Soil biomass also was greater. Bulk density of the Ap horizon appeared to increase under continuous forage, possibly reaching a maximum after 26 years, then decreasing again. The concurrent development of a thick turf layer may have been important to the later decrease in bulk density. It was certainly important to the macro and mesofaunal population

dynamics. The youngest forage stand (that is, the most frequently cultivated soil) had the smallest and least diverse faunal population. With the development of a turf layer, population numbers increased, and a habitat for an enchytraeid population was formed. The microarthropod population became more skewed toward the soil surface, and was almost totally dominated by Acari, particularly Oribatei.

Despite the increased carbon, nitrogen and biomass in the Ap horizon under continuous forage compared with those in the forest Ae horizon, the soil has not developed a mull or proto-mull microstructure typical of Chernozemic soils found under the grasslands of the Great Plains. Fragmic and granic structures produced by cultivation had begun to coalesce in the Ap horizon under Field-3, and were completely coalesced after 26 years under forage. Except for the lack of strong isobanding, and a darker color, the vughy porphyric microstructure of the Ap horizon under long-term continuous forage was more similar to that of the forest Ae than the granic Ahe horizon. Only at the mineral surface and in a few aggrotubules was faunal activity evident in the Ap horizons. Without pedoturbation from larger soil ingesting fauna (whose absence was noted, but unexplained) the faunal role in fabric formation was minimized.

The development of a mull humus-form in the Great Plains region of Canada appears to involve a dynamic process of feedbacks among various fauna, bacteria, micro and macroflora, and physical and chemical processes of the soil. Fabric development in a Gray Luvisolic soil

under continuous forage has not been dominated by such interactions. Whether it is being dominated by the lessivage processes characteristic of the soils of the region (the acidic nature of the turf layer, the processes of breakdown and coalescence of granic units formed by cultivation, and the homogenous, almost bleached appearance of the microfabric may suggest this) or is in a stage in the mull development process not visible under the microscope (conceivably root and microbial biomass and soil organic matter concentration and quality may be approaching a critical level for faunal invasion of the mineral soil) cannot be stated without a dynamic study of the carbon cycling and hydrologic processes of the soil.

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