Moore, Terry A.

SEASONAL FUNGAL BIOMASS DYNAMICS IN AN INTERIOR ALASKAN PAPER BIRCH (BETULA PAPYRIFERA MARSH) AND QUAKING ASPEN (POPULUS TREMULOIDES MICHX.) STAND AND EFFECTS OF LONG-TERM FERTILIZATION

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A

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FUNGAL BIOMASS DYNAMICS IN AN INTERIOR ALASKAN PAPER BIRCH (*Betula papyrifera* Marsh) AND QUAKING ASPEN (*Polulus tremuloides* Michx.) STAND AND EFFECTS OF LONG-TERM FERTILIZATION

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ABSTRACT

Standing crop fungal biomass was measured at bi-weekly intervals for two successive field seasons in contiguous, 50 year old stands of quaking aspen (Populus tremuloides Michx.) and paper birch (Betula papyrifera Marsh) and in contiguous stands of aspen and birch undergoing long-term fertilization by yearly application of inorganic nitrogen, phosphorus and potassium fertilizers. Soil temperature and moisture were monitored throughout the study.

Principal goals were: (1) to delineate seasonal fluctuations in fungal biomass in the forest floor and mineral soils of aspen and birch vegetation sites considered representative of upland, interior Alaskan hardwood taiga; (2) to determine if biomass fluctuations were correlated with fluctuations in soil microclimate; (3) to determine if differences in fungal biomass were correlated with dominant overstory vegetation; i.e., differences in primary or secondary site substrate (resource) quality; (4) to determine if long-term (nine years) application of inorganic fertilizers altered overall standing crop fungal biomass in the two vegetation types studied; and (5) to determine if soil bulk density or microclimate were influenced by vegetation type or fertilization.

Results show that seasonal biomass for both control and fertilized sites was closely correlated with soil moisture and exhibited little or negative correlation with soil temperature.

Unamended aspen soils supported significantly greater fungal biomass than birch soils due to increased soil moisture, a more favorable chemical environment and production of organic matter more conducive to growth of soil fungi. Fertilization significantly decreased fungal biomass in aspen soils indicating that long-term treatment with inorganic fertilizers could be detrimental to mineral cycling in this forest type. Fertilization significantly increased fungal biomass in birch soils due to increased soil organic matter content and increased soil moisture. Hyphae of basidiomycetes was significantly decreased by fertilization in both vegetation types suggesting that basidiomycetes involved in saprotrophic decomposition and/or mycorrhizal associations were adversely affected by fertilization.

The effects of vegetation type and fertilization on soil temperature, moisture and bulk density are discussed.

TABLE OF CONTENTS

	Page
ABSTRACT	3
LIST OF FIGURES	7
LIST OF TABLES	13
ACKNOWLEDGMENTS	16
INTRODUCTION	18
CENTRAL HYPOTHESIS, COROLLARIES AND OBJECTIVES	20
STUDY AREA	22
A. Vegetation	22
B. Soils	24
C. Climate	25
D. Intensive Site Baseline Data	26
EXPERIMENTAL METHODS	
A. Field Methods/Experimental Design	30
B. Laboratory Methods/Experimental Design	34
C. Calculations	46
D. Statistical Treatment	48
RESULTS AND DISCUSSION	
A. Soil Temperature	56
B. Soil Moisture	70
I. Rainfall/Soil Moisture	70
II. Effects of Vegetation Type and Long-Term Fertilization on Soil Moisture	75
C. Soil Bulk Density	92
D. Seasonality, Vegetation and Fertilization Effects	102

Page

I. Seasonal Fluctuations of Fungal Biomass 104

II. Data Presentation: Effects of Vegetation Type and Long-Term Fertilization on Fungal Biomass 172

III. Discussion: Vegetation Effects 183

IV. Discussion: Fertilization Effects 192

V. Effects of Vegetation Type and Fertilization on the Distribution of Basidiomycete Hyphae 199

SUMMARY AND PROSPECTUS FOR FURTHER RESEARCH 203

APPENDIX 209

BIBLIOGRAPHY 213

LIST OF FIGURES

Figures		Page
Figure 1.	Study site location.	23
Figure 2.	Study site rainfall.	27
Figure 3.	Field experiment design.	31
Figure 4.	Laboratory sampling hierarchy: Preparation of soil cores for Level I fungal biomass sampling.	35
Figure 5.	Laboratory sampling hierarchy: Preparation of soil cores for Level II fungal biomass sampling.	36
Figure 6.	Laboratory procedure overview.	40
Figure 7.	Data Hierarchy: Levels of statistical treatment.	49
Figure 8.	Soil temperature for field season 1: Aspen (A) and birch (B), depths 1 (O1 horizon) and 2 (O22/A horizon).	58
Figure 9.	Soil temperature for field season 2: Aspen (A) and birch (B), depths 1 (O1 horizon) and 2 (O22/A horizon).	59
Figure 10.	Soil temperature: Season 1, aspen (A), depths 1 (O1 horizon) and 2 (O22/A horizon).	60
Figure 11.	Soil temperature: Season 1, birch (B), depths 1 (O1 horizon) and 2 (O22/A horizon).	60
Figure 12.	Soil temperature: Season 2, aspen (A), depths 1 (O1 horizon) and 2 (O22/A horizon).	61
Figure 13.	Soil temperature: Season 2, birch (B), depths 1 (O1 horizon) and 2 (O22/A horizon).	61

Figures | Page

Figure 14. Soil temperature: Aspen, site-by-year. 68

Figure 15. Soil temperature: Birch, site-by-year. 68

Figure 16. Soil temperature: Aspen, site-between-year. 69

Figure 17. Soil temperature: Birch, site-between-year. 69

Figure 18. Soil moisture and rainfall: Season 1, aspen and birch. 71

Figure 19. Soil moisture and rainfall: Season 2, aspen and birch. 72

Figure 20. Soil moisture seasonal means. 74

Figure 21. Soil moisture: Birch soil anomaly, season one. 81

Figure 22. Field soil moisture content of aspen and birch soil layers. 87

Figure 23. Soil moisture and rainfall: Season 1, Birch Control and Birch Fertilized sites. 88

Figure 24. Soil moisture and rainfall: Season 2, Aspen Control and Fertilized sites. 89

Figure 25. Soil moisture and rainfall: Season 2, Birch Control and Brich Fertilized sites. 90

Figure 26. Soil bulk density seasonal means: (A). $\overline{X}$ all depths by year, (B). $\overline{X}$ by-year, depth 2 (C). $\overline{X}$ by-year depth 1. 93

Figure 27. Soil bulk density means by site: Birch Control and Birch Fertilized, depth 1. 95

Figure		Page
Figure 28.	Soil bulk density means by site: Birch Control and Birch Fertilized, depth 2.	96
Figure 29.	Season 1 soil bulk density means by vegetation type and soil depth.	97
Figure 30.	Season 2 soil bulk density means by vegetation type and soil depth.	98
Figure 31.	Fungal biomass: Season 1; by vegetation type, by depth.	106
Figure 32.	Fungal biomass: Season 2; by vegetation type, by depth.	107
Figure 33.	Fungal biomass (Aspen Control): Season 1; by plot, by depth.	108
Figure 34.	Fungal biomass (Birch Control): Season 1; by plot, by depth.	109
Figure 35.	Fungal biomass (Aspen Control): Season 2; by plot, by depth.	110
Figure 36.	Fungal biomass (Apsen Fertilized): Season 2; by plot, by depth.	111
Figure 37.	Fungal biomass (Birch Control): Season 2; by plot, by depth.	112
Figure 38.	Fungal biomass (Aspen): Fertilization effects.	113
Figure 39.	Fungal biomass (Birch): Fertilization effects.	114
Figure 40.	Fungal biomass (Birch): Within-plot variability.	115

Figure		Page
Figure 41.	Fungal biomass and soil temperature: Aspen and birch, year 1, depth 1.	119
Figure 42.	Fungal biomass and soil temperature: Aspen and birch, year 1, depth 2.	120
Figure 43.	Fungal biomass and soil temperature: Aspen and birch, year 2, depth 1.	121
Figure 44.	Fungal biomass and soil temperature: Aspen and birch, year 2, depth 2.	122
Figure 45.	Fungal biomass and soil moisture: By year.	130
Figure 46.	Aspen Control fungal biomass and soil moisture: By year.	131
Figure 47.	Birch Control fungal biomass and soil moisture: By year.	132
Figure 48.	Aspen Fertilized fungal biomass and soil moisture: By year.	133
Figure 49.	Birch Fertilized fungal biomass and soil moisture: By year.	134
Figure 50.	Fungal biomass and soil bulk density: By season.	137
Figure 51.	Aspen Control fungal biomass and soil bulk density: By season.	138
Figure 52.	Birch Control fungal biomass and soil bulk density: By season.	139
Figure 53.	Aspen Fertilized fungal biomass and soil bulk density: By season.	140

Figure		Page
Figure 54.	Birch Fertilized fungal biomass and soil bulk density: By season.	141
Figure 55.	Relationship of fungal biomass, soil moisture %, soil bulk density and soil moisture classes: Site Birch Control, season 1.	142
Figure 56.	Fungal biomass/soil moisture: Level II "Profile" samples; by site, by date.	143
Figure 57.	Fungal biomass/bulk density: Profile sample (Aspen Control), season 1.	146
Figure 58.	Fungal biomass/bulk density: Profile sample (Aspen Fertilized), season 1.	146
Figure 59.	Fungal biomass/bulk density: Profile sample (Birch Fertilized), season 1.	147
Figure 60.	Fungal biomass/bulk density: Profile sample (Aspen Control), season 1.	147
Figure 61.	Fungal biomass/bulk density: Profile sample (Birch Fertilized), season 2.	148
Figure 62.	Fungal biomass/bulk density: Profile sample (Birch Control), season 2.	149
Figure 63.	Fungal biomass/bulk density: Profile sample (season 2).	150
Figure 64.	Fungal biomass/bulk density: Profile sample, all sites, day 315.	151
Figure 65.	Fungal biomass/bulk density: Profile sample, all sites, day 225.	152

Figure		Page
Figure 66.	Relationship of fungal biomass, soil moisture and temperature: Site Aspen Control, season 1.	153
Figure 67.	Relationship of fungal biomass, soil moisture and temperature: Site Aspen Fertilized, season 1.	154
Figure 68.	Relationship of fungal biomass, soil moisture and temperature: Site Birch Control, season 1.	155
Figure 69.	Relationship of fungal biomass, soil moisture and temperature: Site Birch Fertilized, season 1.	156
Figure 70.	Relationship of fungal biomass, soil moisture and temperature: Site Aspen Control, season 2.	157
Figure 71.	Relationship of fungal biomass, soil moisture and temperature: Site Aspen Fertilized, season 2.	158
Figure 72.	Relationship of fungal biomass, soil moisture and temperature: Site Birch Control, season 2.	159
Figure 73.	Relationship of fungal biomass, soil moisture and temperature: Site Birch Fertilized, season 2.	160
Figure 74.	Relationship of fungal biomass, temperature, soil moisture and seasonality (adapted from Soderstrom, 1979a).	170
Figure 75.	Effect of vegetation type and fertilization on occurrence of basidiomycete hyphae.	202
Figure 76.	Interaction of soil fungal community, soil matrix, climatic input, vegetation and time.	208

LIST OF TABLES

Table		Page
1.	Study area: Selected ecosystem parameters.	26
2.	Study area rainfall.	28
3.	Field season sample dates.	32
4.	Sample N: Each level of field experiment.	33
5.	Summary: Field and laboratory experiment design.	42
6.	Soil temperature ANOVA: Main effects.	62
7.	By sample date temperature ANOVA: Season 1.	64
8.	By Sample data temperature ANOVA: Season 2.	65
9.	Soil moisture and soil bulk density ANOVA: By season.	77
10.	Soil moisture ANOVA by depth: Duncan's Multiple Range Test.	79
11.	Soil moisture ANOVA by season, by site: Duncan's Multiple Range Test.	80
12.	Soil moisture ANOVA (Season 1) by site, by depth: Duncan's Multiple Range Test.	83
13.	Soil moisture ANOVA (Season 2) by site, by depth: Duncan's Multiple Range Test.	85
14.	Soil bulk density ANOVA: Duncan's Multiple Range Test.	99
15.	Fungal biomass, soil moisture and bulk density means.	123

Table		Page
16.	Regression: Season 1, biotic, climatic and soils data.	125
17.	Regression: Season 2, biotic, climatic and soils data.	127
18.	Regression: Bulk density and soil moisture by sample date.	136
19.	Correlation coefficients: Season 1, moisture percent by sample date.	162
20.	Correlation coefficients: Season 2, moisture percent by sample date.	163
21.	Fungal biomass ANOVA: Combined seasons.	173
22.	Fungal biomass ANOVA: By sample season.	174
23.	Fungal biomass ANOVA: By season, by sample date.	176
24.	Fungal biomass means (ANOVA) by year, date, depth and site.	177
25.	Fungal biomass: Duncan's Multiple Range Test; Combined depths, by site, by year and combined years.	181
26.	Fungal biomass means: Duncan's Multiple Range Test; By site, depth and year.	182
27.	Summary of aspen and birch biotic and abiotic variables in relation to organic matter decomposition.	186
28.	Means for respiration nutrient data from aspen and birch vegetation.	187

Table		Page
29.	Selected aspen and birch soil chemical and biotic data.	188
30.	Site chemical and stemflow data.	189

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INTRODUCTION

The study of interactions of the fungal community and the environment at the ecosystem level is a relatively new addition to classical, taxonomy oriented mycology. For forest soil systems this is due, in part, to the difficulty of *in situ* quantitative assessment of the responses of the microscopic community to variations in physical, chemical and biotic factors. This difficulty is compounded by the fact that any study conducted over time is subject to successional or other response oriented changes; i.e., microarthropod grazing, litterfall, stemflow, etc., which may alter the structure of the population under study. However, current direction in both basic and applied soil microbiology and higher plant ecology require that such studies be undertaken.

In defining structure and function in forest ecosystems in regard to nutrient cycling, productivity and revegetation, it is necessary to determine rates of decomposition, mineralization and nutrient cycling through the decomposer segment of the ecosystem. Basic to these investigations are: (1) the quantification of biomass of the fungal decomposer community; (2) changes in biomass over time and (3) the effect of changes in site quality (natural or induced) on biomass of fungi. This research addresses these three points.

In interior Alaska these areas of research are of particular interest at this time, due to the need for data pertinent to establishment of sound forest management programs prior to further large-scale commercial utilization of timber reserves (Zasada et al., 1977). Of the

interior's 22.4 million acres of commercial lands, quaking aspen (Populus tremuloides Michx.) and paper birch (Betula papyrifera Marsh) are the predominant vegetation on 7.5 million acres (2.4 million acres and 5.1 million acres, respectively) of land categorized as commercial forest land (Hutchinson, 1967). Zasada et al. (1977) state that these high latitude forests are capable of producing fiber and solid wood products on a commercial scale and that little adaptation would be necessary to implement intensive, large scale forest management, including thinning and fertilization, should harvesting for industrial raw materials (pulp, chipboard, paper) increase. They note that research is needed to assess the impact on long-term productivity of these intensive management programs.

The most detailed studies of long-term effects of management of interior taiga vegetation are those of Van Cleve (1971, 1972, 1973, 1974); Van Cleve and Zasada, (1976); Coyne and Van Cleve, (1977); Van Cleve and Moore, (1978) and Van Cleve and Oliver (1982)). This study was carried out in conjunction with long-term fertilization studies by Van Cleve on upland aspen and birch vegetation.

CENTRAL HYPOTHESIS, COROLLARIES AND OBJECTIVES

1. Central Hypothesis

Below ground, standing crop, fungal biomass in upland, permafrost-free interior Alaskan paper birch (Betula papyrifera) and quaking aspen (Populus tremuloides) forests exhibit within-season population changes which are accounted for by changes in microclimatic conditions, specifically soil temperature and soil moisture. Within the confines of dates comprising the field season for this study, soil moisture is thought to be the overriding causative factor for 'seasonal' fluctuations in fungal biomass.

It is to be expected that there are other mediating environmental factors which may influence (or determine) base line fungal biomass and the magnitude of seasonal changes. These factors are addressed by three corollary hypotheses:

2. Corollary 1

The magnitude of fungal biomass is affected by localized differences in soil bulk density, used here as a comparative index of organic matter (substrate) content.

3. Corollary 2

Fungal biomass dynamics which are dependent, in part, upon substrate availability and quality, differ between dominant

overstory vegetation types (aspen and birch) which have been shown to produce organic materials of different quality.

4. Corollary 3

A manipulation of within-site primary and secondary substrate quality by long-term (nine years) additions of N, P and K fertilizers may alter the magnitude of fungal biomass, in comparison with untreated sites, as well as altering fertilized site fungal species composition.

STUDY AREA

Vegetation

The study site is located 40 kilometers NE of Fairbanks, Alaska at 64°52' N latitude and 146°58' W longitude, at an elevation of 198 meters on a 15° south facing slope (Figure 1). The experimental forest is composed of contiguous stands of even-aged, 60-year old birch (Betula papyrifera Marsh.)[a] and aspen (Populus tremuloides Michx.). The site is considered typical of the upland birch-aspen vegetation type which occupies a dominant position in boreal forest succession (Van Cleve and Sprague, 1971) and which accounts for approximately 79% of the 3.9 million hectares of commercially available hardwood forests and 43% of the 9.1 million hectares of hardwood and softwood forests of the Alaskan boreal forest (Zasada et al., 1977).

Van Cleve and Viereck (1981) have described a seven stage successional sequence for this type of mesic, upland south facing slope:

Successional Stage	Time Span	Vegetation
I	0-1 years	Newly burned
II	2-5	Herb-tree seedlings
III	6-25	Shrub-tree saplings
IV	26-50	Dense hardwoods (aspen and birch)
V	51-100	Mature hardwoods
VI	100-200	Mixed hardwood - white spruce
VII	200-250+	Mature white spruce - moss

[a]Vascular flora nomenclature follows Hultén (1968).

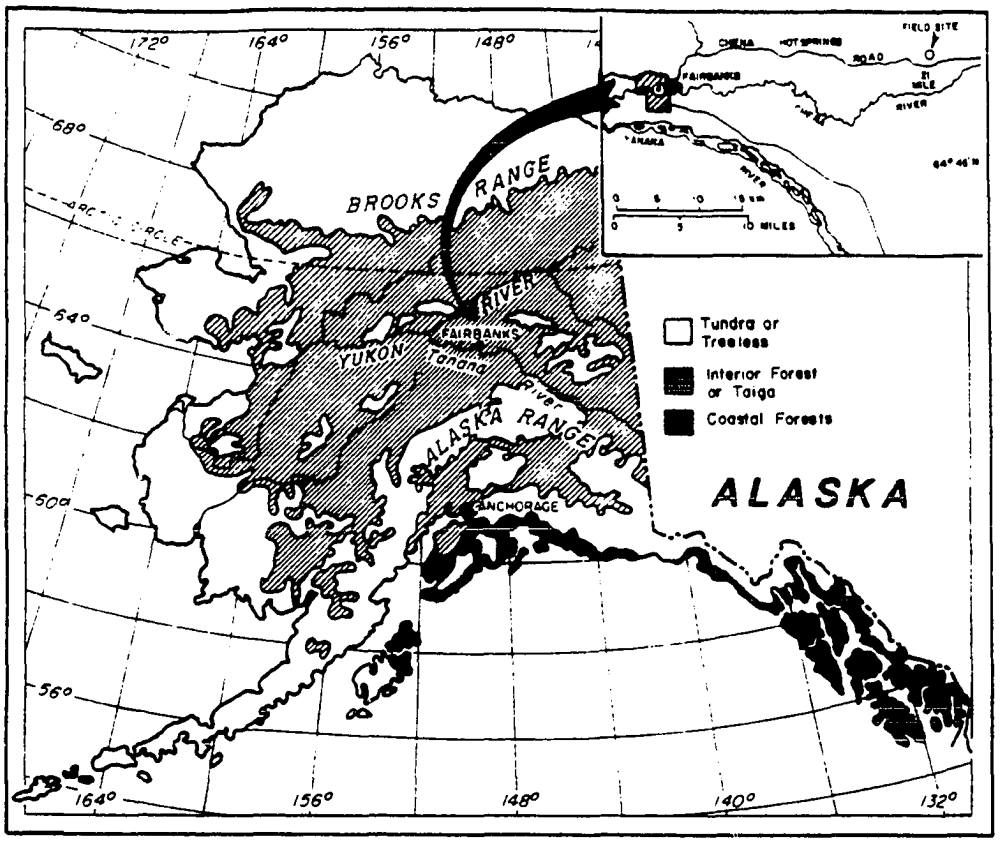


Figure 1. Study site location (adapted from Viereck et al., 1983).

The research site for this study is best described as an intermediate of successional stages IV and V. The dense hardwood canopy, low herbaceous ground cover, lack of a continuous forest floor moss cover and an increase in density of evergreen seedlings are characteristic of late stage IV and early stage V successional stages.

The vegetation of the aspen site is characterized as a Populus tremuloides/Viburnum edule/Linnae borealis complex. In addition to Viburnum edule, shrubs in the stand are Alnus crispa (Ait.) Pursh and Rosa acicularis with a total ground cover of 10%. Linnae borealis L. occurs with a 5% cover. Mosses and lichens are scattered (Viereck et al., 1983).

The birch site is characterized as a Betula papyrifera/Alnus crispa/Calamagrostis complex. Tall shrubs include Alnus crispa (4% cover), and Rosa acicularis (1% cover). Low shrubs and herbs include Vaccinium vitis-idaea, Linnae borealis, Calamagrostis canadensis and scattered Lycopodium annotium L. (Viereck et al., 1983).

Soils

Soil for the aspen site is a moderately shallow phase of the Steese silt loam series (Alphic Cryochrept) with a slightly deeper organic layer than the birch site. Depth to bedrock (Birch Creek Schist, a Precambrian formation of quartz-mica and quartzite schist) is approximately one meter.

Soil for the birch site is a moderately deep phase of the Fairbanks silt loam series (Alphic Cryochrept). Depth to bedrock

is assumed to be considerably greater than 1 meter.

Table 1 is a summary of vegetation and soil ecosystem parameters for both study sites.

Climate

The generalized climate for interior Alaska may be characterized as dry and cold (Continental). Annual precipitation for Fairbanks averages 287 mm, of which approximately 62% falls during May-September as rain. The remainder, falling as snow during winter months, covers the ground from mid-October until mid to late April with maximum accumulations of 75 to 100 cm. The mean average temperature is -3.4°C. Yearly temperature extremes range from a high of 33.9°C to a record low of -51°C. July, the warmest month, averages 15°C. January, the coldest month, averages -24°C (U.S. Dept. Commer., 1970). The average last day of freezing temperature is May 21 and the average first occurrence of freezing temperatures is August 30, resulting in an average growing season of 100 frost free days (U.S. Dept. Commer., 1977).

Figure 2 shows rainfall during both field seasons for this study. Accumulations were 12.93 cm for 1974 (May to October) and 15.53 cm for 1975 (May to October). Table 2 presents a month by month comparison of rainfall accumulation for the sample periods.

TABLE 1. Selected ecosystem parameters of the study area

Ecosystem Parameter [1]	Aspen [2]	Birch [3]
Age (yrs)	60	60
Slope (%) and aspect	15-S	15-SSE
Depth to permafrost	None	None
Maximum rooting depth (cm) measured from organic-mineral soil interface	90	>100
Generalized soil profile description:		
01 horizon - recently deposited litter	7-4 cm	7-4 cm
021 horizon - partially decomposed leaf material	4-0 cm	4-0 cm
A horizon - silt loam	0-3 cm	0-3 cm
Total tree density (NO. $\cdot ha^{-1}$)	3981	2101
Aspen (NO. $\cdot ha^{-1}$)	1891	683
Birch (NO. $\cdot ha^{-1}$)	1841	1050
Spruce (NO. $\cdot ha^{-1}$)	249	368
Sapling density (NO. $\cdot ha^{-1}$)		
Aspen (NO. $\cdot ha^{-1}$)	0	13
Birch (NO. $\cdot ha^{-1}$)	102	0
Spruce (NO. $\cdot ha^{-1}$)	70	102
Tree basal area ($m^2 \cdot ha^{-1}$): Total each site	30.1	33.5
basal area ($m^2 \cdot ha^{-1}$) of dominant tree species	21.0	24.2
Tree height (m)	20	16
Tree diameter (dbh $\cdot cm^{-1}$)	11.9	17.1
Annual productivity ($g \cdot m^{-2} yr^{-1}$)	760	343
Aboveground tree biomass ($g \cdot m^{-2}$)	17,490	9,121
Annual litterfall ($g \cdot m^{-2} yr^{-1}$)	222	233
Average leaf area ($m^2 \cdot tree^{-1}$)	10.3	8.2

[1]Data from Viereck et al., (1983)
[2]Aspen site #15 (Viereck et al., 1983)
[3]Birch site #16 (Viereck et al., 1983)

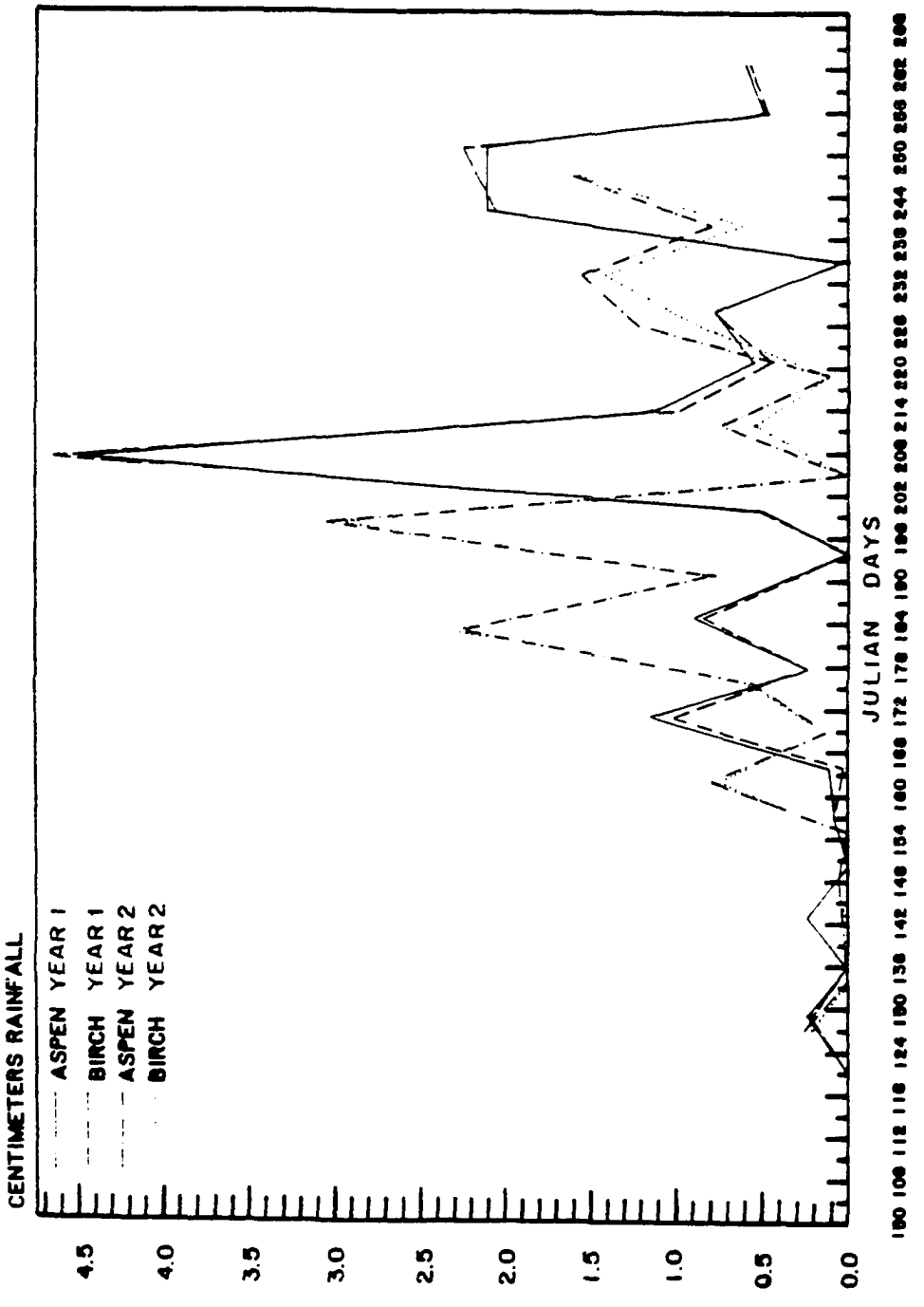


Figure 2. Study site rainfall.

TABLE 2. Study Area Rainfall.[1]

Month	1974	1975
May	0.26 cm	0.48 cm
June	3.76	2.18
July	4.26	6.15
August	4.65	3.17
September	0.00	3.55
Total Rainfall	12.93 cm	15.53 cm

The first occurrence of 0°C or greater in 1974 was recorded prior to Julian day 127 and for 1975 prior to day 129. The first day of temperature minima less than 0°C was day 235 for 1974 and day 258 in 1975.

Intensive Site Baseline Data

Both the aspen and birch study sites have received a number of years of study (Van Cleve and Sprague, 1971; Van Cleve, 1971, 1974; Van Cleve and Noonan, 1975; Viereck et al., 1983). As part of the intensive site study, one 1/10 acre (0.04 hectare) treatment plot was established within each vegetation type (aspen and birch) during the 1967 field season. Plots were selected for uniformity of site conditions including slope, aspect, vegetation age and soil type (Van Cleve and Noonan, 1971). The treatment plots received additions of nitrogen, phosphorus and potassium just after spring snow melt (mid-May) of each year from 1967 through 1975 at the rate of 111 $kg \cdot ha^{-1}$ nitrogen as NH_4NO_3, 55 $kg \cdot ha^{-1}$ phosphorus as treble super phosphate and 111 $kg \cdot ha^{-1}$ potassium as KCl.

[1]Data on file wth Forest Soils Laboratory

This manipulation of primary and secondary substrate quality is part of an intensive site study by Van Cleve, directed towards assessing rates of forest biomass accumulation and turnover and the effects on ecosystem properties of manipulation of organic matter quality by long-term fertilization (Van Cleve, 1971; 1972; 1973; Van Cleve and Noonan, 1971; Van Cleve and Sprague, 1971).

EXPERIMENTAL METHODS

Field Methods and Experimental Design

Climate

All temperature and rainfall data is taken from published and unpublished data routinely recorded by Forest Soils Laboratory personnel. Temperature, rainfall and snowfall were recorded from stations located in aspen control and birch control sites in the immediate study area. Air temperature was recorded every six days using U.S. Weather Bureau standard air temperature thermometers. Soil temperatures were measured with a tele-thermometer (Yellow Springs Instrument model 425C), with thermisters at the soil surface, at the organic soil mineral soil interface and at depths of 15 cm, 30 cm, and 60 cm below the soil surface. Rainfall was recorded directly from U.S. Forest Service standard specification rain gauges.

Field Experimental Design/Core Sampling

Within each of the four existing Chena Hot Springs Road Experimental Forest Vegetation/Treatment sites:

Site 1 Aspen Control

Site 2 Aspen Fertilized

Site 3 Birch Control

Site 4 Birch Fertilized

two 4 meter by 4 meter plots were established (Figure 3). These eight plots were selected for uniformity of site conditions, including understory vegetation, ground cover, apparent drainage patterns and tree density.

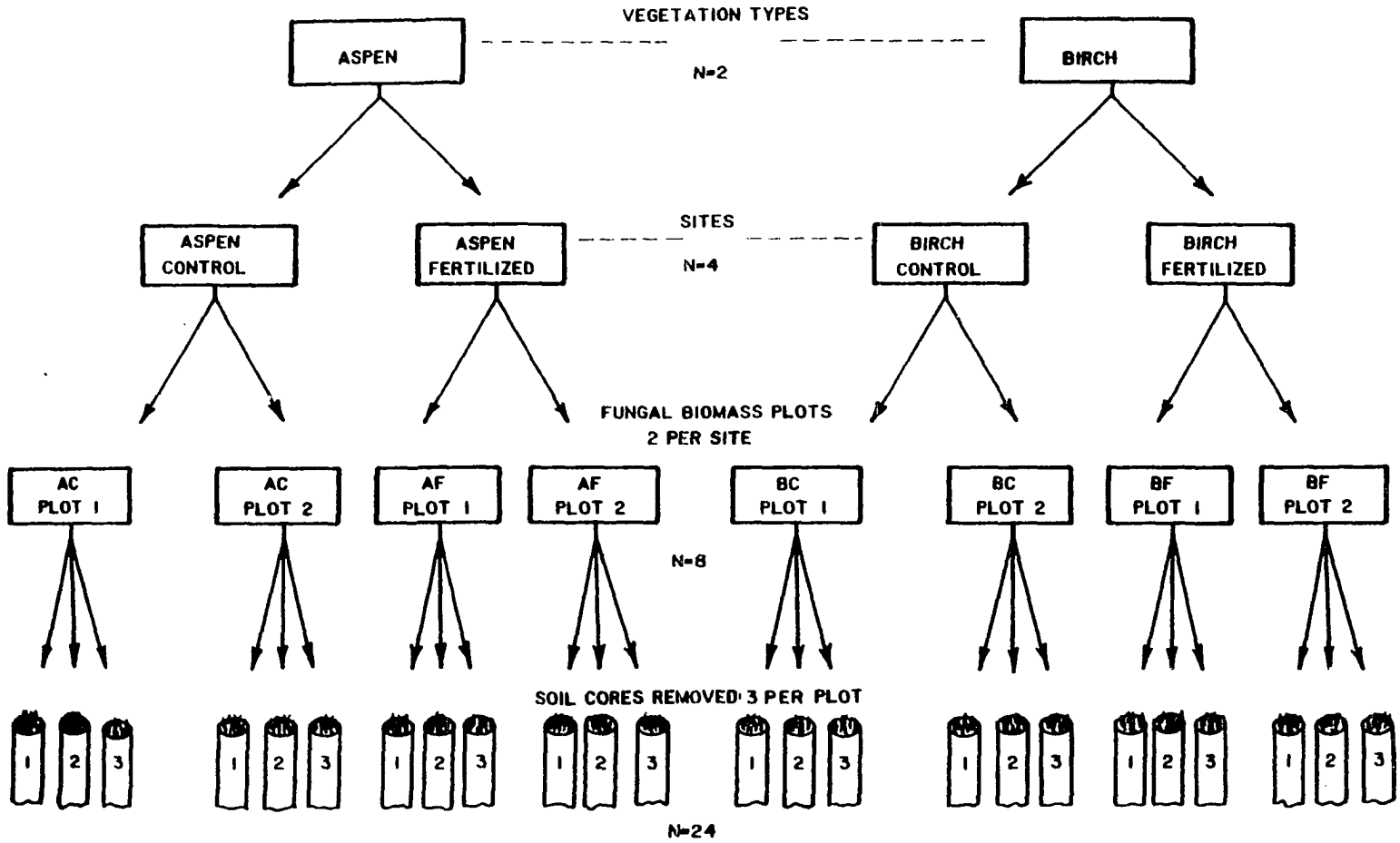


Figure 3. Field experiment design.

Within these eight plots, sampling for standing crop fungal biomass began after spring snow melt (early to mid-May) for each of the two field seasons. During each field season samples were collected as frequently as laboratory processing would allow. Ten samples were collected from May 12 through September 9 during the 1974 season and eight samples (May 13 through November 12) were collected in 1975 (Table 3).

TABLE 3. Two year field sample dates.

Field Season 1			Field Season 2		
Sample	Calendar Date	Julian Date	Sample	Calendar Date	Julian Date
1	5/12/74	132	1	5/13/75	133
2	5/24/74	144	2*	5/27/75	147
3*	6/ 5/74	156	3	6/12/75	163
4	6/20/74	171	4	6/26/75	177
5	7/ 2/74	183	5	7/22/75	203
6*	7/18/74	199	6*	8/13/75	225
7	8/ 1/74	213	7	8/26/75	237
8	8/14/74	226	8*	11/12/75	315
9*	8/30/74	242			
10	9/ 9/74	261			

*Level II sampling intensity (Figure 5)

On each sample date three contiguous cores, 5.08 cm in diameter and 10-12 cm in length, were removed from the vicinity of a randomly

selected point within each of the eight plots. Cores were placed directly into 18 oz Twirl-Pac polyethylene bags, 7.62 cm diameter, from a stainless steel tube type soil corer. The corer was designed to fit snugly into the Twirl Pacs so that the cores could be pushed into the bag without disturbing the structural integrity of the core. The bags were sealed and taped until rigid and placed in a Freeze Safe containing Blue Ice packets during transport to the laboratory. Table 4 shows the number of samples within each tier of the nested field design (Figure 3) and cummulative numbers of samples.

TABLE 4. Sample size for levels of field experimental design.

For each sample date:

1.	Number of vegetation types sampled	N = 2	
2.	Number of sites (1 control and 1 fertilized per vegetation type)	N = 4	
3.	Number of fungal biomass plots (2 per size)	N = 8	
4.	Number of cores removed per plot	N = 3	
5.	Number of cores per plot used for biomass determinations	N = 2	
6.	Number of cores per plot used for soils data measurements	N = 1	
		Biomass	Soils
7.	Total cores per date	N = 16	8
8.	Total cores per vegetation type	N = 8	4

Laboratory Methods and Experimental Design

The two levels of laboratory sampling intensity used during each of the two sample years are illustrated in Figures 4 and 5.

Level I Sampling Intensity: Figure 4

On each of the ten sample dates for year one and each of the eight sample dates for year two, three cores from each of the eight plots were sampled in 1 cm increments at 1-2 cm below the core surface and 6-7 cm below the core surface. A 5.08 cm x 1 cm wafer was removed at these two depths using a soil miter box (Laursen, 1976). Two cores were used to estimate fungal biomass and the third core was used for determination of dry weight moisture percent and bulk density. Level I sampling yielded 32 biomass samples per sample date.

Level II Sampling Intensity: Figure 5

The object of Level II sampling was to augment Level I sampling (sample depths 1-2 cm and 6-7 cm) with additional biomass data from the soil surface (O1 horizon) through mineral soil (A horizon). Three times during each sample season roughly corresponding to early, mid and late field season one of the two biomass cores from plots Aspen Control #1 (AC1), Aspen Fertilized #1 (AF1), Birch Control #1 (BC1) and Birch Fertilized #1 (BF1) was sampled from the core surface to a depth of 7 cm in 1 cm increments; that is, a 5.08 x 1 cm slice was removed from the core at depths of 0-1 cm, 1-2 cm, 2-3 cm, 3-4 cm, 4-5 cm, 5-6 cm, and 6-7 cm and processed for fungal biomass. These cores are referred to in this text as profile cores and the dates on which they were collected as profile dates. The second fungal biomass core from AC1, AF1, BC1, and

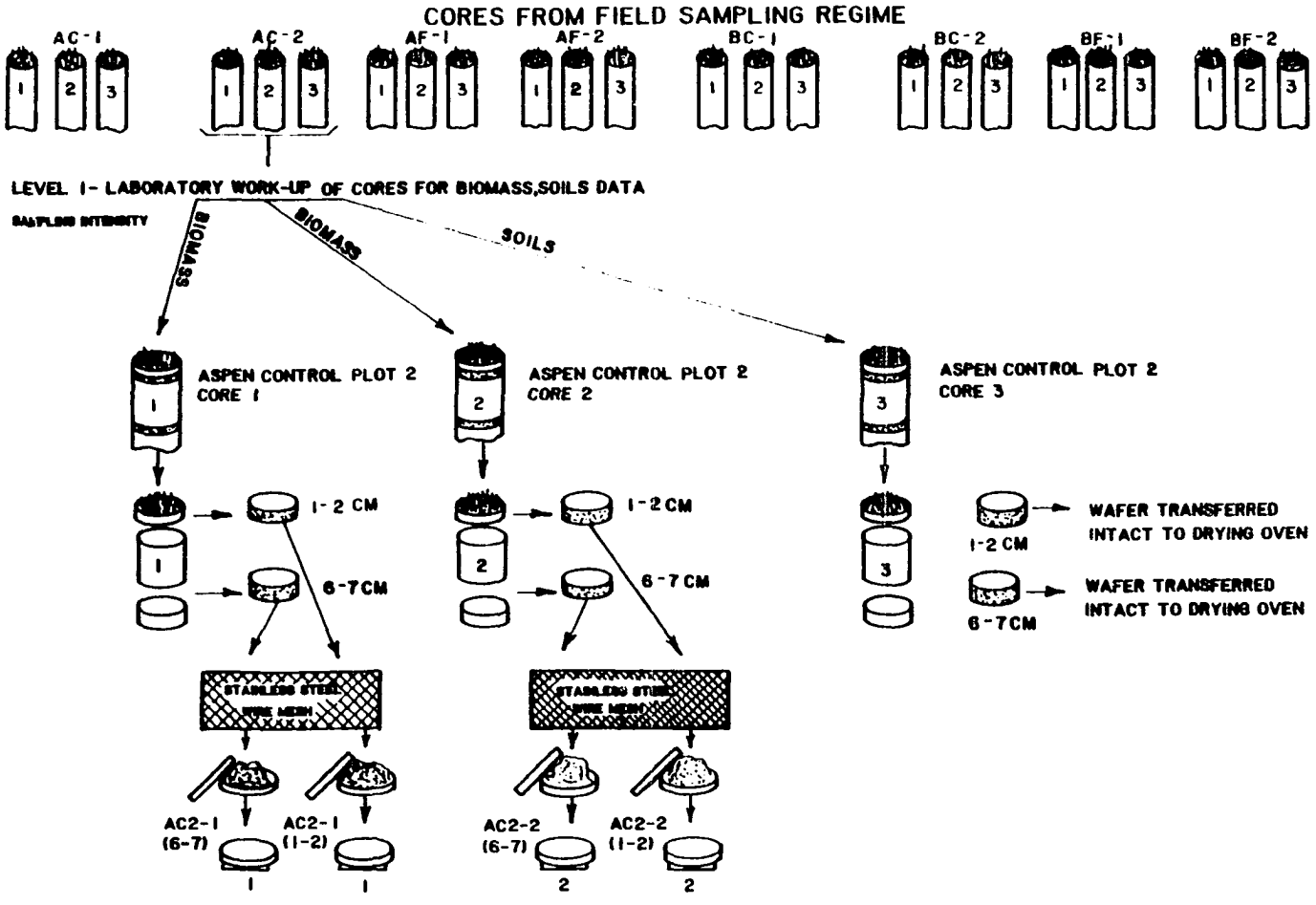


Figure 4. Laboratory sampling hiearchy: Preparation of cores for level I (1-2 cm and 6-7 cm below forest floor surface) fungal biomass sampling.

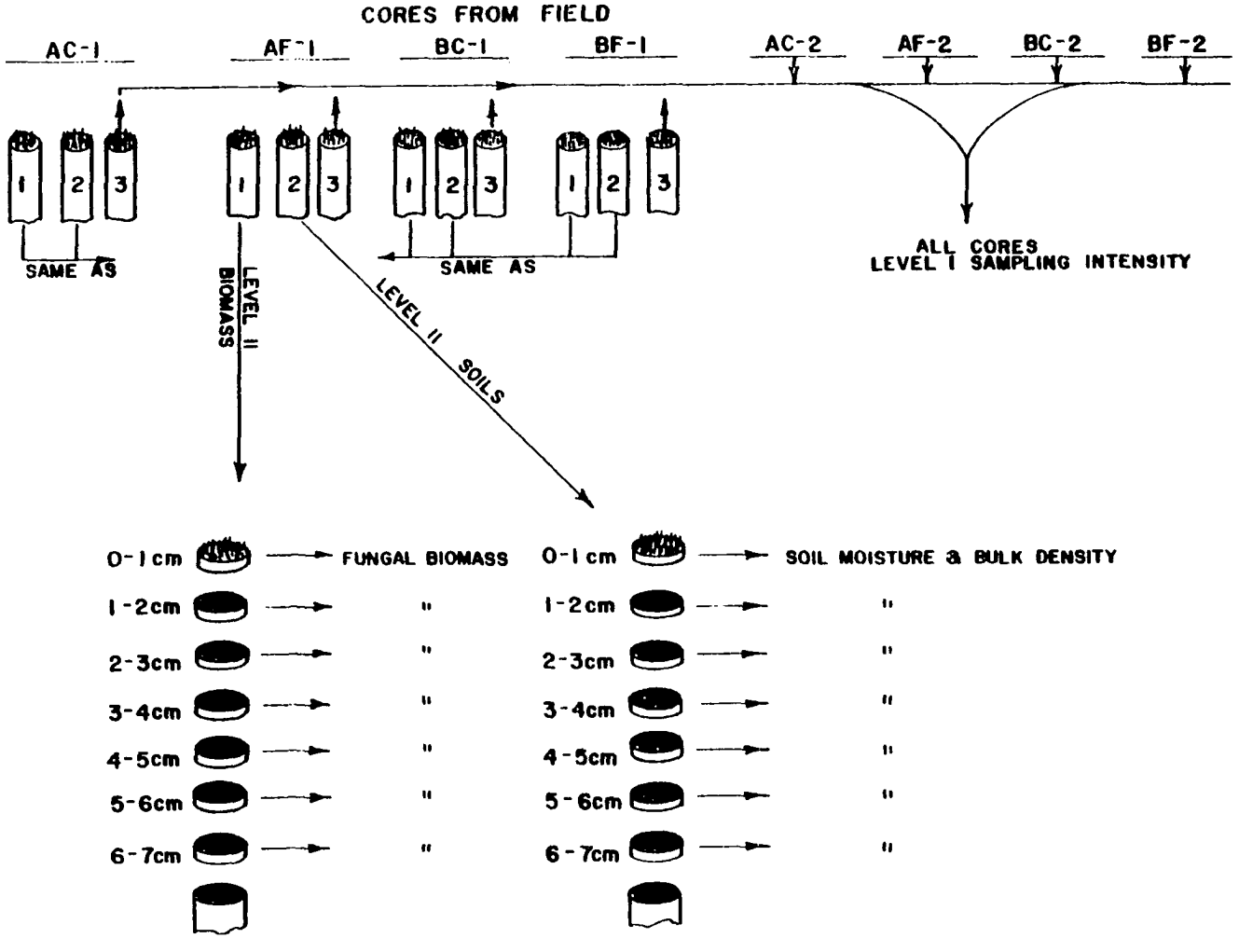


Figure 5. Laboratory sampling heiarchy. Preparation of soil cores for level II (forest floor surface through 7 cm below surface) fungal biomass sampling.

BF1 and replicate cores from AC2, AF2, BC2 and BF2 were sampled at Level 1 intensity. The third core collected from each plot on all dates was sectioned into 1 cm increments which corresponded to the biomass increments to be sampled, and used for soil dry weight moisture percent and bulk density determinations. Level II sampling yielded 12 cores sampled at Level I intensity and 4 cores sampled at Level II intensity for a total of 52 biomass samples per profile date.

In all cases soil dry weight moisture percent and soil bulk density were determined gravimetrically after drying the soil wafers at 105°C for 24 hours.

Fungal Biomass Methods

Total fungal mycelium (standing crop fungal biomass) was determined using the agar-film method of Jones and Mollison (1948). The agar-film technique has been favorably reviewed by a number of authors including: Thomas, et al., (1965), Nicholas and Parkinson (1967), Swift (1973), Frankland (1976), Frankland (1975), Frankland and Lindley (1978). Bååth and Söderström (1979), comment that incorporating modifications of Thomas et al., (1965) and Frankland (1974), the agar-film method is still among the most commonly used techniques for determination of total mycelium in soil. Ineson and Anderson (1982), in a comparison of direct measurement of soil fungal biomass (Jones and Mollison, 1948) and indirect biomass assay (soil respiration primed by an initial addition of glucose), found that from time zero through twenty days of direct and indirect biomass measurements there was a significant

(R=0.69, N=11) correlation between the two methods.

A shortcoming of the agar-film method, as used for this study is that no distinction between living and dead or quiescent tissue can be made. All references in this study to fungal biomass should be interpreted as standing crop biomass (living and dead, undecomposed tissue). Recent studies using the agar-film method of Jones and Mollison (1948), with modifications, include those of Martinez and Ramirez (1978), Berg and Söderström (1979), Bååth and Söderström (1979) Holm and Jenson (1980) Bååth (1980), Flanagan (1981), and Ineson and Anderson (1982).

A discussion of techniques used for quantitative soil mycology studies prior to the advent of the Jones and Mollison (1948) technique, which include; dilution plate methods, soil plating methods, slide immersion techniques and direct observation methods, may be found in Laursen, (1976). Brunburg (1980) reviews more recent quantitative methods including acridine orange staining, autoradiography, X-ray fluorescence spectrometry, ATP luciferase interaction and fluorescine diacetate staining. Sundman and Silvea (1978) and Flanagan (1981) review the membrane filter technique of Hansen et al., (1974) with suggestions for improving the method. Flanagan (1981, 1983) describes a method for vital staining of fungal hyphae using aceto-orecin stain.

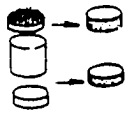
For this study, soil samples were forced through a 2 mm mesh stainless steel sieve and stored in sealed containers at 5°C until processed (Figure 4). Processing (cycling individual samples through the Jones and Mollison (1948) biomass procedure) from the time samples were sifted to the completion of measurements on the last sample took an average

of 10 to 12 days. Test samples were run prior to finalizing the experimental design. These estimates show no statistically significant differences (Alpha = .05) in biomass when conducted on the same sample after 15 days storage of seived material at 5°C.

Sieved samples (Figure 6) were placed in a 1.1% non-nutritive agar solution and agitated at 250 excursions per minute in a reciprocal shaking water bath kept at 55°C. Agar films were prepared from the homogenate by pipeting the suspension onto a hemacytometer with cover glass fixed in place. The suspension was not introduced at point A and B (Figure 6), as is normally the case, since early tests for this study indicated that introduction of a suspension of organic soils along this single edge led to a "straining" effect due to organic matter buildup. For this study the suspension was introduced at points C and D, the lateral overflow troughs, which led to an even dispersal of the suspension on the face of the counting chamber. Fungal hyphal lengths were directly measured, without transfer of the agar films from the hemacytometer, using transmitted light microscopy at a magnification of 625 X. Mycelial length measurements were made using an ocular micrometer and a calibrated measurement grid, similar to a whipple disc, superimposed upon the microscope visual field by a Leitz drawing tube. I believe that this method of measurement is more accurate than tracing hyphal lengths found within the visual field and later measuring the tracings with a map tracer.

Since no attempt was made to distinguish live from dead or metabolically active from inactive hyphae, fungal biomass figures given in

Figure 6. LABORATORY BIOMASS MEASUREMENT: OVERVIEW

(1)  A soil wafer 1 cm thick by 5.08 cm diameter is removed from the core.

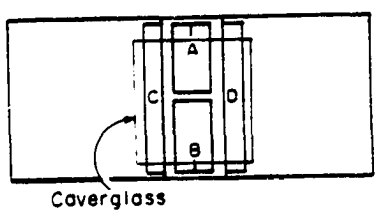
(2) Passed through stainless sieve (2 mm^2 mesh)

(3) 2.5 gm net weight of sample placed in 125 mm Erylenmeyer flask

(4) Using a 1.1% non-nutritive agar, the volume of the suspension is brought to 50 ml.

(5) Suspension agitated for 15 minutes at 50°C

(6) Suspension pipetted onto a hemacytometer (blood counting chamber) with a cell volume of 5.82 x 10^{-3} cc (each cell is: 8.75 mm long by 6.65 mm wide by 100 micrometers deep)



(7) The slide is placed on the microscope and using a drawing tube (system of prisms and mirrors) a calibrated grid of known size is superimposed on the field of vision of the microscope. At a magnification of 625X the lengths of hyphae falling within this visual field on the grid - are measured in micrometers. Fifty to twenty grids were counted per slide.

this study represent total standing crop fungal biomass at the time of sampling. A notation was made during the measurement of hyphae of the total length attributable to clamped hyphae. Those hyphal lengths shown to have clamp connections under microscopic examination can be noted as being of basidiomycete origin.

Following the method of Laursen (1976), 50 visual fields were measured for total hyphal length present from each core sample for 1974 data. Statistical analysis indicated that sampling intensity could be decreased from 50 fields to 20 fields without significantly affecting variability. Twenty visual fields were measured per core subsample in 1975. Approximately 21,000 microscope fields were measured in 1974 and 10,040 fields in 1975.

Table 5 is an abbreviated overview of the complete field and laboratory experimental design used in this study for each field season.

Although fungal biomass was calculated for all data as dry weight mass per dry weight soil and dry weight mass per unit area (Calculations: [5], [6] and [7]) in addition to calculations of lengths of hyphae per gram dry soil, all discussion, graphs and statistical treatments presented are confined to the expression of fungal biomass in unit lengths per dry weight of soil (Calculations: [1]). This figure is not a true biomass expression but actually an expression of relative fungal lengths or concentration of fungi in the soil. Historically the expression of fungal lengths per dry weight mass of soil has been referred to as 'biomass' (Parkinson, 1973; Bååth, 1980; Bååth

Table 5. Summary of Field and Laboratory Experimental Design.

(1) 1974 Field Season
- 10 sample dates
  - 4 sample sites (Aspen Cont., Aspen Fert., Birch Cont., Birch Fert.)
    - 8 sample plots (2 per sample site)
      - 2 cores per plot sampled for biological data and 1 core sampled for soils data
        - 2 depths per core sampled on all dates and full profile (7 depths) sampled from selected cores from each sample site on 3 dates for each field season
          - 50 visual fields per sample depth recorded to give average fungal biomass per slide

(2) 1975 Field Season
- 8 sample dates
  - 4 sites
    - 8 plots
      - 2 cores per plot
        - 2 depth samples on all dates
          - 7 depths sampled on profile dates
            - 20 visual fields per depth counted

and Söderström, 1980; Holm and Jensen, 1980; Frankland and Lindley, 1978; Söderström, 1979a; Söderström, 1979b; Laursen, 1976). Söderström (1979a) points out that though technically mycelial lengths (lengths · m^{-2}) is not a true biomass expression it is used synonymously. This convention is followed in this study:

1.) For ease of comparison with work being done, at the inception of this project, by Laursen and Miller (1977) in Alaskan tundra.

2.) Accuracy of fungal biomass figures expressed as grams dry weight fungal hyphae per mass soil or area soil can vary as much as 30% depending upon the method used for estimating fungal biovolume and dry weight mass of measured lengths of mycelium (Bååth and Söderström, 1979a).
In standard calculations, biovolume is calculated as average cross section (ACS) multiplied by the total length of hyphae measured. Usually, a random sample of hyphae are measured for diameter and the mean is calculated.

$$\frac{\Sigma\, di}{N} \qquad [1]$$

where di equals the diameter of the individual hyphal segment measured and N is the number of segments measured. From [1] the average cross section is calculated

$$ACS = \frac{\frac{\Sigma\, di}{N}}{2} \times \pi \qquad [2]$$

This method has traditionally yielded a wide variety of hyphal widths used for biomass calculations: 1.8 µm (Whitkamp, 1974), 2.66 µm to 3.01 µm (Visser and Parkinson, 1975), 2.746 µm (Laursen, 1977) and 4.0 µm (Holm and Jensen, 1980). This variation, unless all constants arrived at are supplied to the reader, makes comparisons between studies and habitats difficult. This method of calculation does not take into consideration the possibility of unequal distribution of thick and thin walled hyphae, nor does it address the possibility of differential fragmentation of thin and and thick walled hyphae during the preparation of soils for biomass estimations. In this study thick walled, clamped and darkly pigmented hyphae were consistently of larger diameter than thin walled hyaline hyphae. If thick walled hyphae do not fragment as readily as thin walled hyphae, biomass figures based on a random measurement of fragments would give an underestimate. Although a number of studies do make some distinction between hyphal diameters measured from mineral or organic soil (Bååth and Söderström, 1979a; Söderström, 1977) or between differing vegetation types (Laursen, 1976) most use an average figure for calculations. It is my observation that hyphal diameters not only differ in relationship to the soil horizon being sampled but there is the possibility of a 'time' effect normally not considered when using average figures. Although no statistical tests

have been applied to determine the significance of such factors as soil horizon, vegetation type and seasonality on hyphal width, it appears from measurements made over the summer field season for this study that successional patterns exist which involve fungi of sufficiently differing diameters to alter total biomass figures. In short, since there remains some doubt concerning the effect of vegetation type, treatment, soil horizon and time on average hyphal diameter, it appears that, considering the comparisons which must be made over a gradient of biotic and climatic variables, comparisons must be made which include as few of these variations as possible. From this argument it follows that the logical unit of comparison is length per gram dry soil.

CALCULATIONS

The data generated from the procedures includes:

A. Soil and Climatic data

Bulk Density = BD

BD = Grams dry soil $\cdot$ cm^{-3} = soil wafer dry weight in grams $\cdot$ r^{-2} $\cdot$ h^{-1} (1)

$r^2 = 6.45\ cm^2$

h = solid wafer depth increment = 1 cm

Dry weight moisture percent = % H_2O

$$\%\ H_2O = \frac{\text{Sample wet weight - sample dry weight}}{\text{sample dry weight}} \times 100 \quad (2)$$

$GDSM^2$ = Grams dry solid per meter square to a depth of 1 cm (3)

$GDSM^2$ = Sample bulk density $\cdot$ 1×10^4 cc $\cdot$ m^{-2}

B. Fungal Biomass Data

Meters of mycelium per gram dry soil = MMYCGM

MMYCGM = Meters mycelium measured per slide $\cdot$ ((A x B x C) $\cdot$ D) (4)

A = total number fields counted per slide

B = sample dry weight

C = measurement grid volume in cc

D = total sample solution volume in ml assuming 1 ml = 1 cc

Meters mycelium per meter square to a depth of 1 cm = $MMYCM^{-2}$

$$MMYC \cdot M^{-2} = MMYCGM \times A \times B \quad (5)$$

A = number of cc in one square meter to a depth of 1 cm

B = sample bulk density

Grams dry weight fungal mycelium per gram dry soil = GMYCGM

$$GMYCGM = MMYCGM \times A \times B \quad (6)$$

A = wet weight of 1 meter fungal hyphae (6.534×10^{-6}): from Laursen (1976)

B = % dry weight of hyphae (0.115) per 1 g · wet weight

Grams dry weight fungal mycelium per meter square to a depth of 1 cm = $CMYCM^2$

$$GMYCM^2 = MMYCGM \times A \times B \times C \times D \quad (7)$$

A = wet weight in grams of 1 meter fungal hyphae

B = % dry weight of hyphae

C = 1×10^4 cc · m^{-2}

D = BD of sample in g · cc^{-1}

C. A complete set of sample biomass calculations may be found in Appendix 1.

STATISTICAL METHODS

Statistical reduction and manipulation of data was, in varying stages, done at Virginia Polytechnic Institute and State University, The University of Alaska - Fairbanks, and the Institute of Statistics, Texas A & M University.

Modified Statistical Analysis Systems programs (S.A.S.) similar to those used for the reduction of raw data for this study can be found in Laursen (1976). Generation of line graphs and descriptive statistics for the seasonality section of this work was accomplished by use of a re-programmed versions of BMDØ1D and the Hewlett-Packard 125 systems.

Scatter graphs and contour plots were generated using re-programmed S.A.S. routines.

Statistical analysis of the data may be divided into three categories:

1. Analysis of variance (ANOVA)
   Analysis of variance (Duncan's Multiple Range Test)
2. Regression
3. Correlation

1. Analysis of Variance (ANOVA)

Figure 7 is a diagram of the nested field and laboratory experimental design. ANOVA was applied to each level and where applicable to pooled data.

For both years the sources of variability or classification variables are:

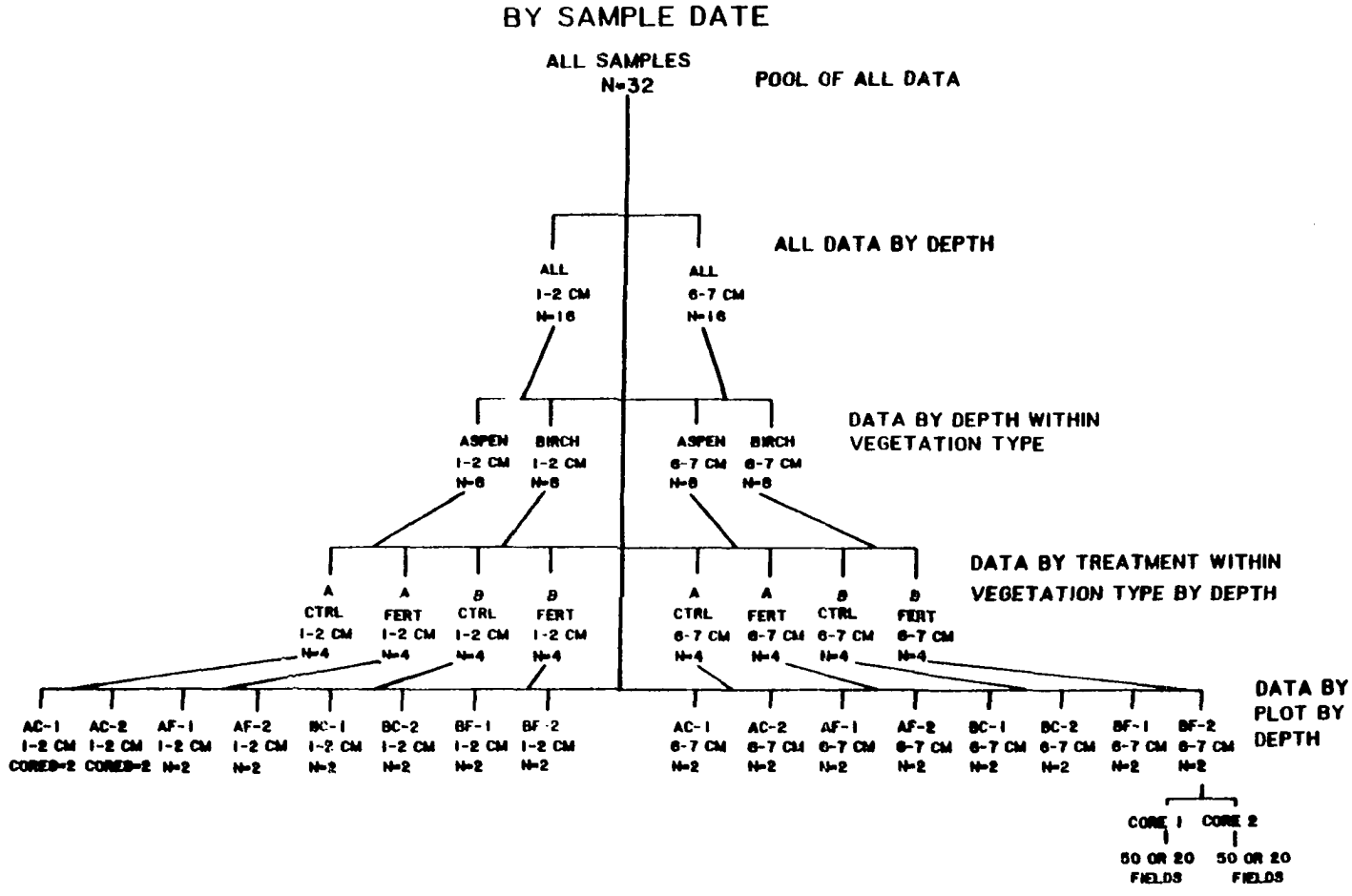


Figure 7. Data hiearchy: Levels of statistical treatment. A = Aspen, B = Birch, CTRL and C = control, FERT and F = fertilized, 1-2 and 6-7 = forest floor sample depths.

Sources

*Sites = 4 levels

Aspen treated
Aspen untreated
Birch treated
Birch untreated

*Plots = A class composed of 8 levels

AC1, AC2, AF1, AF2, BC1, BC2, BF1, BF2

Cores = Class composed of 2 levels per plot for a total of 16 levels
AC1 core 1, AC1 core 2, AC2 core 1, etc.

Depths = 2 depths per core for all sample periods, plus either 6 or 7 depths per core on specific dates

Day = Julian Day: 10 sample dates in 1974, 8 sample dates in 1975

The dependent variables for both years are:

1. bulk density in $g \cdot cc^{-1}$
2. soil moisture in dry wt. % water
3. soil temperature
4. meters of mycelium per gram dry soil
5. grams mycelium per gram dry soil
6. meters per meter squared to depth of 1 cm
7. grams per meter squared to depth of 1 cm
8. % clamped hyphae = percentage of total hyphae attributable to basidiomycetes

For the sake of accuracy and ease of comparison with existing literature only number 4 above, meters of mycelium per gram dry soil, is used hereafter as the descriptive term for the biotic variable - biomass. All graphs use this form of the biotic variable.

Notation for the statistical model for ANOVA (sources of variability and interaction terms) is as follows:

NOTATION:

Sites = S with variability given by $\emptyset s$

Plots within sites = P(S); $\emptyset p(s)$

Cores within plots within sites = C(PS); $\sigma^2_{C(PS)}$

Depth = D; $\emptyset d$

Sites by Depth = S*d; $\emptyset s*d$

Depth * Plots within sites = D*P(S); $\emptyset d*p(s)$

Depth * Cores = (PS) = D*C(PS); $\sigma^2_{d*c(ps)}$

Days = Day; $\emptyset day$

Sites * Days = S*Day; $\emptyset s*day$

Plots within Sites * Days = P(S)*Day; $\emptyset p(s)*Day$

C(PS) * Day; σ^2 c(ps)*day

Depths * Days = D*Day; $\emptyset d*day$

Sites * Depths * Days = S*D*Day; $\emptyset s*d*day$

P(S) * Depth * Day = P(S)*D*Day; $\emptyset p(s)*D*day$

C(PS) * Depth * Day = C(PS)*D*Day; $\sigma^2_{c(ps)*d*day}$

Random Error = Σ; σ^2

The main sources of variability are sites, plots, cores, depths and days. Plots are nested within sites and cores are nested within plots and sites. Depths, days and sites are all crossed with one another. The generalized model for this ANOVA is:

$$y_{ijklmn} = \mu + S_i + P_{j(i)} + C_{K(ij)} + D_\ell$$

$$+ (SD)_{i\ell} + P(D)_{j\ell(i)} + (CD)_{K\ell(ij)}$$

$$+ Day_m + (S\ Day)_{im} + (P\ Day)_{jm(i)}$$

$$+ (C\ Day)_{Km(ij)} + (D\ Day)_{\ell m}$$

$$+ (S\ D\ Day)_{i\ell m} + (C\ D\ Day)_{jkm(i)}$$

$$+ (C\ D\ Day)_{K\ell m(ij)} + \Sigma_N(ijklm)$$

where:

i = number of sites = 1, 2, 3, 4

j = number of plots per site = 1, 2

K = number of cores per lot = 1, 2

ℓ = number of depths samples per core = 1, 2

m = number of days (samples) per year:

= 1, 2, 3, 4, 5, 6, 7, 8, 9, 10 for 1974

= 1, 2, 3, 4, 5, 6, 7, 8 for 1975

Terms, other than the main effects and Σ, represent interactions of i, j, k, ℓ, m. For example, $(S\ Day)_{im}$ represents the possible interaction between site and days. If there is an interaction then the trends in the response, seen over sites, is <u>not</u> the same for all days.

The F-test is used for comparison of variances of two independent samples giving a test for equality of the two variances and estimates of the ratio of the two population variances. The generation of the F-test statistic, the P-value, gives the actual calculated α for that comparison (the probability of wrongly rejecting the null hypothesis).

Analysis of Variance (Duncan's Multiple Range Test)

Duncan's multiple range test developed by D. B. Duncan between 1951 and 1955 (Steel and Torrie, 1960; Sokal and Rohlf, 1969) is one of several multiple comparison tests for comparing each treatment mean with every other treatment mean using the range of treatment means as a test criterion. The standard error ($s_{\bar{x}}$) of each treatment mean is calculated along with a significant range (least significant range - LSR) for each entry. Individual means are compared in the order; largest minus smallest, largest minus second smallest, etc., with each difference declared significant if the value exceeds the calculated LSR. The single exception is that no difference between two means can be declared significant if both means are combined in a larger subset with a non-signficant range. The ordinary convention is to array the data from largest magnitude to least magnitude flanked by lines used to show non-significant groups as follows:

CODE		MEAN	GROUPING
Aspen Control	(AC)	1278	|
Birch Fertilized	(BF)	1147	|
Aspen Fertilized	(AF)	994	|
Birch Control	(BC)	946	|

From the example one may interpret that AC and BF are not significantly different from each other, but do differ from AF and BC. In simplest terms, the test may be looked upon as a test of homogeneity of sample means or those means that are most alike or most different.

2. Multiple Linear Regression Analysis

Data sets for each of the years were constructed by averaging over the core and plot values within sample periods. This averaging was done to see if the observations taken over the course of the field season were close enough together to exhibit autocorrelation, the basis for time series models. However, the data showed no significant autocorrelation, and standard regression models were fit. The regression equations are as follows:

The independent variables are soil temperature, bulk density, dry weight water content and the interaction term - bulk density * dry weight water content. The dependent variable is meters mycelium · gram dry soil^{-1}. The regression models were fit (i) to all of the data; (ii) to the data for each day; and (iii) to the data for each day-depth combination. The estimated equations are of the form

$$Y_j = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_y X_4$$

where

Y_j = meters·gram^{-1}

X_1 = bulk density

X_2 = dry weight %

X_3 = bulk density * dry weight %

X_4 = soil temperature

In a standard regression model, the usual assumptions are that the errors or residuals are independent with constant variance. In a few instances the biotic variables violated this constant variance assumption.

That is, the variability in the data increased as Y increased (the usual remedy is to transform the observations to equalize the variance). A log transformation was used, after which the variances were found to be substantially equalized.

3. Correlation

The primary purpose for applying linear correlation analysis to the data (from S.A.S. routines) is to measure the strength of relationships between the soils data (moisture %) and the biotic data (biomass). The analysis yields the coefficient of linear correlation (r) which reflects the consistency of the effect that a change in one variable has on another; for example, the effect of increased soil moisture percent on standing crop fungal biomass. The value for r is obtained from the formula:

$$r = \frac{\Sigma (X - \overline{X})(Y - \overline{Y})}{(N-1) S_x S_y}$$

where S and Y are the standard deviation of the X and Y variables and N = sample Number.

RESULTS AND DISCUSSION

Information necessary for the interpretation of the effects of dominant overstory vegetation, fertilization and time on the dependent variable fungal biomass includes:

A. Site temperatures: homogeneity and interactions of independent variables.

B. Site moisture regimes: homogeneity and interactions of independent variables.

C. Site bulk densities (as a gross indication of organic matter content): homogeneity and interactions of independent variables.

These factors are considered individually, prior to the discussion of the main effects of vegetation type, fertilization and time on fungal biomass patterns and biomass interactions with (A), (B) and (C) above.

Each section begins with a brief statement of main points drawn from this research, followed by specific observations and discussion.

A. Soil Temperature

Overview:

1. Temperature data is available for control sites only.
2. Field season one shows a significant vegetation effect for temperature (birch > aspen), field season two and combined seasons data does not.

3. The relationship of rise and fall in temperature magnitude, at both soil depths sampled, between aspen and birch control sites, is analogous for field season one and two.

Figures 8 and 9 show soil temperature cycles in the soil O1 layer (depth 1) and the interface of the O22/A soil layer (depth 2) for 1974 and 1975 respectively. For both years the birch control site at depth 1 (B1) shows temperatures generally higher than aspen soils at the same depth (A1). This trend, birch (depth 1) greater than aspen (depth 1), is consistent during 1974 except for a single point (Day 236) when birch and aspen were equal, and consistent during 1975 except for 3 measurements (Days 210, 237 and 285) when aspen temperatures were slightly greater than or equal to those of birch. For both field seasons differences between Depth 1 and Depth 2 temperatures for both vegetation types are greater in magnitude for the early field season (Day 132 through day 226 for the 1974 season and Day 132 through 202 for the 1975 season, Figures 10, 11, 12 and 13). Aspen depth 1 and aspen depth 2 are closer together in magnitude for both years than are birch temperatures for the two depths (Figures 8 and 9). This pattern gives a 'bracketing' effect for birch temperatures that is quite consistent for both years.

For 1974 the main effects soil temperature ANOVA (Table 6A) shows a significant difference (P valve = .0116) between sites (aspen > birch), this effect must be interpreted in light of the significant interaction

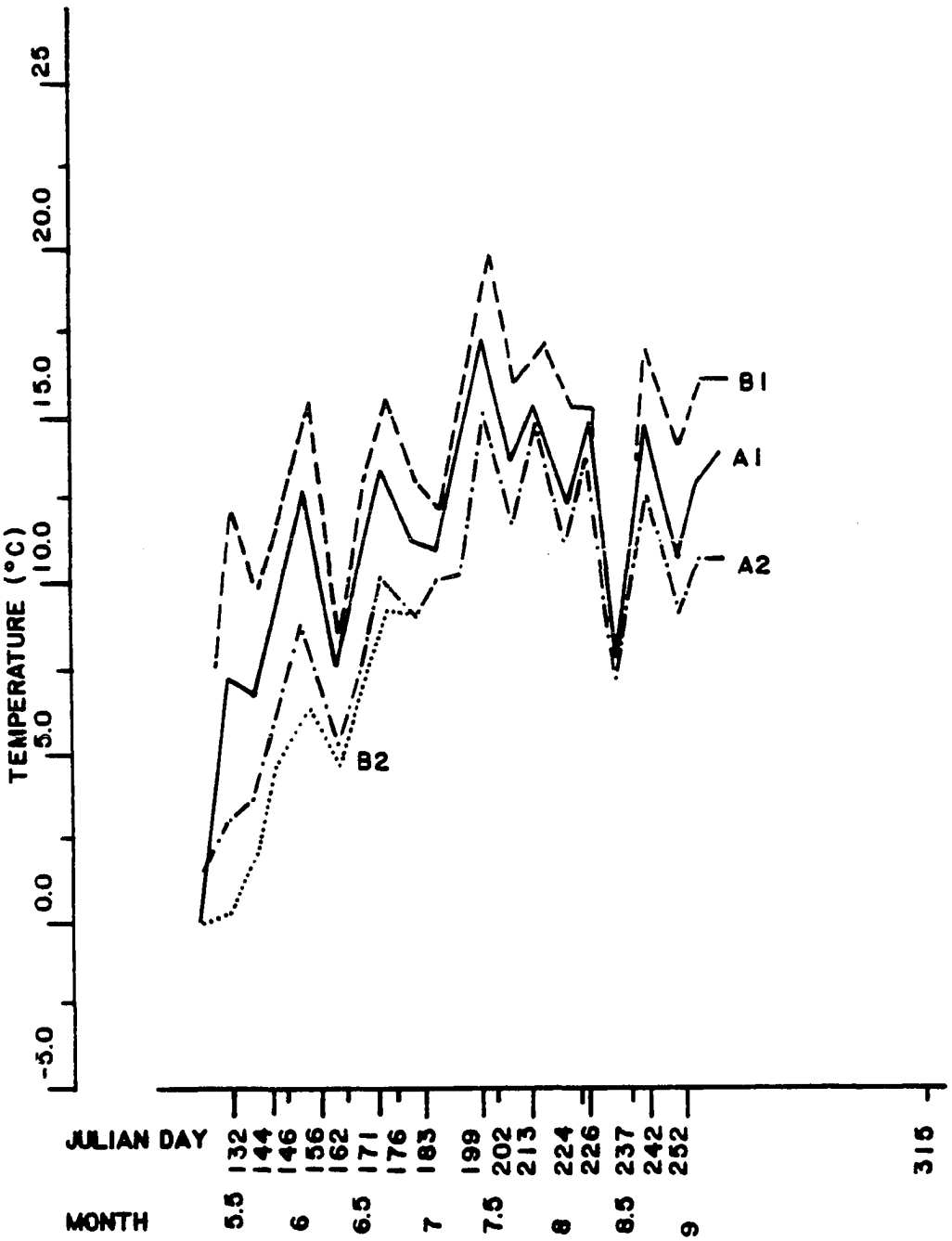


Figure 8. Soil temperature for field season 1: A = Aspen, B = Birch. Soil depths sampled: 1 (01 forest floor horizon) and 2 (022/A horizon).

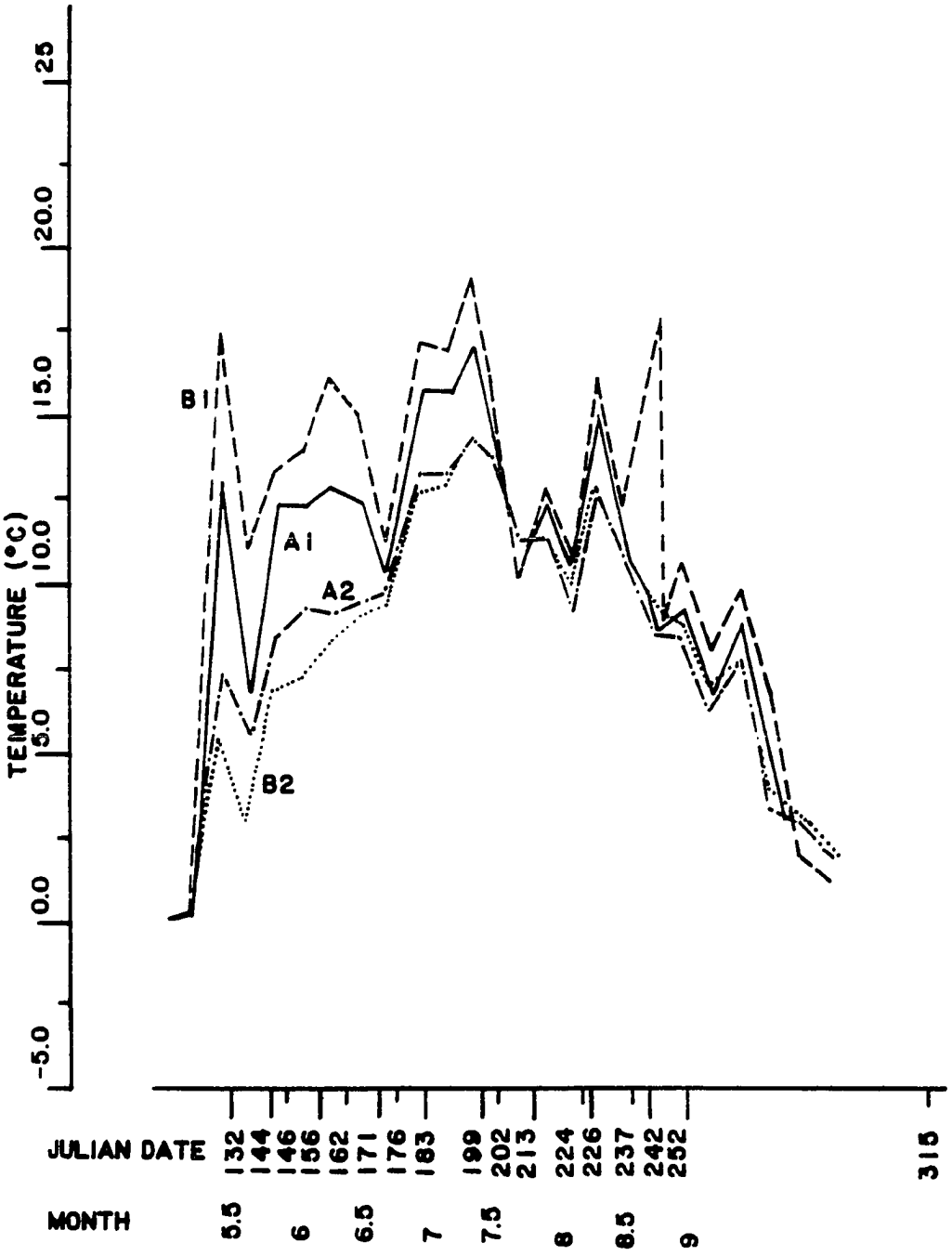


Figure 9. Soil temperature for field season 2: A = Aspen, B = Birch. Soil depths sampled: 1 (01 forest floor horizon) and 2 (022/A horizon).

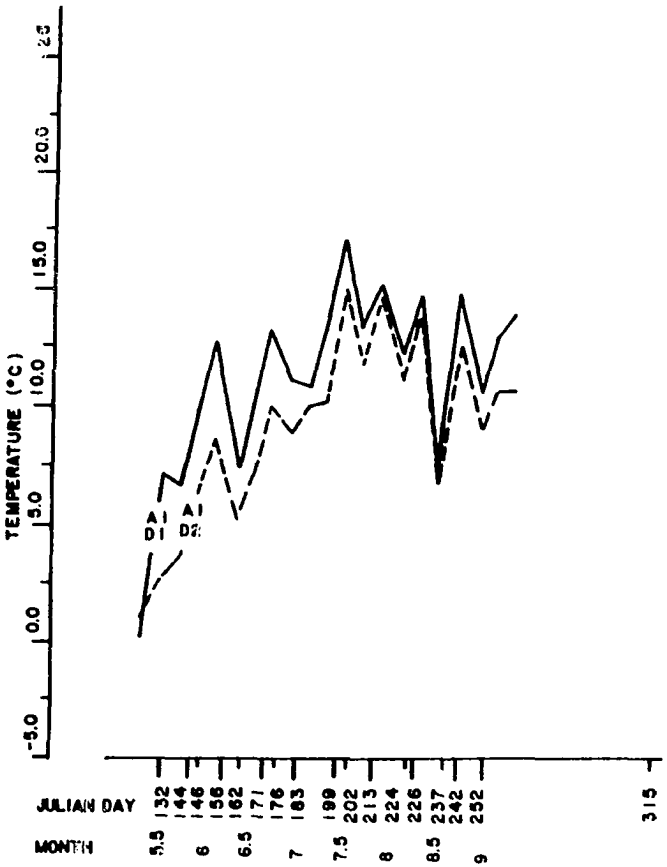


Figure 10. Soil temperature: Season 1, A = Aspen, D1 = Depth 1 (01 horizon), D2 = Depth 2 (022 - A horizon interface).

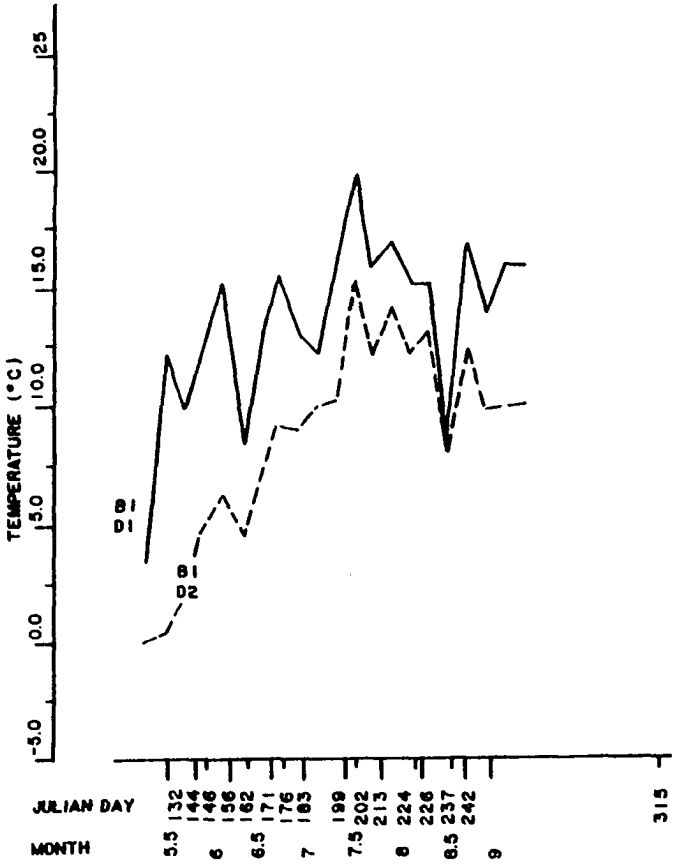


Figure 11. Soil temperature: Season 1, B = Birch, D1 = Depth 1 (01 horizon), D2 = Depth 2 (022 - A horizon interface).

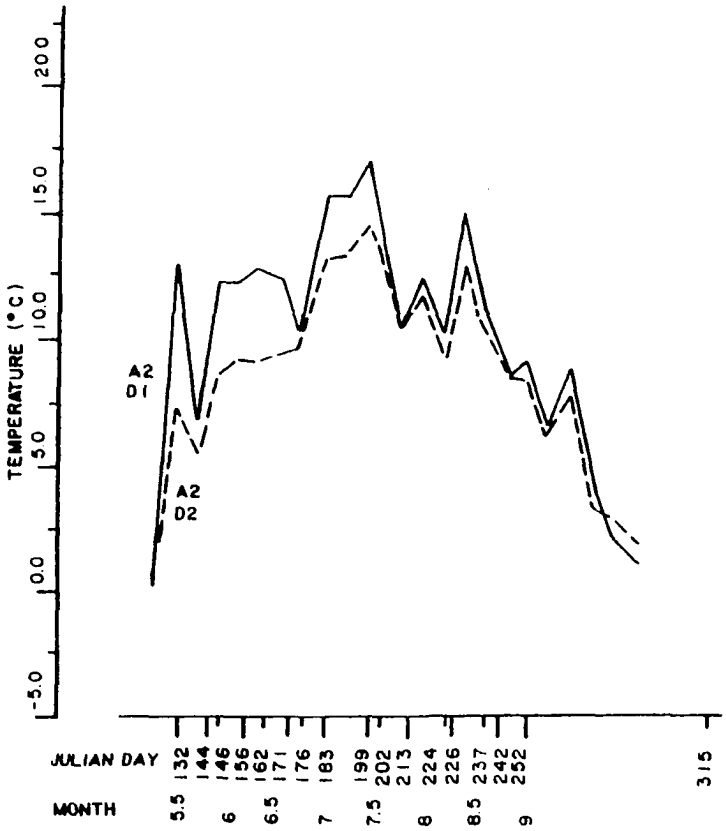


Figure 12. Soil temperature: Season 2, A = Aspen, D1 = Depth 1 (01 horizon) D2 = Depth 2 (022 - A horizon interface).

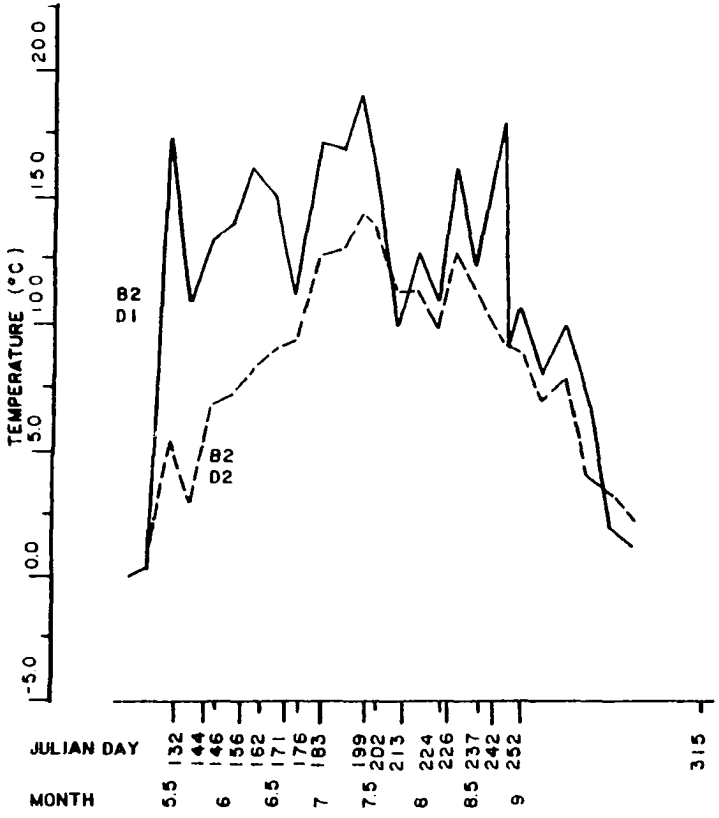


Figure 13. Soil temperature: Season 2, B = Birch, D1 = Depth 1 (O1 horizon), D2 = Depth 2 (O22 - A horizon interface).

Table 6. Soil temperature ANOVA.

A. Main effects and interactions

Error Term Source	Season 1 P-Value	Season 2 P-Value
Site	.0116	.5678
Depth	.0001	.0001
Day	.0001	.0001
Site * Depth	.0013	.0437
Site * Day	.8007	.0289
Depth * Day	.0341	.0303

B. Means Contributing to ANOVA

	Season 1		Season 2	
Site:	Aspen	9.86 °C	Aspen	10.41 °C
	Birch	10.73 °C	Birch	10.78 °C
Depth:	1 (01)	12.40 °C	1 (01)	11.94 °C
	2 (022/A)	8.54 °C	2 (022/A)	9.54 °C
Site * Depth				
	Aspen D1	10.90 °C	Aspen D1	11.31 °C
	Aspen D2	8.81 °C	Aspen D2	9.52 °C
	Birch D1	13.90 °C	Birch D1	12.56 °C
	Birch D2	8.26 °C	Birch D2	9.60 °C

of site with depth (P valve = 0.0013) and depth by day (P valve = 0.0341). Sites analyzed at each of the depth by day combinations show that aspen and birch temperature significantly differed (α = .05) for only two of the ten sample periods:

(i) Day 131, Depth 1 Birch > Aspen

(ii) Day 251, Depth 1 Birch > Aspen

Depths were analyzed at each of the site by day combinations. Temperatures at the two sample depths (D1 and D2) within each vegetation type for sample season one differed significantly (α = .05) as follows (Figure 10):

Vegetation	Sample No.	Day	Vegetation	Sample No.	Day
Aspen D1 > D2	3	155	Birch D1 > D2	1	131
Aspen D1 > D2	4	170	Birch D1 > D2	2	143
Aspen D1 > D2	5	182	Birch D1 > D2	3	155
Aspen D1 > D2	6	198	Birch D1 > D2	4	170
			Birch D1 > D2	5	182
			Birch D1 > D2	6	198
			Birch D1 > D2	7	212
			Birch D1 > D2	8	225
			Birch D1 > D2	10	251

Days were also analyzed at each vegetation type - by day combination. For aspen depth 1, samples number 1, 2 and 9 were significantly less (α = .05) than samples 3, 4, 5, 6, 7, 8 and 10 (Table 7).

For season two (Table 6, Table 8, Figure 11) there is no overall significant difference in temperature between aspen and birch control sites (P valve = .5678, Table 6) seasonal temperature means for aspen

Table 7. Temperature ANOVA: Season One, by sample number and day. Those days which have a common underscore do not differ significantly (α =.05).

Site = Aspen Depth = 1

Sample No.	6	8	7	3	10	5	4	9	2	1
Julian Day	198	225	212	155	251	182	170	241	143	131

Site = Aspen Depth = 2

8	7	10	6	5	3	4	9	2	1
225	212	251	198	182	155	170	241	143	131

Site = Birch Depth = 1

10	6	7	8	3	5	4	2	9	1
251	198	212	225	155	182	170	143	241	131

Site = Birch Depth = 2

8	7	10	6	5	9	4	3	2	1
225	212	251	198	182	241	170	155	143	131

Table 8. Temperature ANOVA: Season Two, by sample number and day. Those days which have a common underscore do not differ significantly (α =.05).

Site = Aspen Depth = 1

Sample No.	5	7	3	1	6	4	2
Julian Day	202	237	162	132	224	176	146

Site = Aspen Depth = 2

5	7	6	4	3	2	1
202	237	224	176	162	146	132

Site = Birch Depth = 1

5	3	6	4	2	7	1
202	162	237	176	146	224	132

Site = Birch Depth = 2

5	7	6	4	3	2	1
202	237	224	176	162	146	132

over all depths = 10.41°C and the corresponding birch temperature mean = 10.78°C, (Table 6-B). However, as with 1974 data, means calculated by depth show a seasonal elevation (not statistically significant) of birch D1 temperatures ($\overline{X}$ = 12.56°C) in comparison to aspen D1 temperatures ($\overline{X}$ = 11.31°C).

Additionally, there are fewer between depth differences within vegetation types for 1975 in comparson with 1974. Analysis done between depths within vegetation type shows that D1 significantly D2 as follows:

Vegetation	Sample No.	Day	Vegetation	Sample No.	Day
Aspen D1 > D2	1	132	Birch D1 > D2	1	132
Aspen D1 > D2	3	162	Birch D1 > D2	2	146
			Birch D1 > D2	3	162
			Birch D1 > D2	4	176

Significant differences between aspen and birch temperatures are confined to Sample 1, D1 birch > aspen and aspen D2 > birch D2. From Table 8 there are a few clearly defined significantly different temperature patterns over the course of the field season. Samples 5, 6, 3 and 7 predominate as season highs over vegetation types and depths. Sample 1 for birch D1 and D2 is significantly less than all other dates.

CONCLUSIONS/SUMMARY

1. In general, birch soil temperatures at the soil surface (O1 layer) are greater than aspen temperatures at the same depth

for both seasons, although differences are statistically significant in few cases. This trend is most noticable in early to mid season samples.

2. There is consistently less difference in temperature between depth 1 and depth 2 in aspen soils than in birch soils for both field seasons.
3. Comparison of temperature graphs by site between seasons (Figures 14, 15, 16 and 17) show a marked similarity of temperature patterns between years.

DISCUSSION

A possible explanation for the slightly elevated soil surface layer temperatures for birch in comparison to aspen can be found in Table 1: Selected ecosystem parameters. Average leaf area per tree is greater in aspen than in birch (10.2 $m^2 \cdot tree^{-1}$ vs 8.2 $m^2 \cdot tree^{-1}$), as is total tree density (aspen = 3981 trees $\cdot ha^{-1}$, birch 2101 trees $\cdot ha^{-1}$) which could result in greater solar intercept by the aspen canopy than the birch canopy. This greater shading effect in aspen sites would be expected to result in decreased soil surface temperatures.

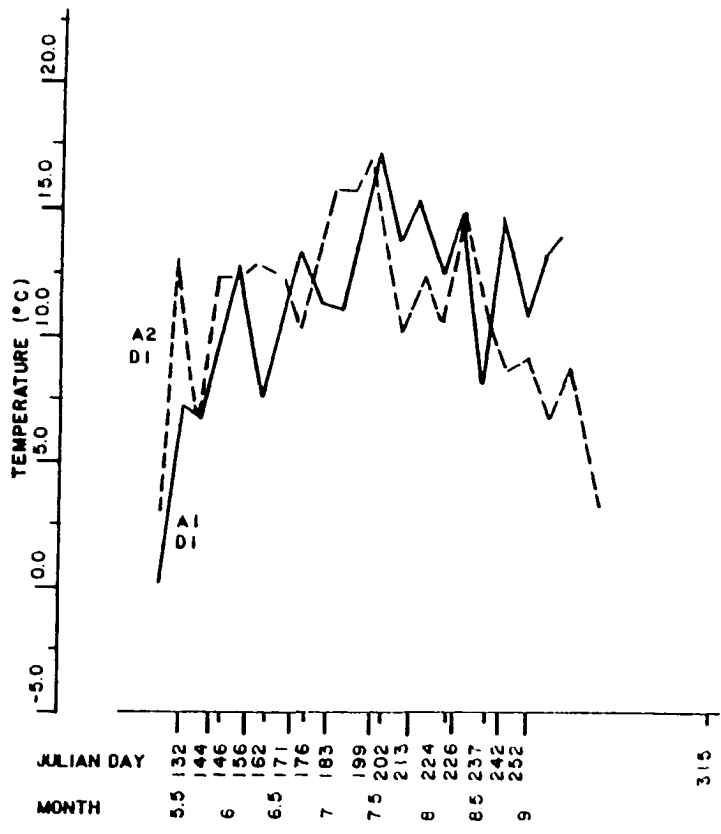


Figure 14. Soil temperature comparisons by site and year: A1 = Aspen, season 1; A2 = Aspen, season 2; D1 = Depth 1 (O1 horizon).

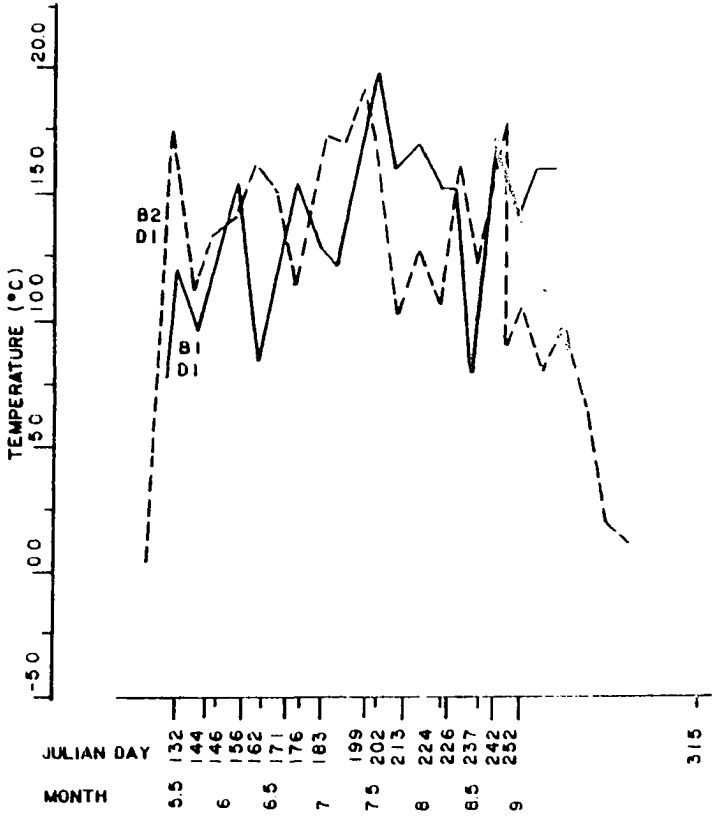


Figure 15. Soil temperature comparisons by site and year: B1 = Birch, year 1; B2 = Birch, year 2; D1 = Depth 1 (O1 horizon).

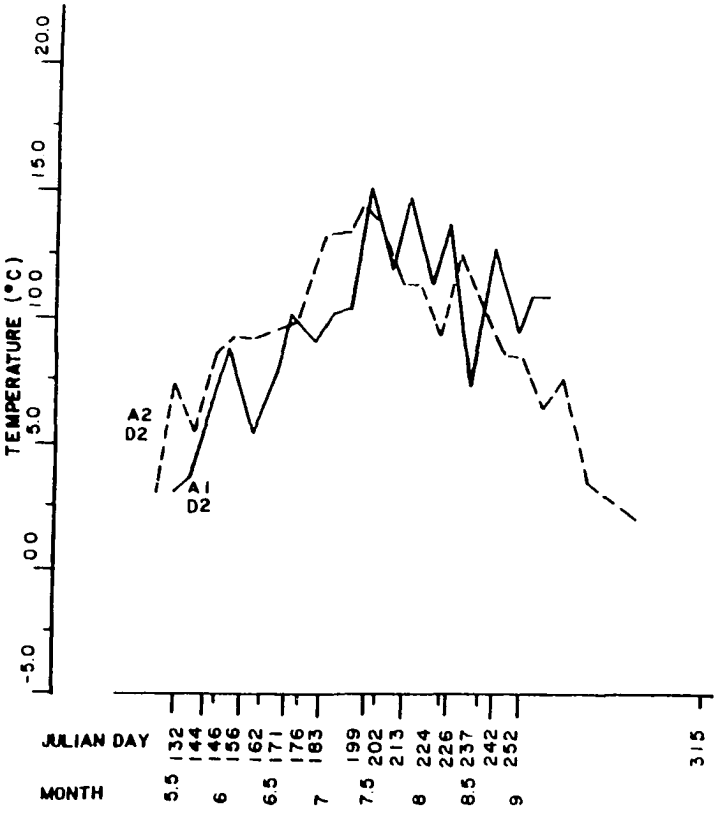


Figure 16. Soil temperature comparisons by site and year: A1 = Aspen, season 1; A2 = Aspen, season 2; D2 = Depth 2 (O22 - A horizon interface).

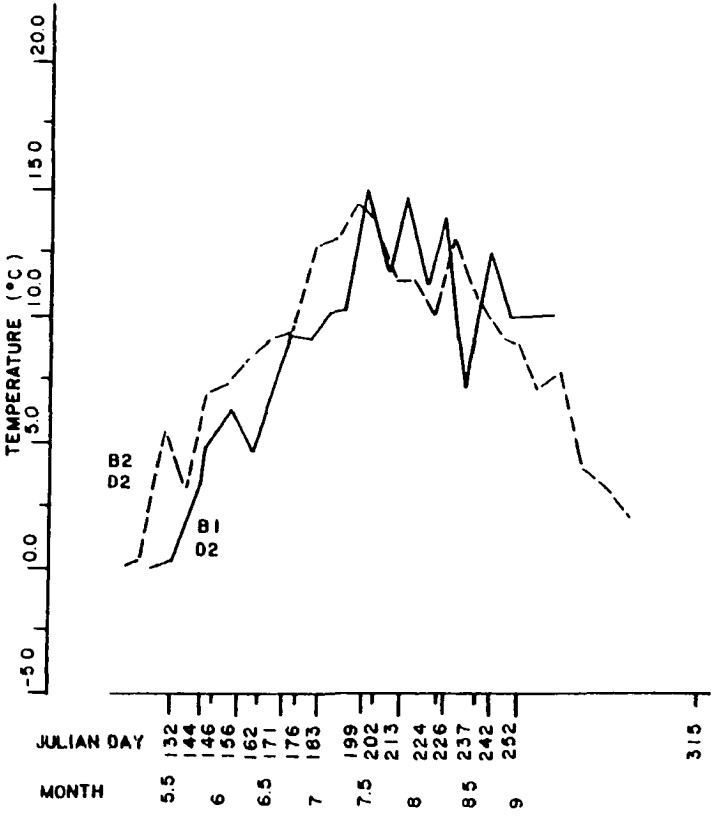


Figure 17. Soil temperature comparisons by site and year: B1 = Birch, season 1; B2 = Birch, season 2; D2 = Depth 2 (O22 - A horizon interface).

B. SOIL MOISTURE

I. Rainfall/Soil Moisture

Overview:

1. Within year comparisons show that for both sample seasons, differences in rainfall between aspen and birch sites were negligible and most probably biologically insignificant.
2. Sample season two showed significantly greater rainfall than season one.
3. Rainfall input and soil moisture percentages are positively correlated for organic soils; mineral soils moisture percentages are not shown to be correlated with rainfall events.

Figure 2 (site description section) shows that, although there are several points during both field seasons when birch site rainfall was slightly less than aspen rainfall, the difference is of insignificant magnitude. Total rainfall for the 1975 field season was significantly greater than the 1974 field season (α = .05: 1974 mean rainfall = 12.93 cm, 1975 mean rainfall = 15.53 cm).

Figures 18 and 19 (seasonal soil moisture curves in relationship to rainfall) show, as expected, a direct relationship between rainfall events and soil moisture fluctuations at the 1-2 cm soil depth, although the response is not immediate. Soil moisture sampling intervals were not coincidential with precipitation measurements, rainfall readings were made every 6 or 7 days and represent a cumulative deposition for that interval. Without daily measurements for both variables a more precise assessment of the response time is not possible.

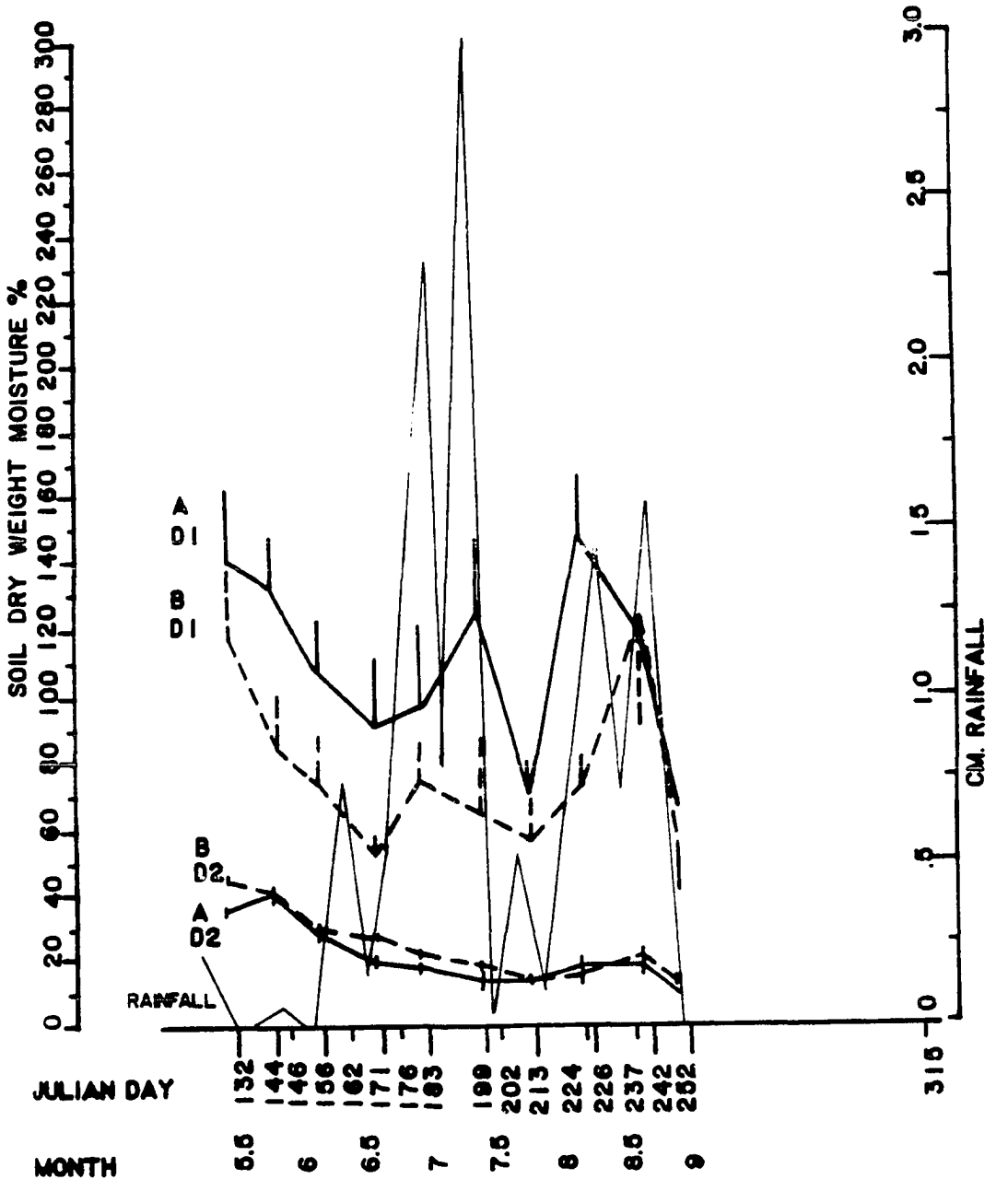


Figure 18. Soil moisture and rainfall for field season 1 (ten sample periods): A = Aspen, B = Birch, D1 = Depth 1 (1-2 cm below forest floor surface), D2 = Depth 2 (6-7 cm below forest floor surface).

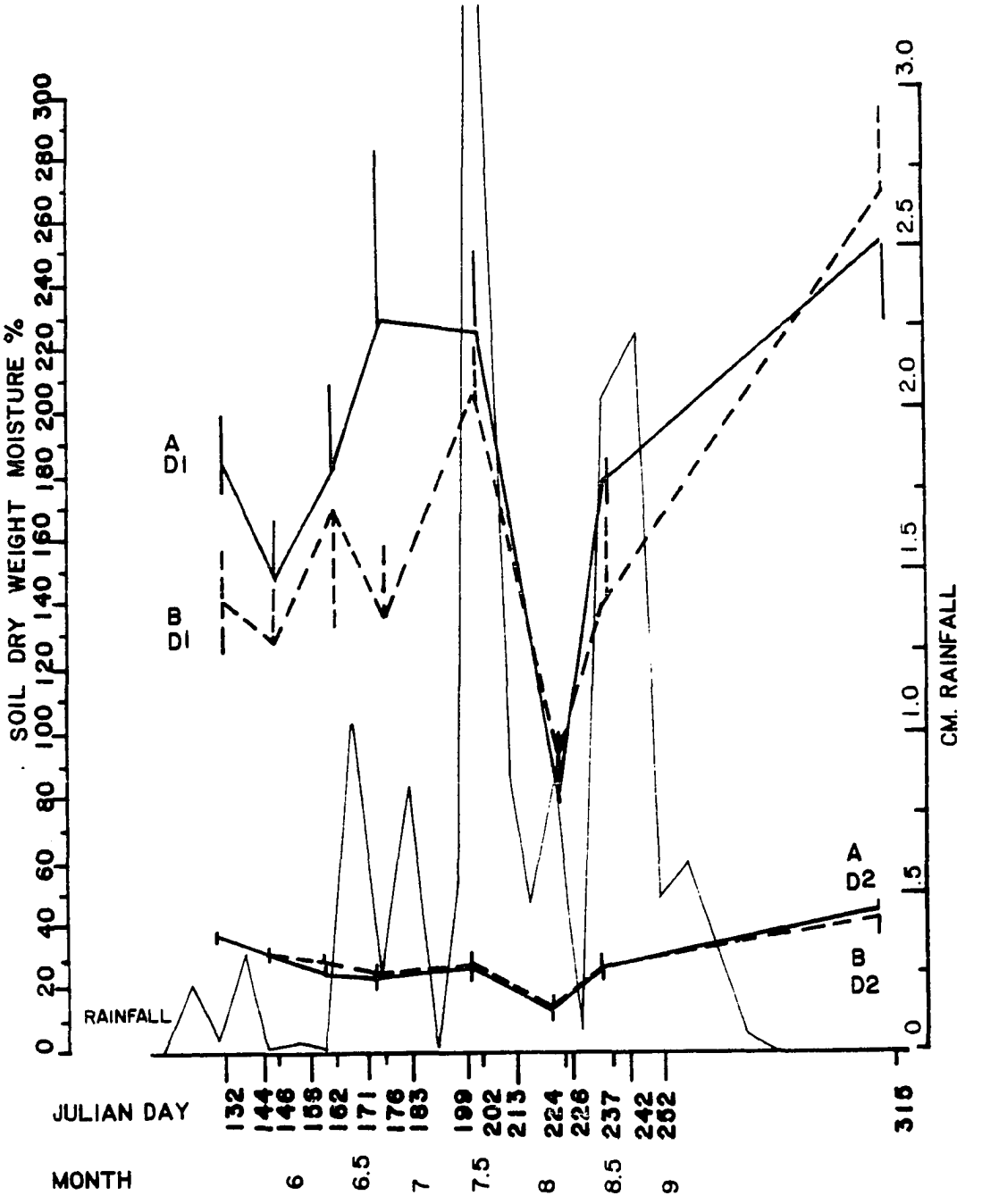


Figure 19. Soil moisture and rainfall for field season 2 (8 sample periods): A = Aspen, B = Birch, D1 = Soil Depth 1 (1-2 cm), D2 = Soil Depth 2 (6-7 cm).

Figure 20: 1974 Rainfall and Soil Moisture (1-2 cm below soil surface)

Figure 20 shows an early season soil moisture high of 132% (0.26 cm rainfall input prior to this sample date) with a steady decline over the first four sample dates to 72%. By sample day 198 (July 18) soil moisture in the 1-2 cm soil level rose to 96% following 3 major rainfall events totaling 8.49 cm. By sample day 212 (August 1) soil moisture dropped to 65% with rainfall input of only 0.64 cm. By sample day 241 (August 30) soil moisture rose to 123% in response to 4.55 cm rainfall. Soil moisture tapered off sharply by sample day 251 (September 9) to 63% in response to 0.00 cm rainfall.

Figure 20: 1975 Rainfall and Soil Moisture (1-2 cm below soil surface)

After an initial drop in soil moisture from 166% on day 132 (May 12) to 139% on day 146 (May 26) there was an increase in soil moisture to 220% by day 202 (July 21). This increase corresponded to a total rainfall of 7.75 cm for the interval. The rainfall trough between days 213 and 229 correspond with a drop in soil moisture to a season low of 84%. There is a late season rise in soil moisture to 163% on sample day 237 (August 25) and a final increase to a season high of 266% on day 315 (November 11). Total rainfall for this period was 7.87 cm. There was a total snow fall accumulation of 2.0 cm prior to sample day 315.

Figure 20: 1974 6-7 cm soil moisture/rainfall interaction

For 1974, soil moisture response in the 6-7 cm layer of the soil profile was not as clearly defined as in the 1-2 cm layer. There was a

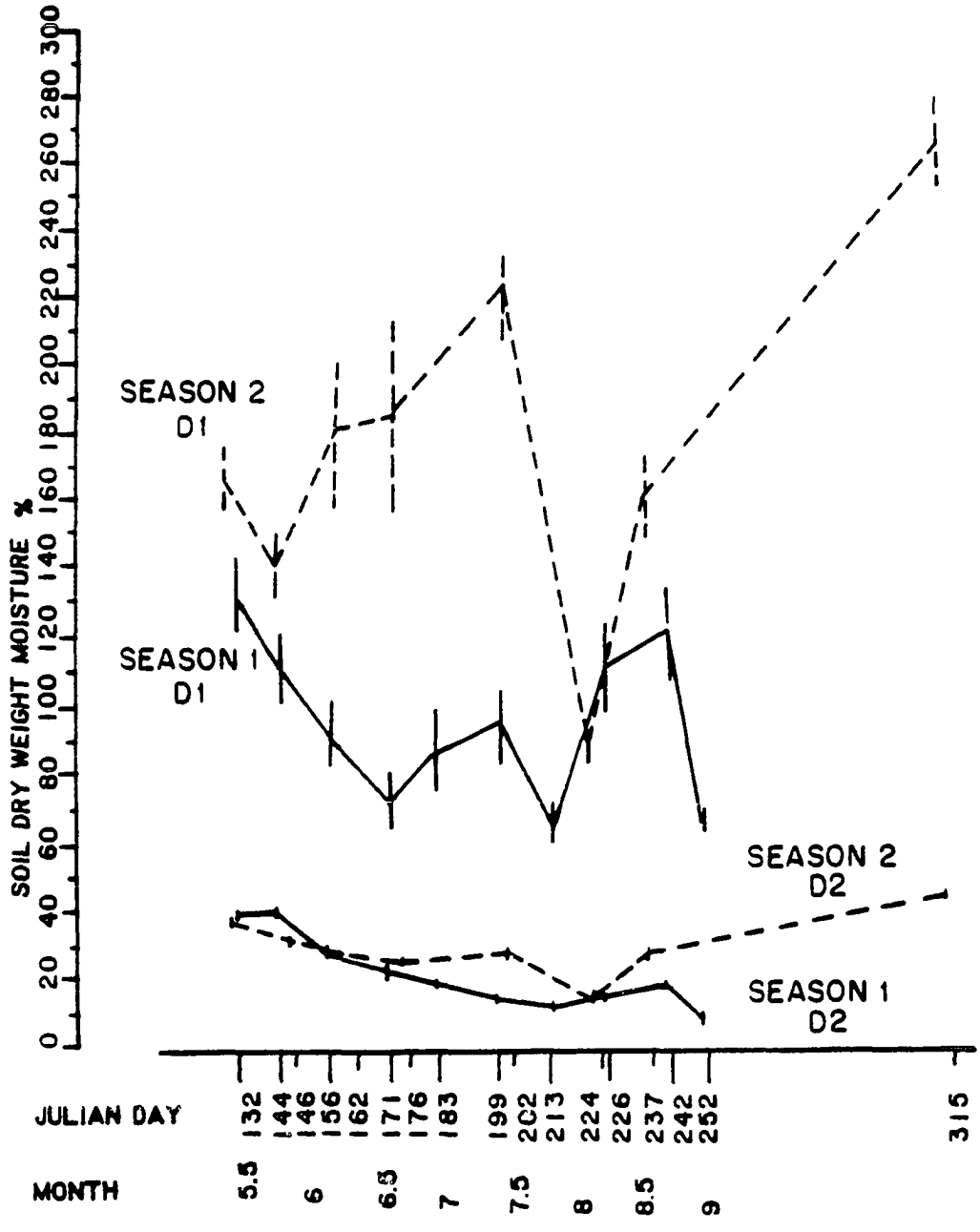


Figure 20. Soil moisture seasonal means for field season 1 and 2: D1 = Depth 1 (1-2 cm below forest floor surface), D2 = Depth 2 (6-7 cm below forest floor surface).

gradual decrease in soil moisture from 40% on date 131 (May 12 - sample 1) to 14% on sample date 212 (sample number 7 - August 1) even though there were 2-3 major rainfall events for this period with a total precipitation of 8.38 cm. The soil moisture peak for this period is clearly evident at 1-2 cm while there is a net decrease in soil moisture at 6-7 cm. By sample day 241 (sample number 9 - August 30) soil moisture increased to 20% and dropped to a season low on date 10 (day 251 - September 9) of 12%.

Figure 20: 1975 6-7 cm Soil Moisture/Rainfall Interaction

Figure 18 shows a gradual decline in soil dry weight moisture percent between sample days 132 (May 12) and 202 (July 21) from 35% to 27.4%. This corresponded with total rainfall of 5.62 cm for this interval. There was no response (elevation) to this input. A season low of 14.2% recorded on day 224 (August 12) at the 6-7 cm soil level corresponds with a 1-2 cm soil moisture minimum for the same period, the only noticable correlation of 1-2 cm and 6-7 cm soil moisture.

II. Effects of Vegetation Type and Longterm Fertilization on Soil Moisture Patterns

Overview

1. Analysis of variance using Duncan's Multiple Range Test indicates that the consistently greater soil moisture values ($\overline{X}$ = 47% greater) recorded from aspen soils are statistically significantly greater than birch soil moisture means (α = .05) at the 1-2 cm soil depth.

2. There is no significant vegetation type effect on soil moisture for the more highly mineralized soil fraction (A, O22/A interface) sampled.
3. There is no statistically significant moisture effect attributable to long-term fertilization.
4. Soil moisture for sample season two is significantly greater than sample season one.

Interpretation of the main effect of SITE (vegetation type and treatment) from the by year ANOVA (Table 9) is made difficult by the significant interaction of SITE * Depth (P value = .0164 and .0003 for field season 1 and 2 respectively) which indicates that results were not consistent between depths over sites. Additional significant interactions include Depth, Day and Depth * Day. In isolating the effects of site and depth over both field seasons the means:

Site	Depth	DWT%
AC	1-2 cm X =	150.7%
AF	1-2 cm X =	154.3%
BC	1-2 cm X =	103.8%
BF	1-2 cm X =	127.9%
AC	6-7 cm X =	23.8%
AF	6-7 cm X =	27.4%
BC	6-7 cm X =	28.2%
BF	6-7 cm X =	26.4%

Point out a considerable difference in soil moisture content between aspen and birch control sites at the 1-2 cm soil depth (150.7% vs. 103.8%, respectively) which is of sufficient magnitude ($\overline{X}$ = 46.90%

Tabel 9. ANOVA by Season: Soil Dry Wt.
Moisture % and Bulk Density ($g \cdot cc^{-1}$)

	Season 1 P-Values		Season 2 P-Values	
Error Source	Bulk Den.	DWT %	Bulk Den.	DWT %
Site	.1991	.3783	.2672	.0618
Depth	.0020	.0122	.0001	.0001
Site * Depth	.0122	.0164	.0164	.0003
Day	.0001	.6218	.0001	.1032
Site * Day	.1169	.7161	.4488	.5739
Depth * Day	.0123	.0025	.0003	.0124
Site * Depth * Day	.2452	.3911	.4806	.4910

to be of biologic importance in the interpretation of fungal biomass figures by site.

Although aspen and birch sites exhibited the same general response pattern in seasonal soil moisture for both years (Figures 18 and 19), aspen site moisture for 1974 ranged from 12% to 75% soil moisture greater than birch for 8 of 10 sample periods and 10% to 95% soil moisture greater on 6 of 8 sample periods in 1975. This relationship (aspen > birch) was pursued by application of Duncan's Multiple Range Test (Table 10). For both field seasons combined; aspen fertilized, aspen control and birch fertilized, as a group, are not significantly different from each other at the 1-2 cm soil depth, but as a group do show significantly higher moisture values than birch control sites. This observation is confirmed by Table 11 - a breakdown of sites by year which shows that moisture percents for birch sites for 1974 are the "most different" of all other combinations. This variability in site data may be further defined (Figure 21). Of the two plots within the birch control site, Birch Control plot 2 was found to have a buried mineral soil layer at the 1-2 cm soil level. Consequently, soil moisture values were inordinately low for this site and depth. This case is treated in detail in the Soil Moisture/Bulk Density interaction section of this chapter. Further discussion of soil moisture is presented at the level of vegetation type by year and, where necessary, by vegetation type by sample date.

TABLE 10. Duncan's Multiple Range Test.

Soil Moisture Percent: 2 Season Average

α =0.05 DF=4

Any means encompassed by the same line are not significantly different.

$\bar{x}$ all 1-2 cm

Mean (DWT %)	N	Site	Grouping
154.3	56	AF	
150.7	56	AC	
127.9	56	BF	
103.8	56	BC	

$\bar{x}$ all 6-7 cm

Mean (DWT %)	N	Site	Grouping
28.2	56	BC	
27.4	56	AF	
26.4	56	BF	
23.8	56	AC	

Table 11. Duncan's Multiple Range Test.

Soil Moisture Percent: 1974 and 1975

Alpha = 0.05 DF = 4

Any means encompassed by the same line are not significantly different.

Mean (DWT %)	N	Site	Grouping
106.9	56	Aspen Fert. - 1975	
98.8	56	Aspen Cont. - 1975	
91.2	56	Birch Fert. - 1975	
81.6	56	Birch Cont. - 1975	
75.6	56	Aspen Cont. - 1974	
74.7	56	Aspen Fert. - 1974	
63.1	56	Birch Fert. - 1974	
50.4	56	Birch Cont. - 1974	

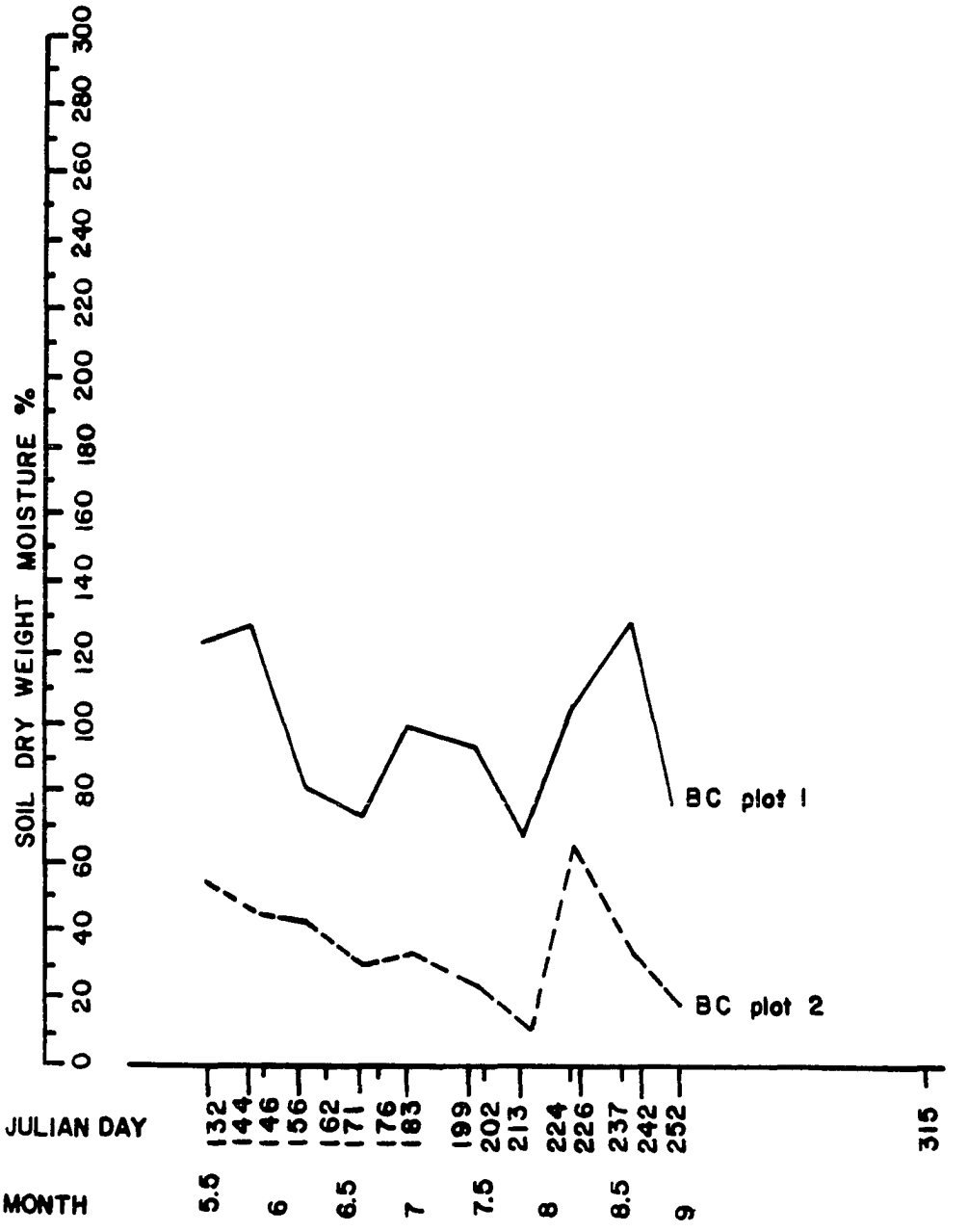


Figure 21. Soil moisture comparisons for Birch Control plots 1 and 2, season 1, 1-2 cm below forest floor surface. BC plot 2 = anomalous' plot with displaced mineral soil layer.

1974 Soil Moisture: Seasonality (Figure 18, Table 12)

ASPEN

A comparison of Figure 18 and Table 12 shows that the moisture peaks (1-2 cm soil level) for samples 1, 6, 8 and 9 ($\bar{X}$ respectively = 144.2%, 134.9%, 127.1% and 149.7%) are not significantly different from each other, but individually and as a group are significantly greater (α = = 0.05) than season moisture lows for dates 4, 5, 7 and 10 ($\bar{X}$ respectively = 91.0%, 97.7%, 72.6% and 66.8%). There is no statistically significant seasonal trend demonstratable for either birch or aspen moisture values at the 6-7 cm soil level for either sample year although there is a trend towards a net decrease in soil moisture over the course of the summer for field season one in both vegetation types. Additionally, field season two, sample period 6, shows the only clear cut response to low rainfall (as reflected by soil moisture percents) at the 6-7 cm soil level.

BIRCH

From Figure 18 and Table 12, sample dates one and nine are significantly greater than all other measurements for the season (moisture percent $\bar{X}$ = 149.7 and 144.2, respectively). The moisture peak at sample number 5 ($\bar{X}$ = 75.9%), though clearly a response to high rainfall preceeding the sample period (and roughly parallel to soil moisture increases in aspen soils for sample 5 and 6) is not significantly (α = .05) greater than moisture troughs corresponding to samples 4, 7 and 10 (moisture percent $\bar{X}$ = 51.6%, 51.8% and 59.1% respectively).

Table 12. Duncan's Multiple Range Test. Soil Moisture Percent

Season 1, Ranked by Date and Depth

$\alpha = 0.05$ DF = 36 N = 8

Any means encompassed by the same line are not significantly different.

Field Season 1

Aspen 1-2 cm Soil Moisture %	Sample No. and Ranking	Aspen 6-7 cm Soil Moisture	Sample No. and Ranking
149.7	8	39.6	2
144.2	1	34.7	1
134.9	2	28.8	3
127.1	6	19.6	4
121.2	9	18.8	9
109.4	3	18.7	8
97.7	5	18.0	5
92.0	4	13.7	6
72.6	7	13.5	7
66.8	10	10.4	10

Birch 1-2 cm		Birch 6-7 cm	
125.3	9	43.6	1
120.3	1	40.6	2
87.0	2	29.2	3
75.9	5	26.8	4
74.5	3	21.5	5
74.5	8	21.0	9
65.6	6	18.1	6
59.1	10	15.8	8
58.1	7	14.7	7
51.6	4	13.5	10

1975 Soil Moisture: Seasonality (Figure 19, Table 13)

ASPEN

Moisture peaks recorded for samples 4, 5 and 8 (moisture percent $\overline{X}$s = 233.7%, 231.0% and 258.9%, respectively) are significantly greater than seasonal moisture lows recorded for samples 2 and 6 ($\overline{X}$ = 151.0% and 80.7% respectively).

Sample periods 1, 2, 3, 5 and 7 are significantly greater than sample 6.

BIRCH

Sample 8 soil moisture is significantly greater than all other recordings. Peaks 3 and 5 (moisture $\overline{X}$ = 175.0% and 209.2% respectively) are greater than samples 1, 2, 4, 6 and 7 ($\overline{X}$ = 143.0%, 128.6%, 136.7% and 142.3%, respectively).

Table 13. Duncan's Multiple Range Test. Soil Moisture Percent

Season 2, Ranked by Date and Depth

$\alpha = 0.05$ DF = 36 N = 8

Any means not encompassed by the same line
are significantly different

Field Season 2

Aspen 1-2 cm		Aspen 6-7 cm	
Soil Moisture %	Sample No. & Ranking	Soil Moisture %	Sample No. & Ranking
258.9	8	47.8	8
233.7	4	36.5	1
231.0	5	31.2	2
189.5	1	27.1	5
186.6	3	26.8	7
183.8	7	24.4	3
151.0	2	23.7	4
80.7	6	14.5	6

Birch 1-2 cm		Birch 6-7 cm	
273.8	8	42.8	8
209.2	5	35.5	1
175.0	3	30.1	2
143.0	1	28.4	3
142.3	7	27.8	5
136.7	4	26.2	7
128.6	2	25.3	4
88.3	6	13.9	6

DISCUSSION

Earlier research on the study sites indicated that soil moisture regimes for the two contiguous vegetation types might be affected by the dominant overstory vegetation (Van Cleve, 1971; Van Cleve and Sprague, 1971; Van Cleve and Noonan, 1971 and 1975 and Viereck et al., 1983). It was noted that birch litter (L) from the sites had a generally greater moisture retention capacity than aspen litter with approximately equal or marginally greater moisture retention in F and H layers as follows:

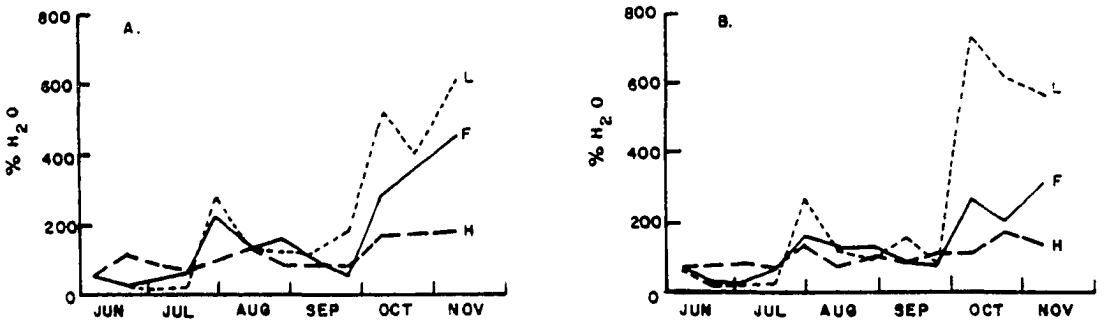
	Moisture % 0.1 atm.	Moisture % 15 atm.
Birch		
L	465.9	168.9
F	202.0	77.8
H	200.5	64.3
Aspen		
L	232.9	101.0
F	186.8	79.2
H	181.2	56.4

(adapted from Van Cleve and Sprague, 1971) Additionally, greater moisture content fluctuation was recorded from the birch L layer than in the aspen L layer, with smaller fluctuations encountered in birch F and H layers than aspen F and H layers. Van Cleve and Sprague (1971) also noted that two discreet periods of minimum litter moisture contents (moisture percent below which biological activity - as measured by

Gilson respirometry - dropped to zero) were evident for both vegetation types with critical moisture minimums higher in birch L soils than aspen (60-70% soil moisture and 50-60% soil moisture, respectively) possibly reflecting differing rates of organic matter wetting in the two soils.

These two periods of minimum moisture content occurred in June-July and August-September

Figure 22. Field moisture content of aspen (A) and birch (B) litter (L), fermentation (F) and humus (H) horizons. Van Cleve and Sprague (1971).



The periods of minimum moisture content for both vegetation types recorded by Van Cleve and Sprague (1971) coincide with the findings of this study (Figures 19, 20, 23, 24 and 25) which indicate a general trend, for both vegetation types, of a day 144 through 190 soil moisture low followed by a mid season (day 190-220) moisture peak followed by a second seasonal low (day 200-230) and a final end of season (day 225-250) moisture peak.

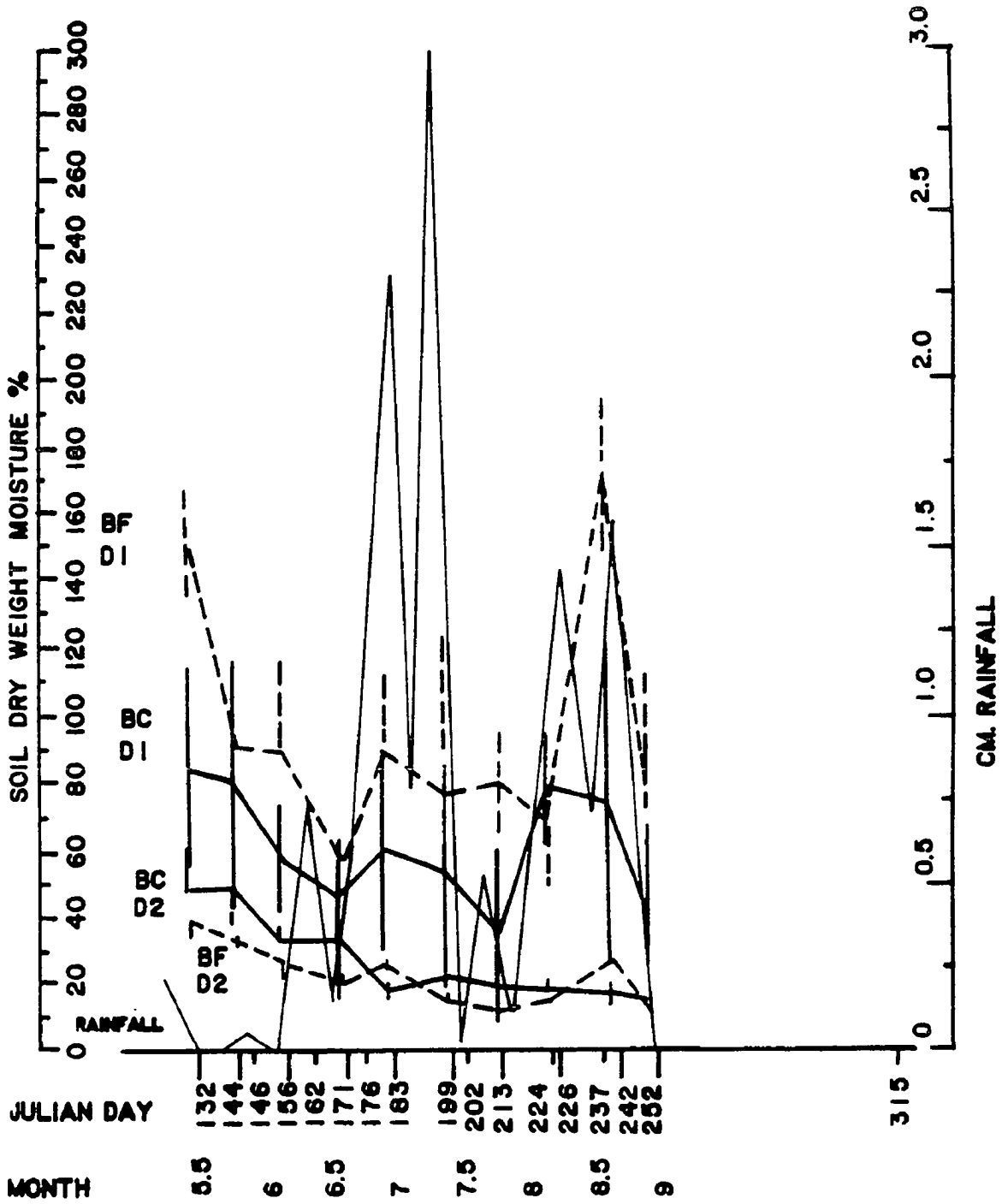


Figure 23. Soil moisture and rainfall for season 1: BC = Birch Control, BF - Birch Fertilized, D1 = 1-2 cm soil depth, D2 = 6-7 cm soil depth.

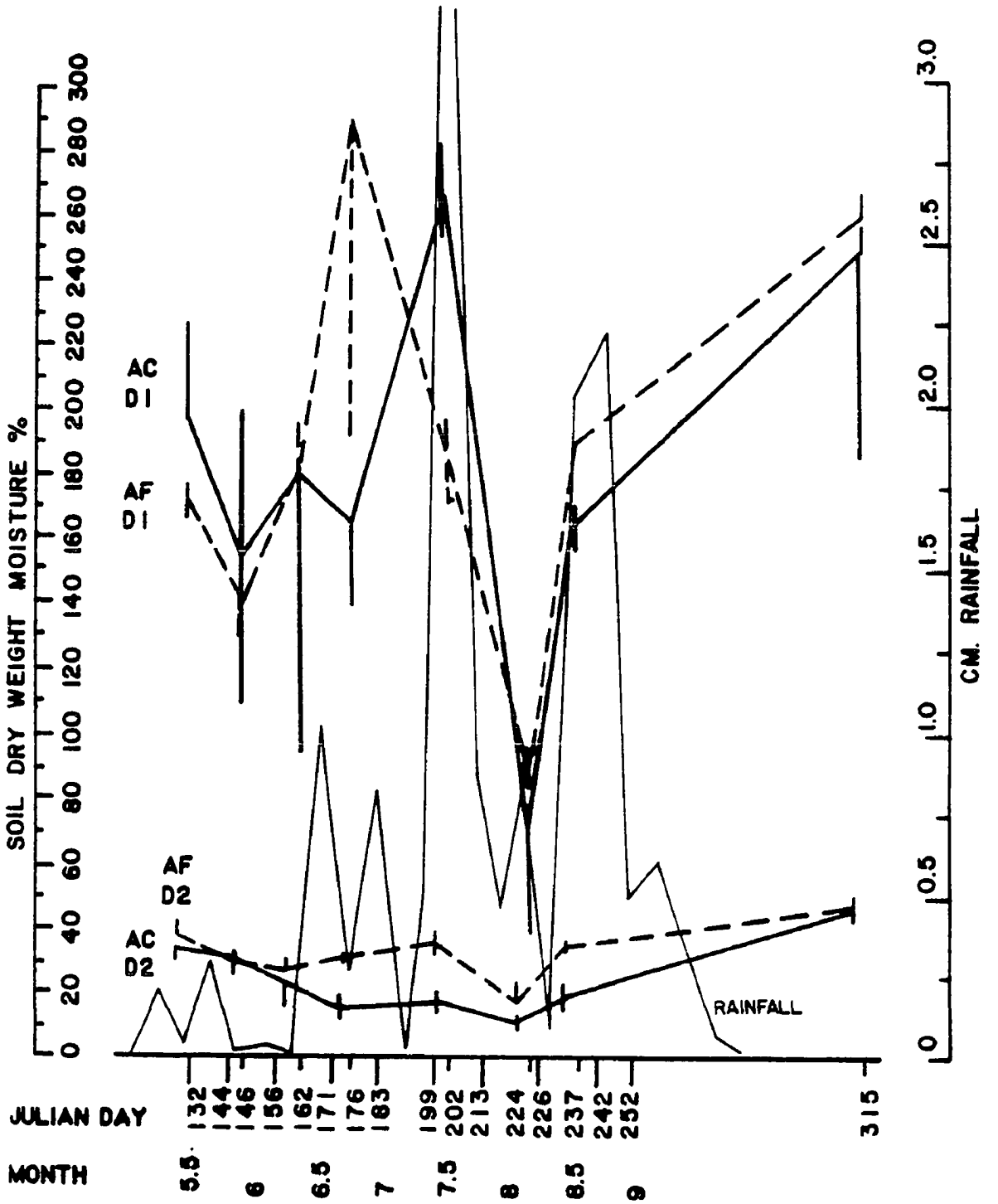


Figure 24. Soil moisture and rainfall for season 2: AC = Aspen Control, AF = Aspen Fertilized, D1 = 1-2 cm soil depth, D2 = 6-7 cm soil depth.

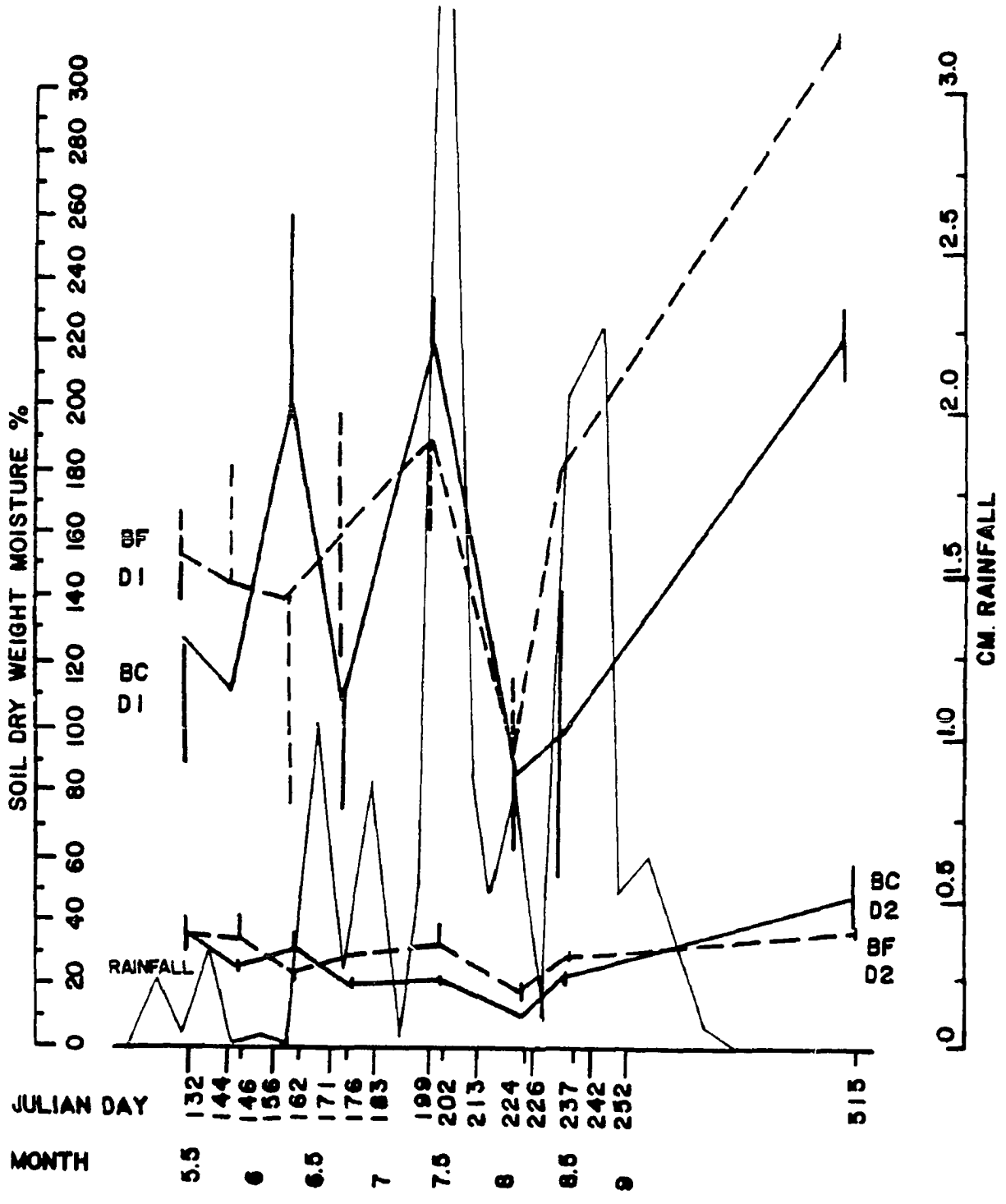


Figure 25. Soil moisture and rainfall for season 2: BC = Birch Control, BF = Birch Fertilized, D1 = 1-2 cm soil depth, D2 = 6-7 cm soil depth.

CONCLUSIONS

1. Differences in rainfall input between aspen and birch sites may be discounted as a factor in assessing significance of differences between aspen and birch soil moisture percents and fungal biomass.
2. Significantly greater soil moisture for season two must be considered in assessing differences in between-season fungal biomass means.
3. Elevated soil moisture values recorded for aspen sites (1-2 cm soil depth) in comparison to birch sites are of sufficient magnitude to be of biological significance in interpretation of differences in fungal biomass means between the two vegetation types.
4. There is no statistically significant effect of long term fertilization on soil moisture.

C. SOIL BULK DENSITY

Effects of vegetation type, fertilization and time (seasonality)

Overview:

1. There is no significant seasonal pattern of fluctuation in soil bulk density.
2. There is no statistically significant vegetation effect on bulk density.
3. Long term application of fertilizers has not affected bulk density.
4. There is a marginally significant year effect (1974 > 1975).
5. There is a significant depth (1-2 cm vs 6-7 cm) effect for all sites for both years.
6. Bulk density is inversely related to soil moisture percent. In comparing seasonal averages those sites that are highest in soil moisture percent are lowest in bulk density.

Figure 26 gives a comparison of 1974 and 1975 bulk density means as well as comparisons of means by depth for the combined forests for both field seasons. A comparison of standard error of the mean bars for both depths and years shows that variability was relatively constant over the sample seasons by depth within years. Means for 1974 (1-2 cm soil depth) are elevated over that of 1975 1-2 cm means (.36697 gm • cc^{-1} and .20209 gm • cc^{-1} respectively). This difference between years is attributable, in part, to significantly higher bulk density figures recorded in 1974 from the previously discussed anomalous birch plot with

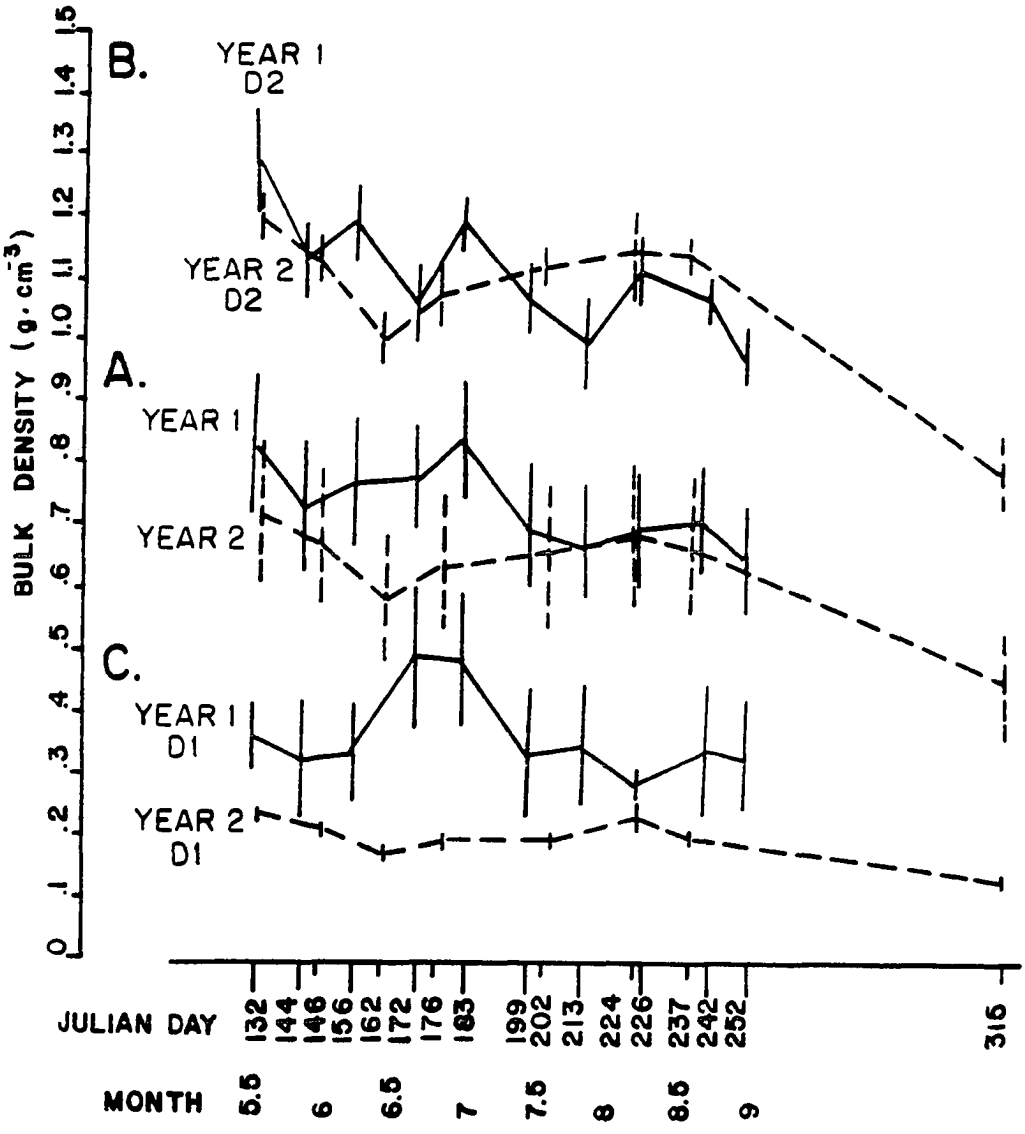


Figure 26. Soil bulk density seasonal means: A = $\overline{X}$ all sites at both depths sampled, B = by year at Depth 2 (6-7 cm below forest floor surface), C = by year at Depth 1 (1-2 cm below forest surface).

a displaced mineral soil layer (Figures 21 and 27). There is a relatively consistent trend, for both sample depths for both years, of a decrease in bulk density over the first two to three sample dates in most of the sites (Figures 26-30). However, for these dates there is no significant effect of vegetation type or fertilization ($\alpha = .05$) on bulk density at any level of comparison. Furthermore, there is no significant ($\alpha = .05$) seasonality effect for either year. A comparison of all sites for both sample years (Table 14 - section D) does indicate that the figure for birch control sites for 1974 differs the most from the overall means. The fact that the abnormally high values recorded from birch control sites in 1974 are not reflected in the by year ANOVA (Table 9) is an indication of the heterogeneity of bulk density across vegetation and treatment sites.

A comparison of bulk density and soil moisture values show that bulk density figures ranked by magnitude yield a sample site array that is the inverse of a by-site moisture percent array:

	Soil Moisture		Bulk Density	
	Mean	Site	Site	Mean
1-2 cm	154.3	AF	BC	0.4280
	150.7	AC	BF	0.2626
	127.9	BF	AC	0.2300
	103.8	BC	AF	0.2139
6-7 cm	28.2	BC	AC	1.1849
	27.4	AF	BF	1.1150
	26.4	BF	AF	1.1091
	23.8	AC	BC	1.0780

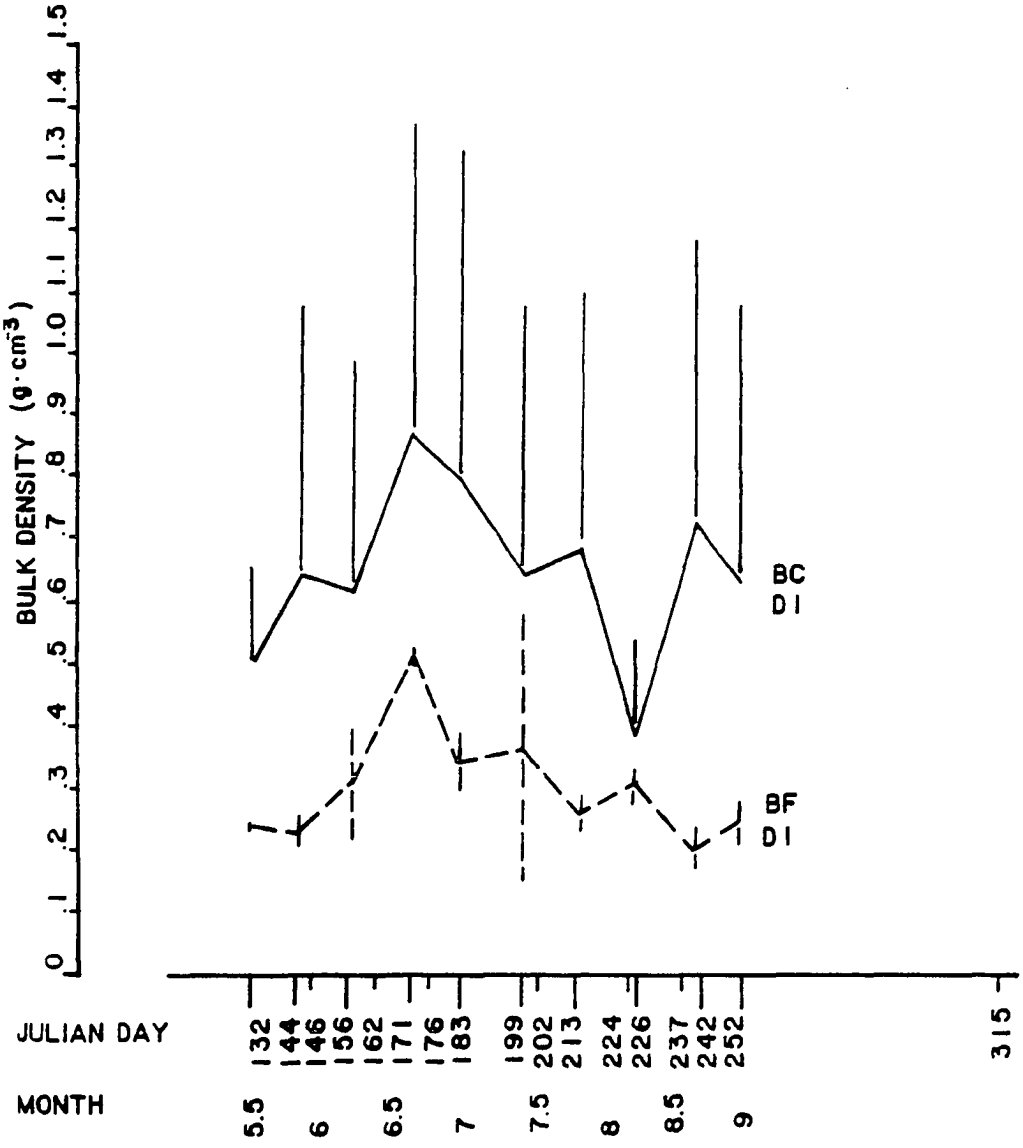


Figure 27. Soil bulk density means: Season 1, BC = Birch Control, BF = Birch Fertilized, D1 = Depth 1 (1-2 cm below forest floor surface).

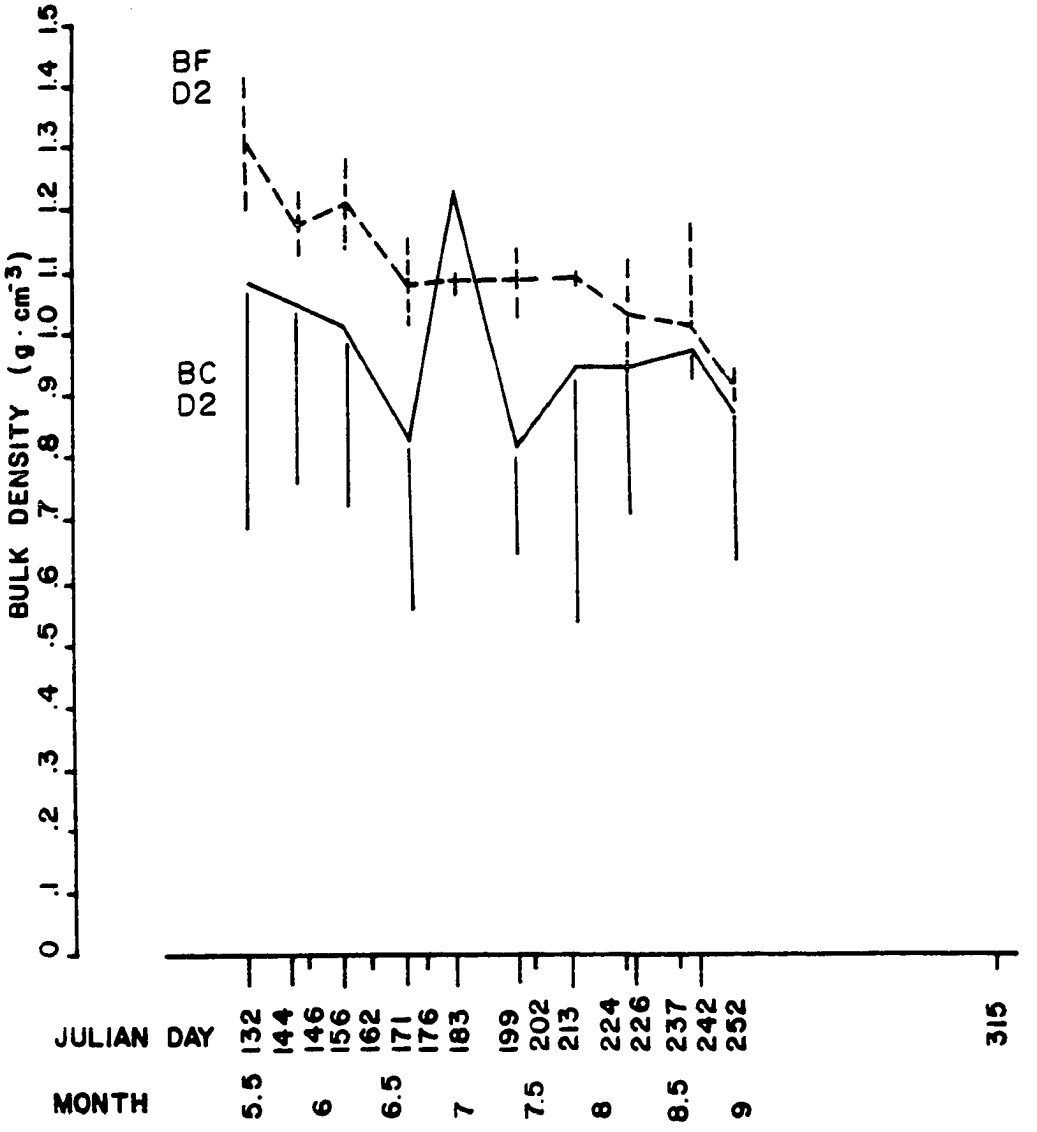


Figure 28. Soil bulk density: Season 1, BC = Birch Control, Birch Control, BF = Birch Fertilized, D2 = Depth 2 (6-7 cm below forest floor surface).

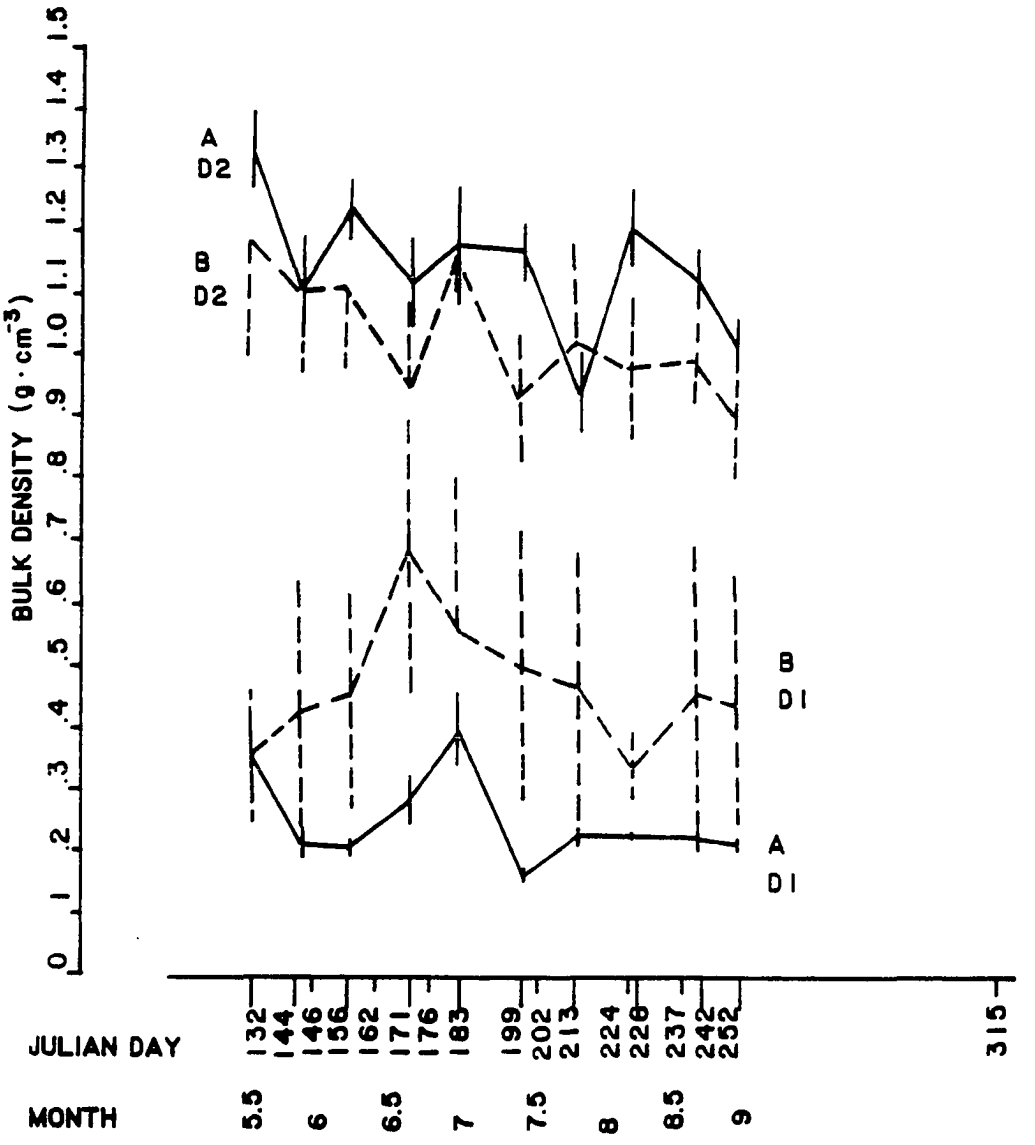


Figure 29. Soil bulk density means by vegetation type: Season 1, A = Aspen; B = Birch, D1 = Depth 1 (1-2 cm below forest floor surface), D2 = Depth 2 (6-7 cm below forest floor surface).

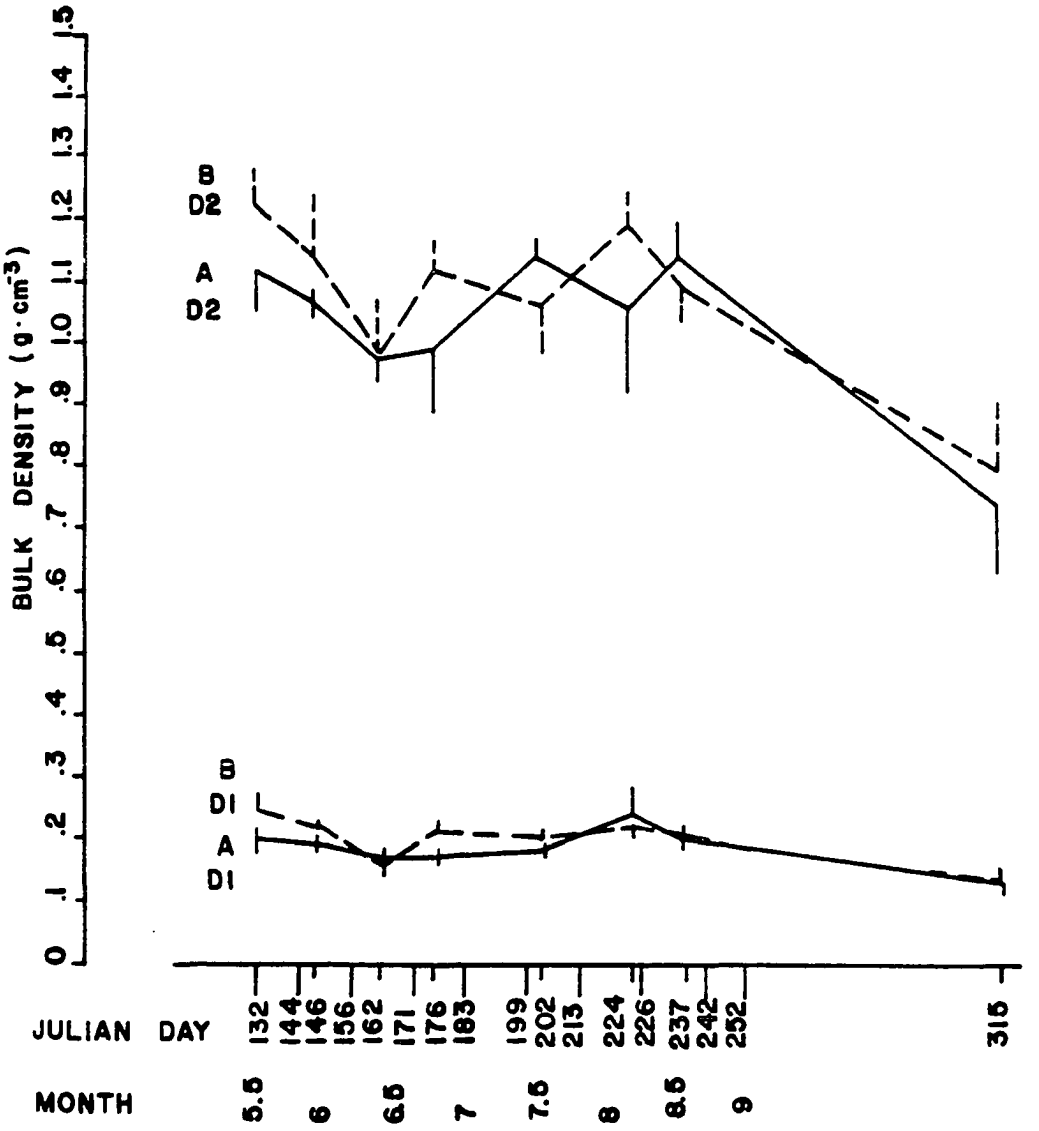


Figure 30. Soil bulk density means by vegetation type: Season 2; A = Aspen, B = Birch, D1 = Depth 1 (1-2 cm below forest floor surface), D2 = Depth 2 (6-7 cm below forest floor surface).

Table 14. Duncan's multiple range test for bulk density ($g \cdot cc^{-1}$). Means sharing a common line (under 'grouping') are not significantly different ($\alpha = .05$).

Bulk Density

Mean & Rank	N	Site	Grouping
0.4280	56	BC	(A)
0.2626	56	BF	
0.2300	56	AC	
0.2139	56	AF	
1.1849	56	AC	(B)
1.1150	56	BF	
1.1091	56	AF	
1.0780	56	BC	
0.7530	112	BC	(C)
0.7072	112	AC	
0.6888	112	BF	
0.6615	112	AF	
0.803071	56	BC-1974	(D)
0.738214	56	AC-1974	
0.727286	56	BF-1974	
0.703464	56	AF-1974	
0.703000	56	BC-1975	
0.676214	56	AC-1975	
0.650232	56	BF-1975	
0.61956	56	AF-1975	

(A) = 1974 and 1975 combined (depth 1-2 cm)
(B) = 1974 and 1975 combined (depth 6-7 cm)
(C) = 1974 and 1975 combined (combined depths)
(D) = 1974 and 1975 by site and year (combined depths)

CONCLUSIONS/DISCUSSION

The conclusion that there is no significant effect of vegetation type or long-term fertilization on soil bulk density must be weighed in light of the demonstrated inherent variability within each site. The ANOVA for 1974 does not indicate a main effect of site even though a plot sampled (Birch Control 2) shows bulk density figures (1-2 cm soil level) 2 to 3 times the average bulk density measurements from all other sites. This observation raises three points:

1. The possibility must be considered that any main effect of vegetation type and treatment is masked by the heterogeneity of within site soil profiles.
2. These results strengthen the argument, presented in the METHODS section of this work, against extrapolating point source biomass measurements (lengths per gram dry soil) to a unit area measurement (lengths or grams per meter^2).
3. Further microbiological studys in these forests and other vegetation types with similar variability in bulk density would benefit from expressing microbial biomass measurements as biomass per gram organic matter per gram soil, as has been done by Brunberg (1980).

The marginally significant year effect (1974 > 1975) can be traced to two factors:

1. Contribution of high bulk density figures from the anomalous birch control site in 1974 which was not sampled in 1975.
2. Significantly greater soil moisture in 1975 than in 1974 for

the 1-2 cm soil depth (175.8 DWT% and 95.4 DWT%, respectively). A moisture difference of this magnitude could have effectively decreased bulk density in the relatively loose, unpacked O1-O21 organic layer due to expansion or swelling of organic matter upon wetting. Since bulk density was calculated gravimetrically upon an excised 1 cm by 6.08 cm soil wafer (see Laboratory Methods), expansion of the organic matter in this layer prior to excision of the 1 cm wafer would have resulted in less mass per wafer.

Other factors which could have affected bulk density in the litter layer such as winter snow load/compaction, effect of microarthropods, and previous years litter fall, are not addressed in this study.

FUNGAL BIOMASS:

D. SEASONALITY*, VEGETATION AND FERTILIZATION EFFECTS

The independent variables: soil temperature, soil moisture, and soil bulk density have been discussed in relationship to effects of vegetation type, fertilization and time, in preparation for addressing the central hypothesis and corollaries:

Central Hypothesis

Below ground standing crop fungal biomass in upland, permafrost-free interior Alaskan taiga vegetation exhibits within season population fluxes which may be accounted for by changes in microclimatic conditions; specifically soil temperature and soil moisture. Within the confines of dates comprising the field season for this study, soil moisture is thought to be the overriding causative factor for 'seasonal' fluctuations in fungal biomass.

Corollary 1

The magnitude of fungal biomass is affected by localized differences in soil bulk density, used here as a comparative index of organic matter (substrate) content.

*In this study the term 'seasonal' refers to Julian Days 131 through 315 (roughly mid-May to mid-November).

Corollary 2

Fungal biomass dynamics which are dependent, in part, upon substrate availability and quality, may be expected to differ between dominant overstory vegetation types (aspen and birch) which have been shown to produce litter of differing quality and soil horizons of differing quality.

Corollary 3

A manipulation of within site primary and secondary substrate quality by long-term (nine years) additions of N, P and K fertilizers may alter the magnitude of fungal biomass, in comparison with untreated sites.

The remaining text is devoted to a discussion of:

I. Cause and effect relationships among temperature, moisture and fungal biomass over time; relationships which define 'seasonal biomass'.

II. The effect of dominant overstory vegetation type on fungal biomass.

III. The effect of long-term application of N-P-K fertilizers on fungal biomass.

IV. The effect of vegetation type and fertilization on the distribution of basidiomycete hyphae.

D. I. SEASONAL FLUCTUATIONS OF FUNGAL BIOMASS

OVERVIEW

1. With some exceptions, seasonal biomass fluctuations plotted by vegetation type, by depth, by treatment and by plot within site show markedly similar patterns of peaks and troughs. The correspondence of means is more pronounced for field season two.
2. Standing crop fungal biomass is significantly correlated with soil moisture, showing a strong linear relationship for field season one.
3. Standing crop fungal biomass is negatively correlated with soil bulk density.
4. Standing crop fungal biomass shows little correlation with soil temperature, over the confines of sample dates for this study, and in some instances biomass and temperature are negatively correlated.

Early in the analysis, it appeared that the data would reflect three periods of peak fungal biomass roughly corresponding to: (1) beginning season sample (mid May), (2)mid season (late June - early July) and (3) late season (mid August - early September). This observation from the raw data was reinforced by twice weekly collections of epigeous sporocarps, for future determination of periodicity of higher fungi fruiting body development. The collections showed above-ground biomass peak periods during early June and late August.

Figures 31-40 show below-ground biomass fluctuations (at varying levels of resolution) over time. The early, mid and late season peaks, at the 1-2 cm soil depth, are evident for both field seasons for aspen sites and to a lesser extent for birch sites (Figures 31, 32 and 34).

For comparison of significance of means (by vegetation type within season) mean value points for Figure 31 and 32 are indicated by sample number (110 for 1974, 18 for 1975).

1974 Aspen Seasonality: $\alpha = .05$ (Figure 31)

1-2 cm soil depth

means 1, 4, 8 and 9 are not significantly different

means 2, 3, 5, 6, 7 and 10 are not significantly different

means 1, 4, 8 and 9 are significantly greater than 2, 3, 5, 6, 7 and 10.

Values for the three biomass peaks: (1) mean 1, (2) mean 4 and (3) means 8 and 9 are significantly greater than all other by sample date means. The first season mean (1866 $m \cdot gm^{-1}$) is significantly greater than the final season mean (1256 $m \cdot gm^{-1}$).

6-7 cm soil depth

There is no significant difference among means for the 10 sample dates.

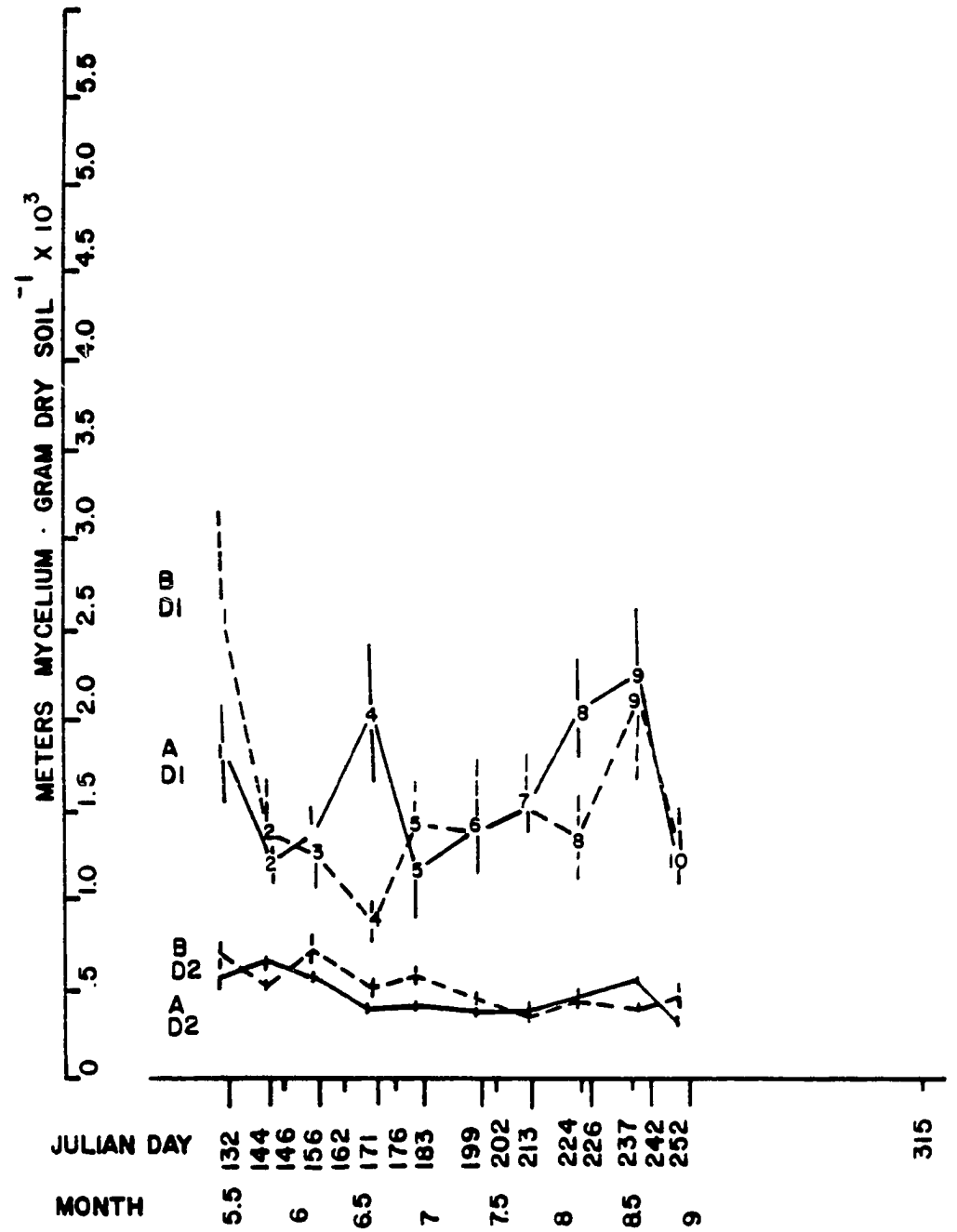


Figure 31. Fungal biomass seasonal means by vegetation type: Season 1; A = Aspen, B = Birch, D1 = Depth 1 (1-2 cm below forest floor surface), D2 = Depth 2 (6-7 cm below forest floor surface). 1-10 = sample dates 1-10.

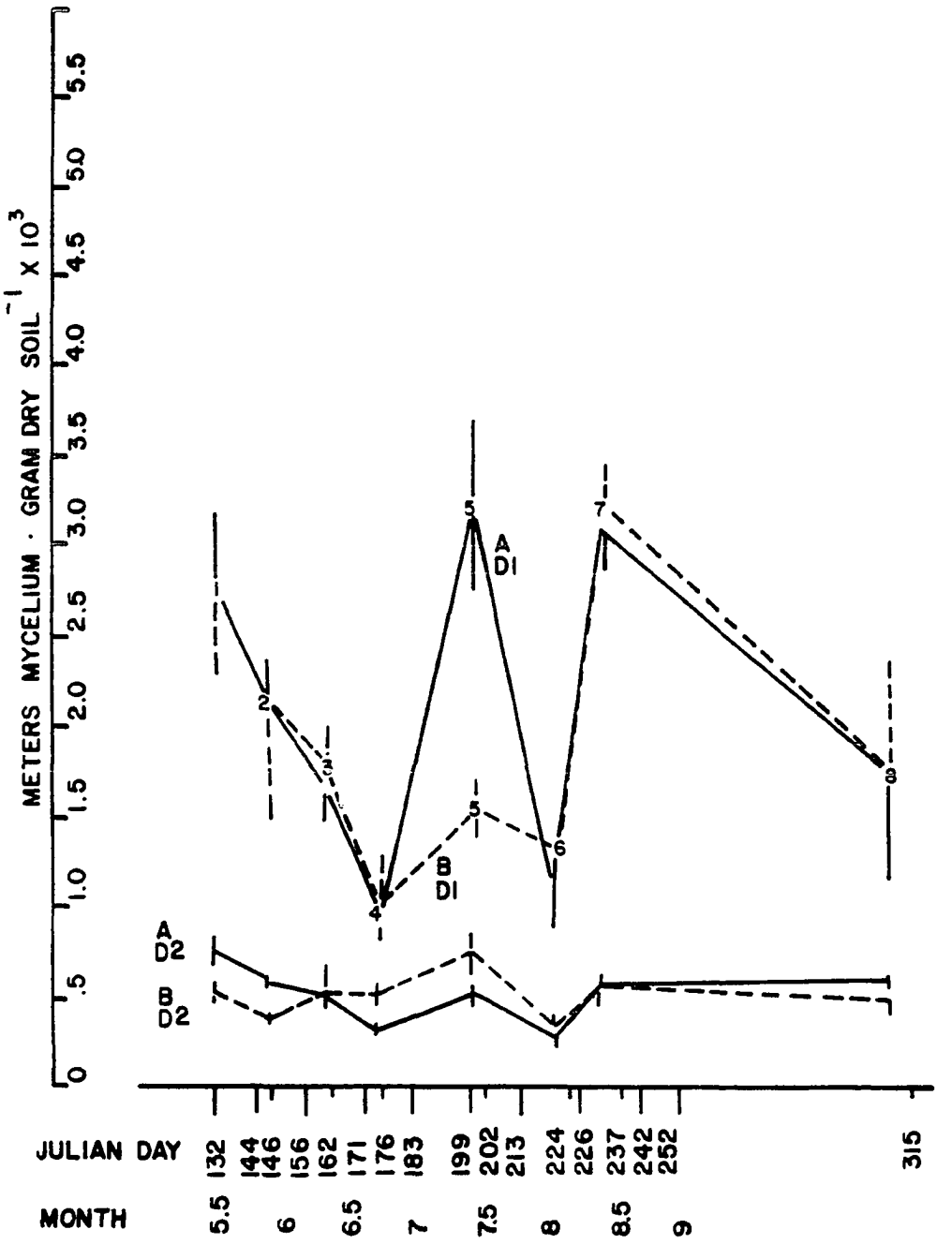


Figure 32. Fungal biomass seasonal means by vegetation type: Season 2; A = Aspen, B = Birch, D1 = Depth 1 (1-2 cm below forest floor surface, D2 = Depth 2 (6-7 cm below forest floor surface). 1-8 = sample dates 1-8.

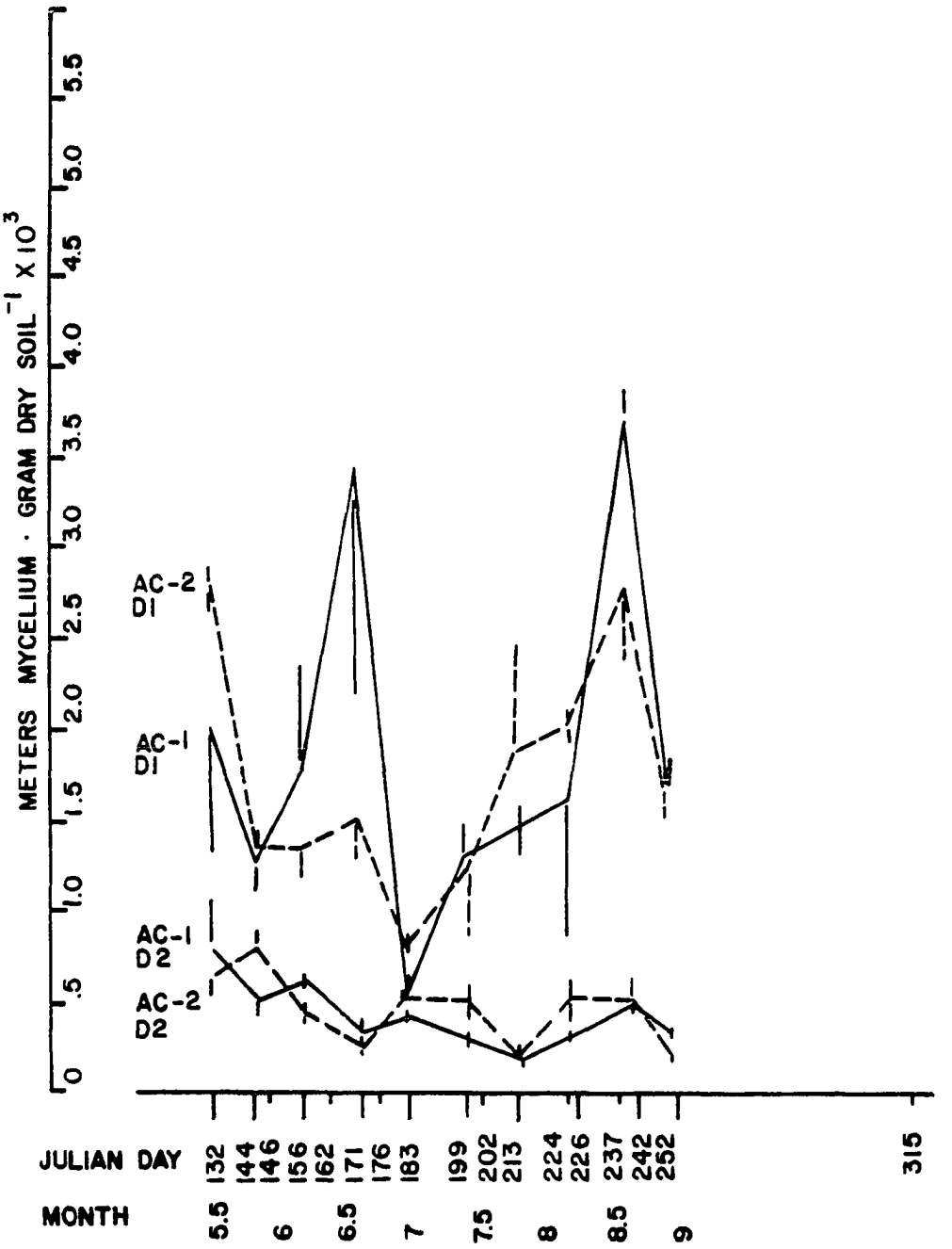


Figure 33. Fungal biomass by plot: Season 1; AC-1 = Aspen Control - plot 1, AC-2 = Aspen Control - plot 2, D1 = Depth 1 (1-2 cm), D2 = Depth 2 (6-7 cm).

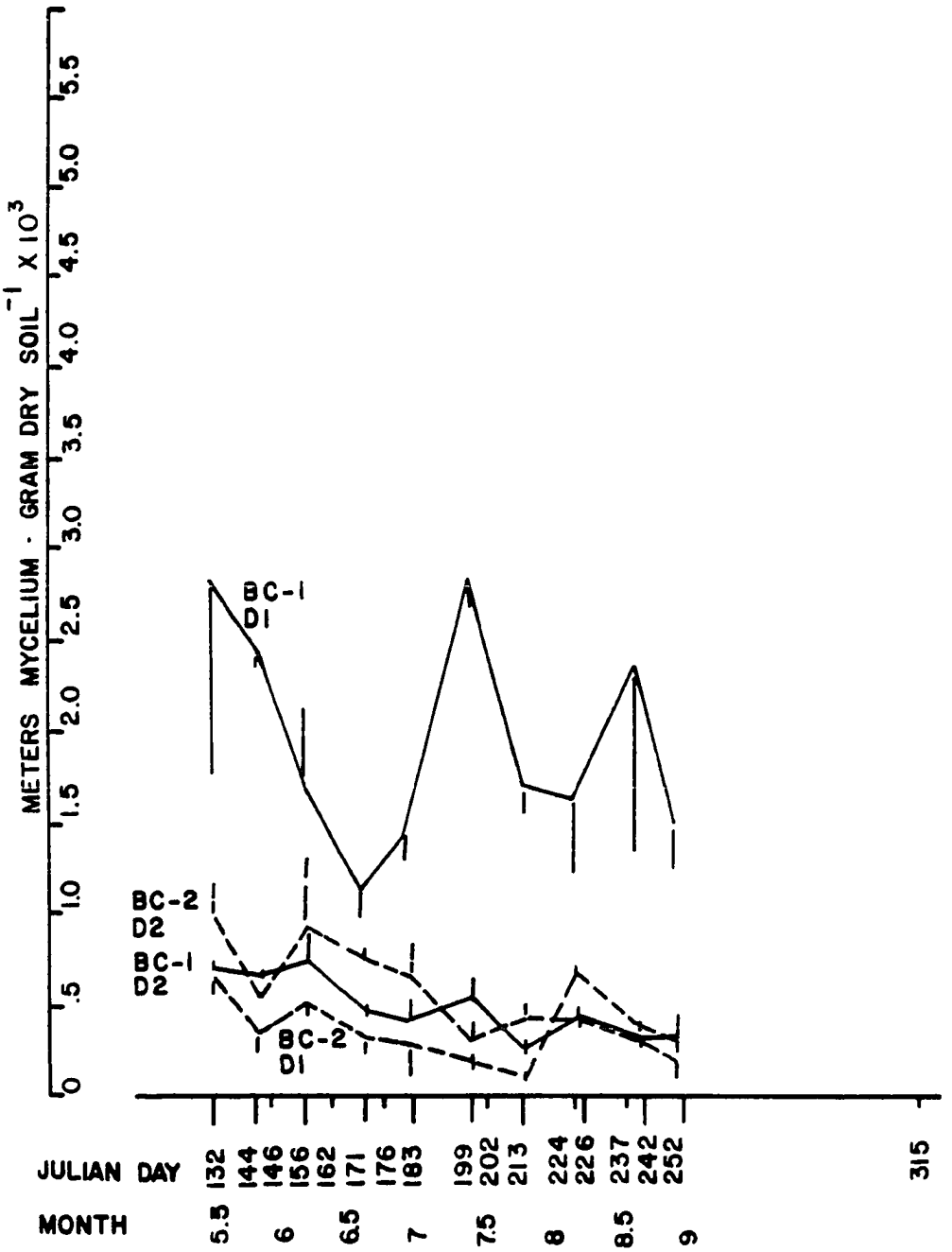


Figure 34. Fungal biomass by plot: Season 1; BC-1 = Birch Control - plot 1, BC-2 = Birch Control - plot 2, D1 = Depth 1 (1-2 cm), D2 = Depth 2 (6-7 cm).

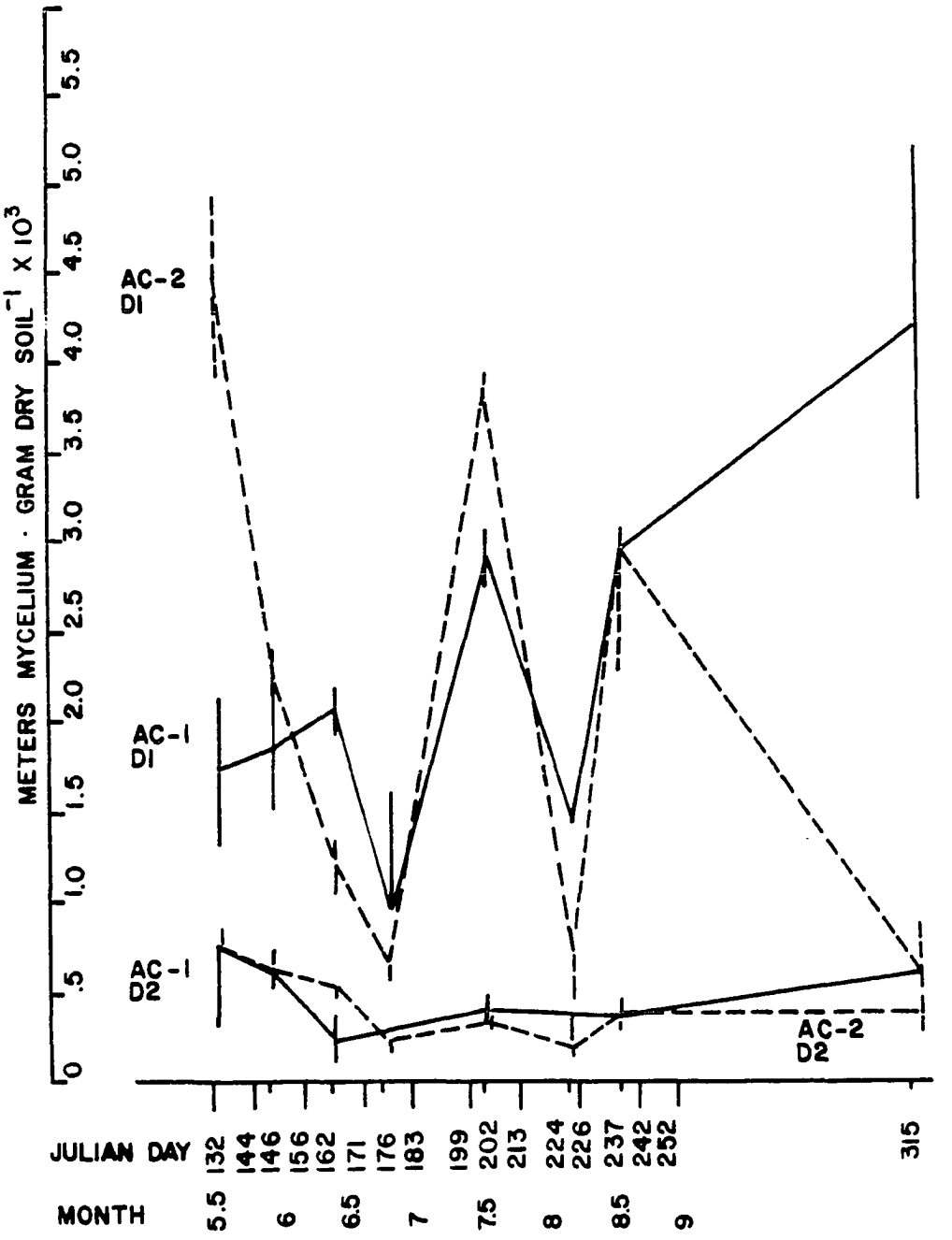


Figure 35. Fungal biomass by plot: Season 2; AC-1 = Aspen Control - plot 1, AC-2 = Aspen Control - plot 2, D1 = Depth 1 (1-2 cm), D2 = Depth 2 (6-7 cm).

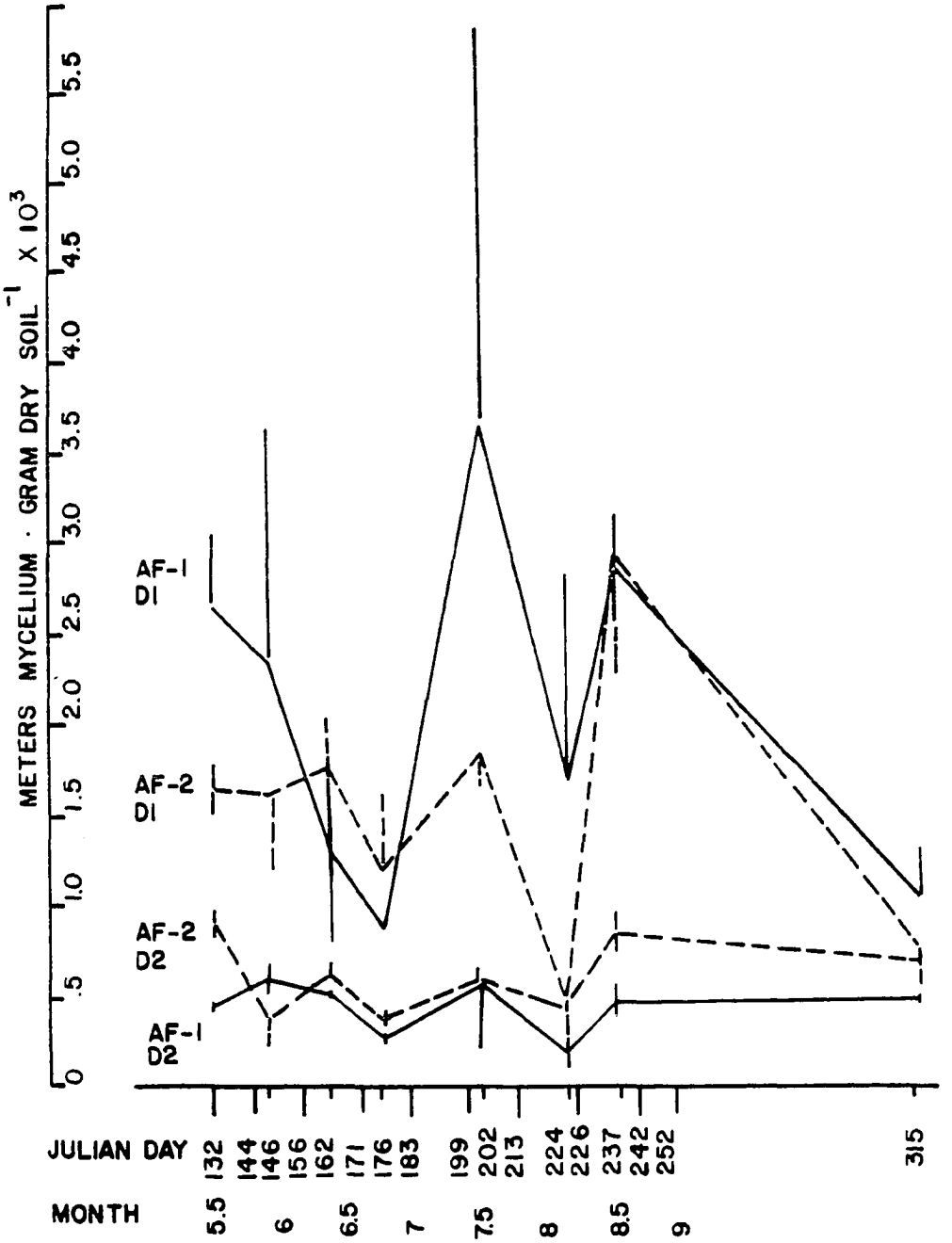


Figure 36. Fungal biomass by plot: Season 2; AF-1 = Aspen Fertilized - plot 1, AF-2 = Aspen Fertilized - plot 2, D1 = Depth 1 (1-2 cm), D2 = Depth 2 (6-7 cm).

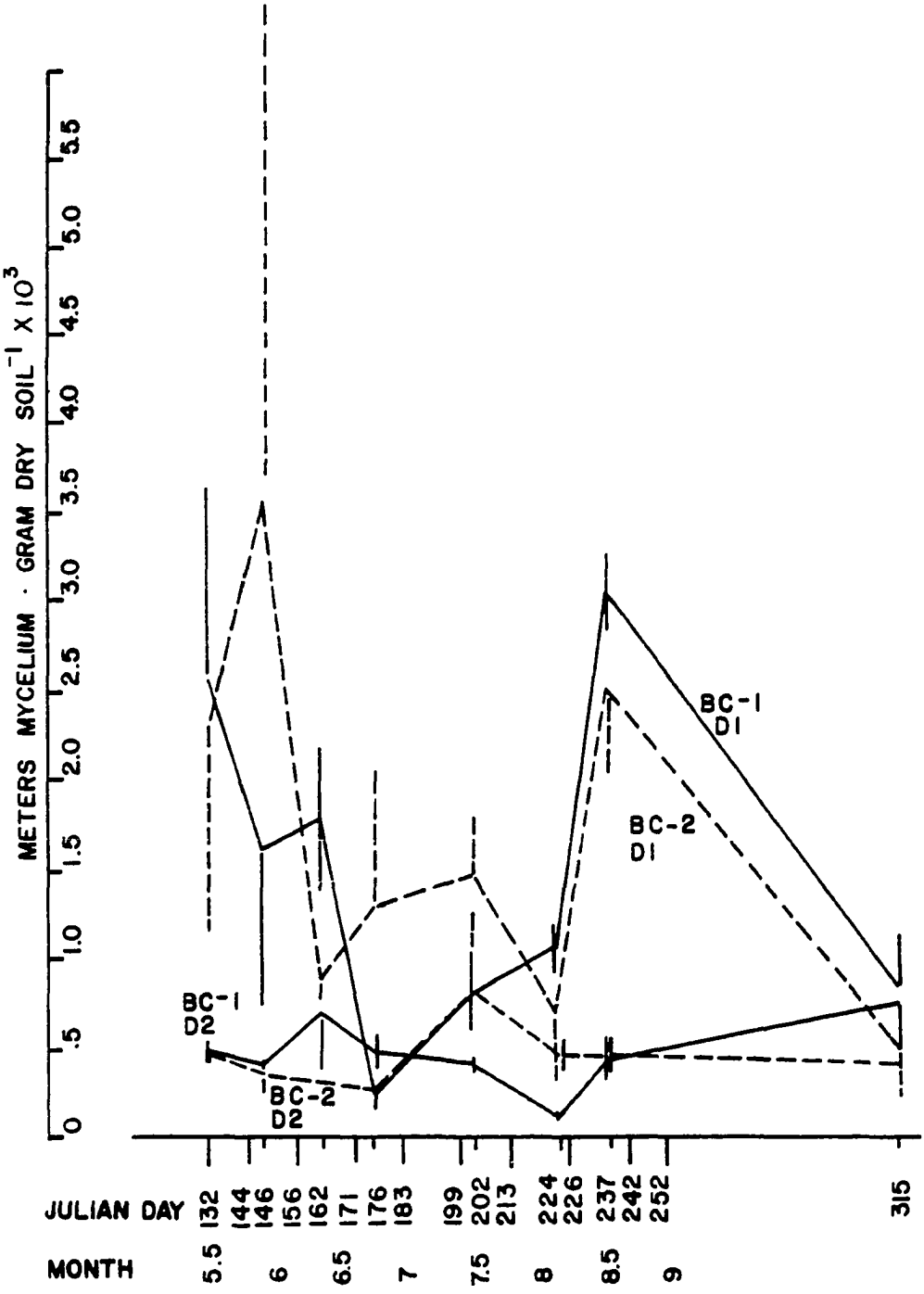


Figure 37. Fungal biomass by plot: Season 2, BC-1 = Birch Control - plot 1, BC-2 = Birch Control - plot 2, D1 = Depth 1 (1-2 cm), D2 = Depth 2 (6-7 cm).

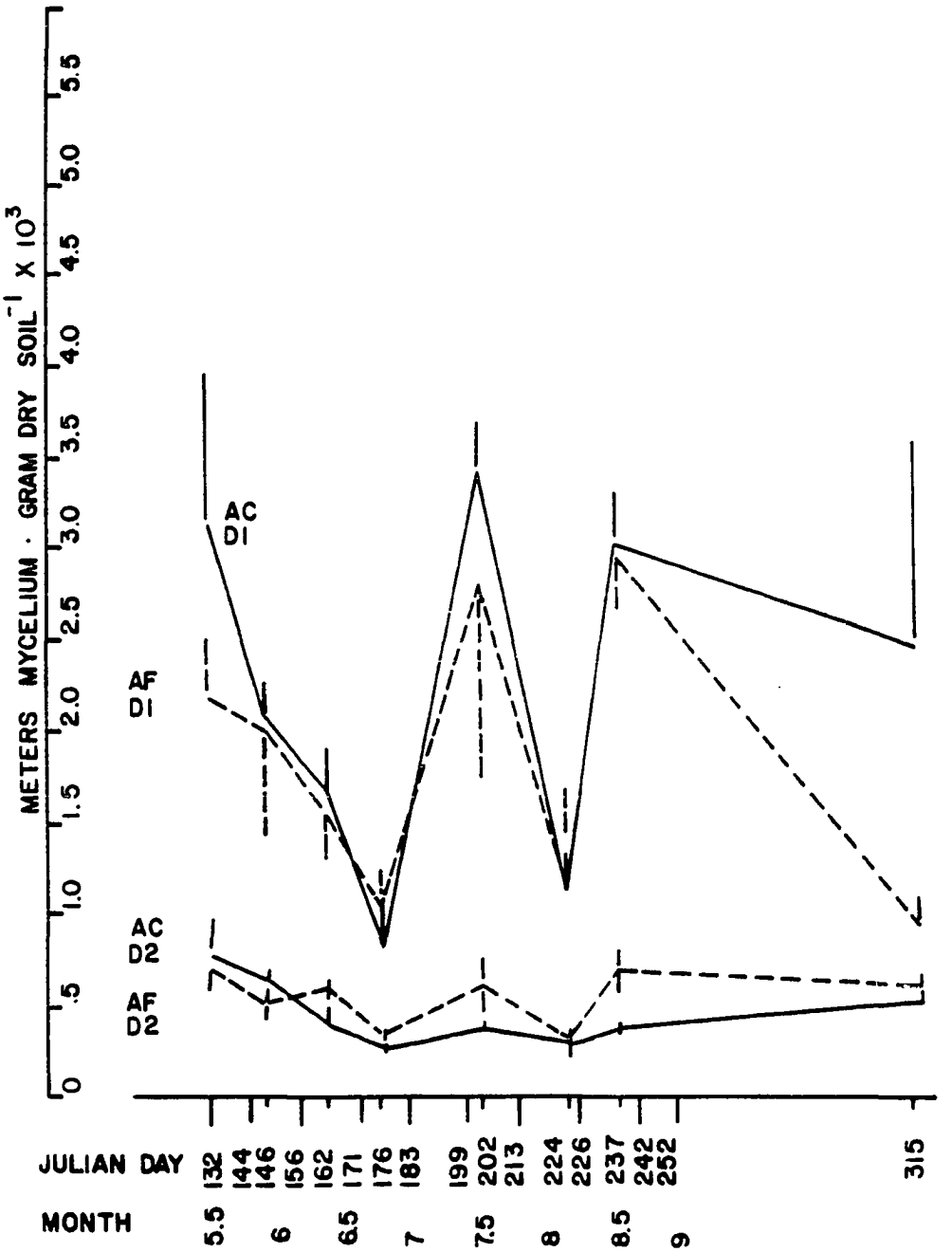


Figure 38. Fungal biomass by site: Season 2; AC = Aspen Control, AF = Aspen Fertilized, D1 = Depth 1 (1-2 cm), D2 = Depth 2 (6-7 cm).

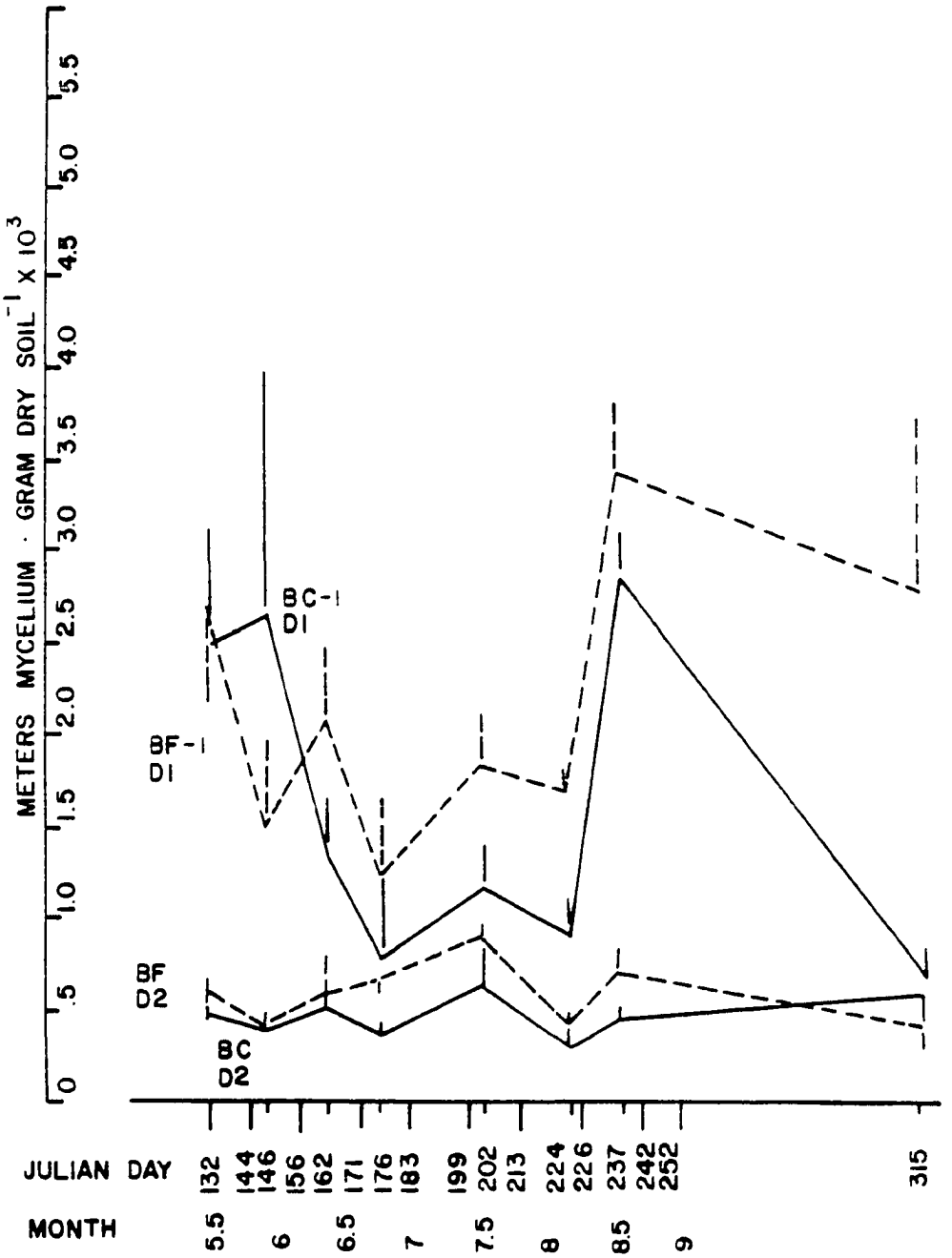


Figure 39. Fungal biomass by plot: Season 2; BC-1 = Birch Control - plot 1, BF-1 = Birch Fertilized - plot 1, D1 = Depth 1 (1-2 cm), D2 = Depth 2 (6-7 cm).

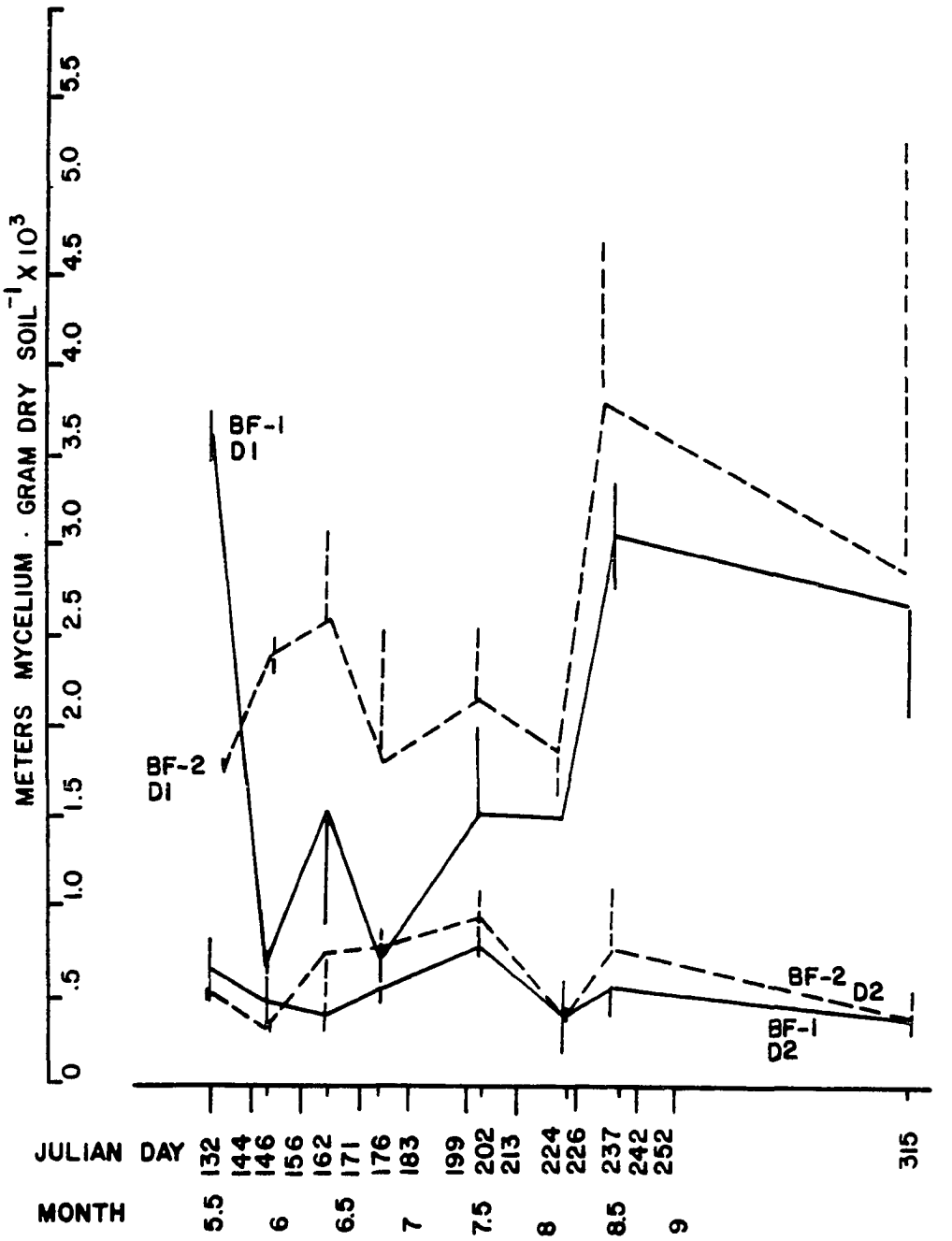


Figure 40. Fungal biomass by plot: Season 2, BF-1 = Birch Fertilized - plot 1, BF-2 = Birch Fertilized - plot 2, D1 = Depth 1 (1-2 cm), D2 = Depth 2 (6-7 cm).

1974 Birch Seasonality: $\alpha = .05$ (Figure 31)

1-2 cm soil depth

Mean 1 significantly greater than 9

Means 1 and 9 significantly greater than 2, 3, 4, 5, 6, 7, 8 and 10.

Mean 4 significantly less than all other means

Birch shows significant early (sample 1) and late season (sample 9) peaks. The mid season elevation of values (samples 5, 6 and 7) while not of the magnitude of samples 1 and 9, is greater than the season low (sample 4). As with aspen the first sample mean (2615 $m \cdot gm^{-1}$) is significantly greater than the final season mean (1274 $m \cdot gm^{-1}$).

6-7 cm soil depth

There is no significant difference in means for the 10 sample dates.

1975 Aspen Seasonality: $\alpha = .05$ (Figure 32)

1-2 cm soil depth

Means 1, 5 and 7 are not significantly different

Means 3 and 8 are not significantly different

Means 1, 5 and 7 are significantly greater than 3, 4, 6 and 8.

As for 1974, aspen shows three biomass peaks (early, mid and late field season) significantly greater than all other by sample date means. Again, sample one (2659 $m \cdot gm^{-1}$) is significantly greater than the final season biomass mean (1676 $m \cdot gm^{-1}$).

6-7 cm soil depth

There is no significant difference among means for the 8 sample dates.

1975 Birch Seasonality: $\alpha = .05$ (Figure 32)

1-2 cm soil depth

Means 1 and 7 are not significantly different

Means 3, 8 and 2 are not significantly different

Means 1 and 7 are significantly greater than 3, 4, 5, 6 and 8.

The seasonal fluctuation in biomass for 1975 is the same as for 1974. Birch shows significant early (sample 1) and late (sample 7) season biomass peaks. Although there is a mid season (sample 5) elevation in biomass the mean is not significantly different than samples 3, 4 and 6. As for 1974 aspen and birch and 1975 aspen, 1975 birch sample 1 mean (2667 $m \cdot gm^{-1}$) is significantly greater than the final season sample (1715 $m \cdot gm^{-1}$).

6-7 cm soil depth

There is no significant difference among means for the 8 sample dates.

The variability of biomass between plots within sites for 1974 is illustrated by Figures 33 and 34. Figures 35, 36, 37, 38, 39, and 40 show the degree of correspondence of within-site between-plot biomass for field season 2. Considering the varying degrees of ground cover, tree density, root biomass and potential for bulk density variation within sites, the by plots seasonal biomass graphs showed a surprising

degree of similarity, particularly for season 2. A by-year comparison of the seasonal graphs shows greater within-site variation for 1974 than for 1975, including the anomalous birch control plot #2 (Figure 34). Additionally, 1975 shows greater correspondence of peaks and troughs between depths within sites (correspondence of peaks and troughs between 1-2 cm and 6-7 cm soil depth) (Figures 35, 36, 38 and 39).

DISCUSSION:

Contribution of site microclimate to seasonal biomass fluctuations

Figures 41-44 address the relationship between fungal biomass and temperature by sample date. For 1974 at soil depth 1-2 cm, fungal biomass for dates 1 (May 12) and 9 (August 30) from both birch and aspen (Figure 41) correspond to the lowest soil temperatures recorded for the field sample period, 5^0C to 7^0C. It is interesting to note that the individual biomass measurements on these dates yielded seasonal biomass peaks, and that sample dates 7, 8 and 10 (bracketing the low temperature/high biomass values for sample 9) show an average decrease in biomass with an increase in temperature. The pattern is approximately the same for 1975 (Figure 43) at the 1-2 cm soil depth. In addition, elevated birch O1 layer temperatures (Figures 8 and 9) are not reflected in elevated biomass. In fact, the opposite is the case; birch is greater than aspen (1-2 cm) in soil temperature (Table 6-B) but aspen is significantly greater than birch in fungal biomass (Table 15-C). A comparison of biomass and temperature for both vegetation types at 6-7 cm soil depth (O22/A interface) for 1974 and to a lesser extent 1975, indicates

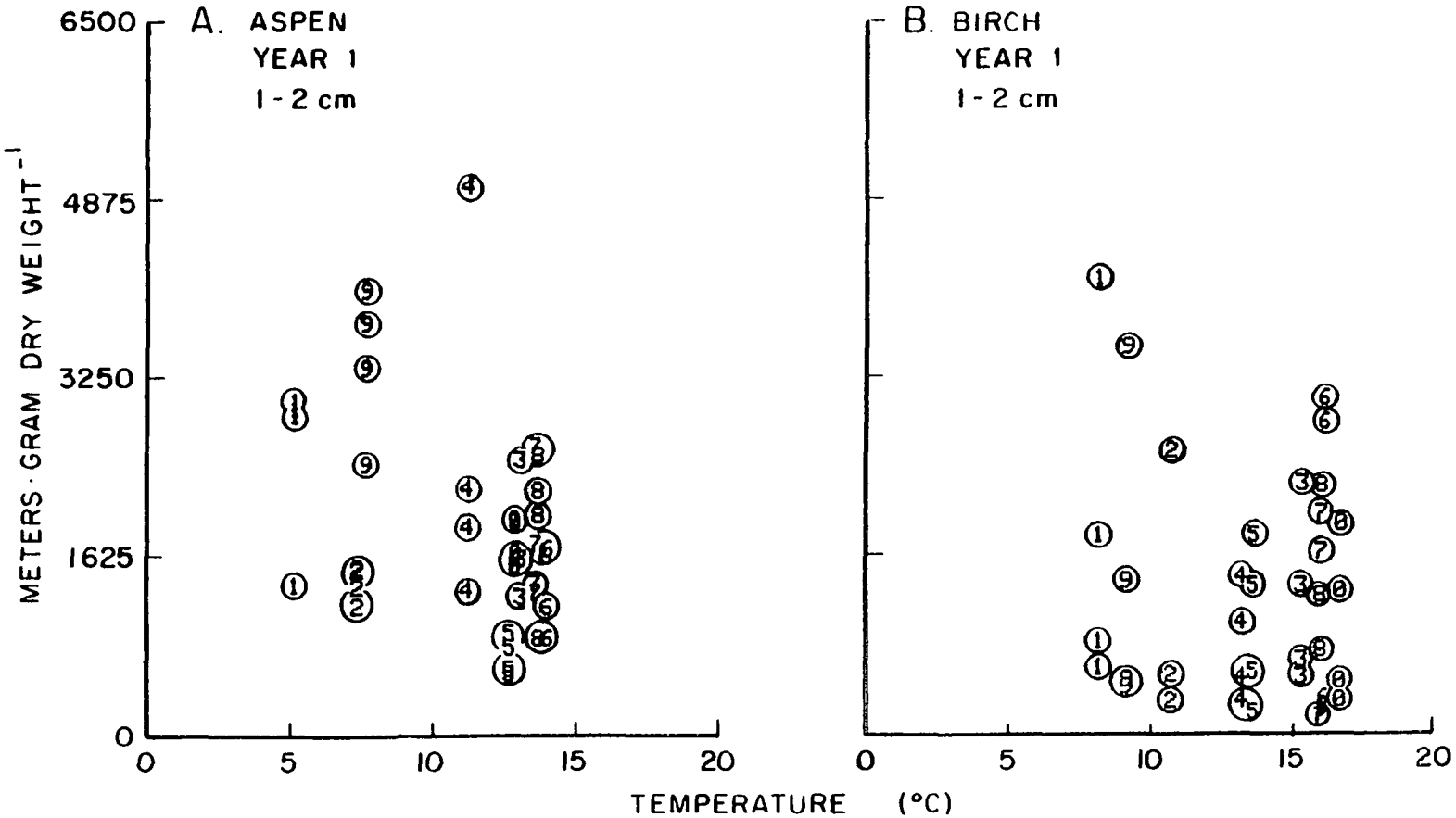


Figure 41. Fungal biomass and soil temperature: Circled data points 1-0 = sample dates 1 - 10.

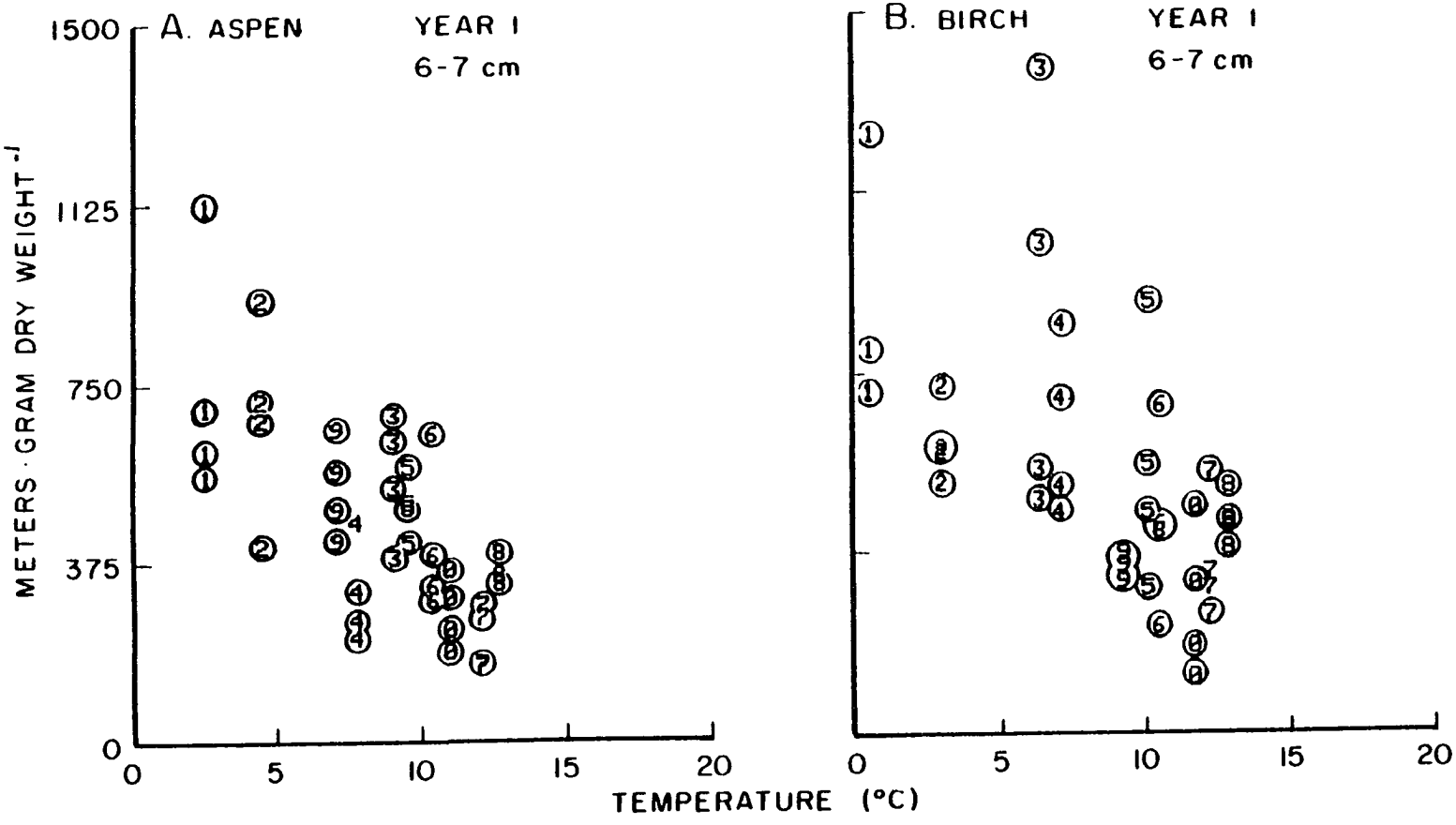


Figure 42. Fungal biomass and soil temperature: Circled data points 1-0 = sample dates 1 - 10.

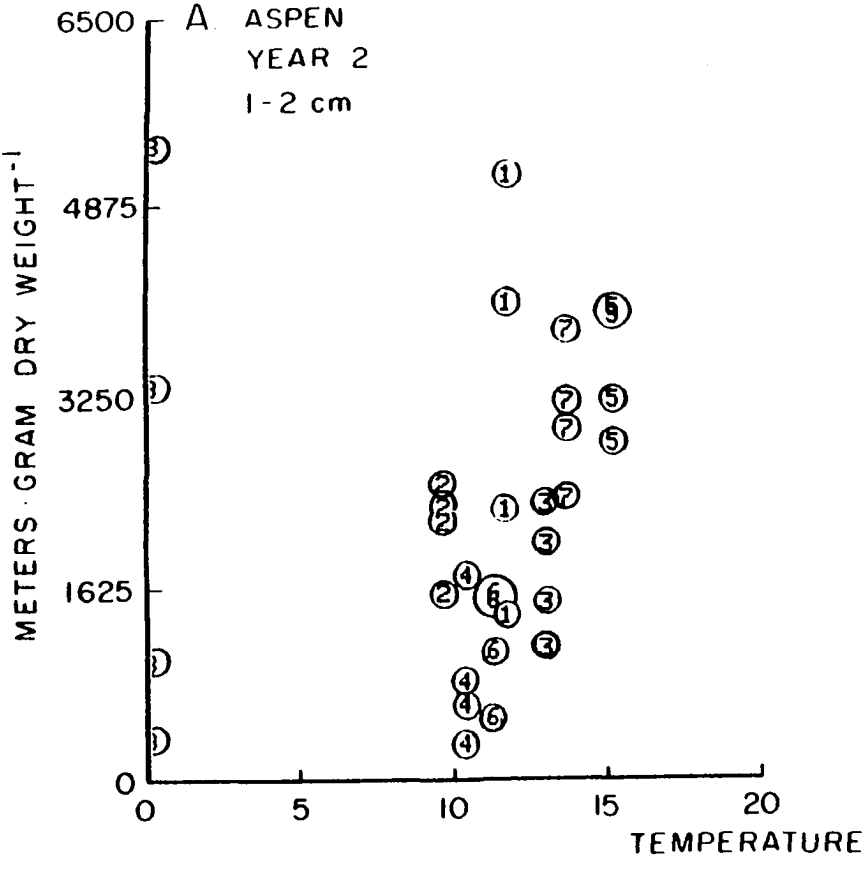
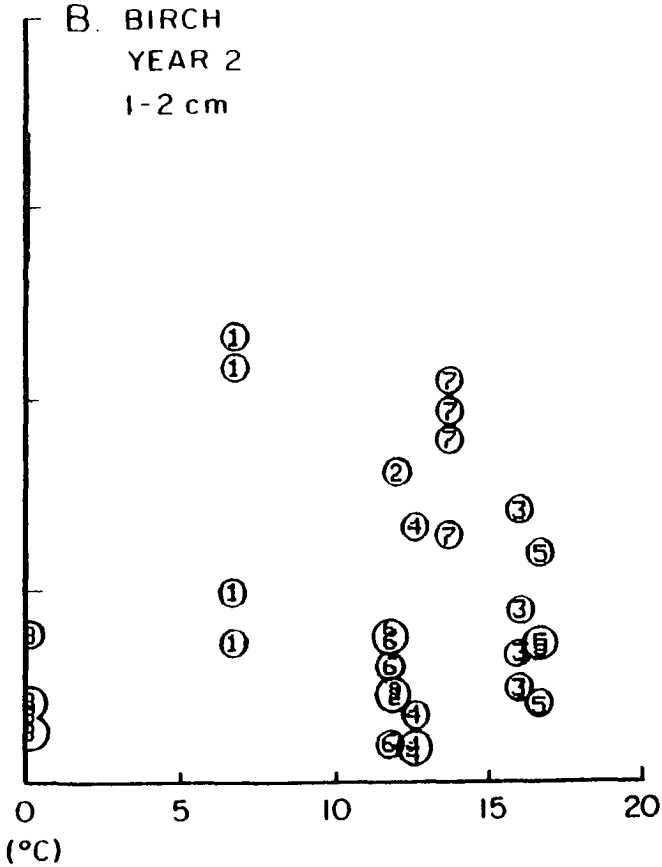


Figure 43. Fungal biomass and soil temperature: dates 1 - 8.



Circled data points 1-8 = sample

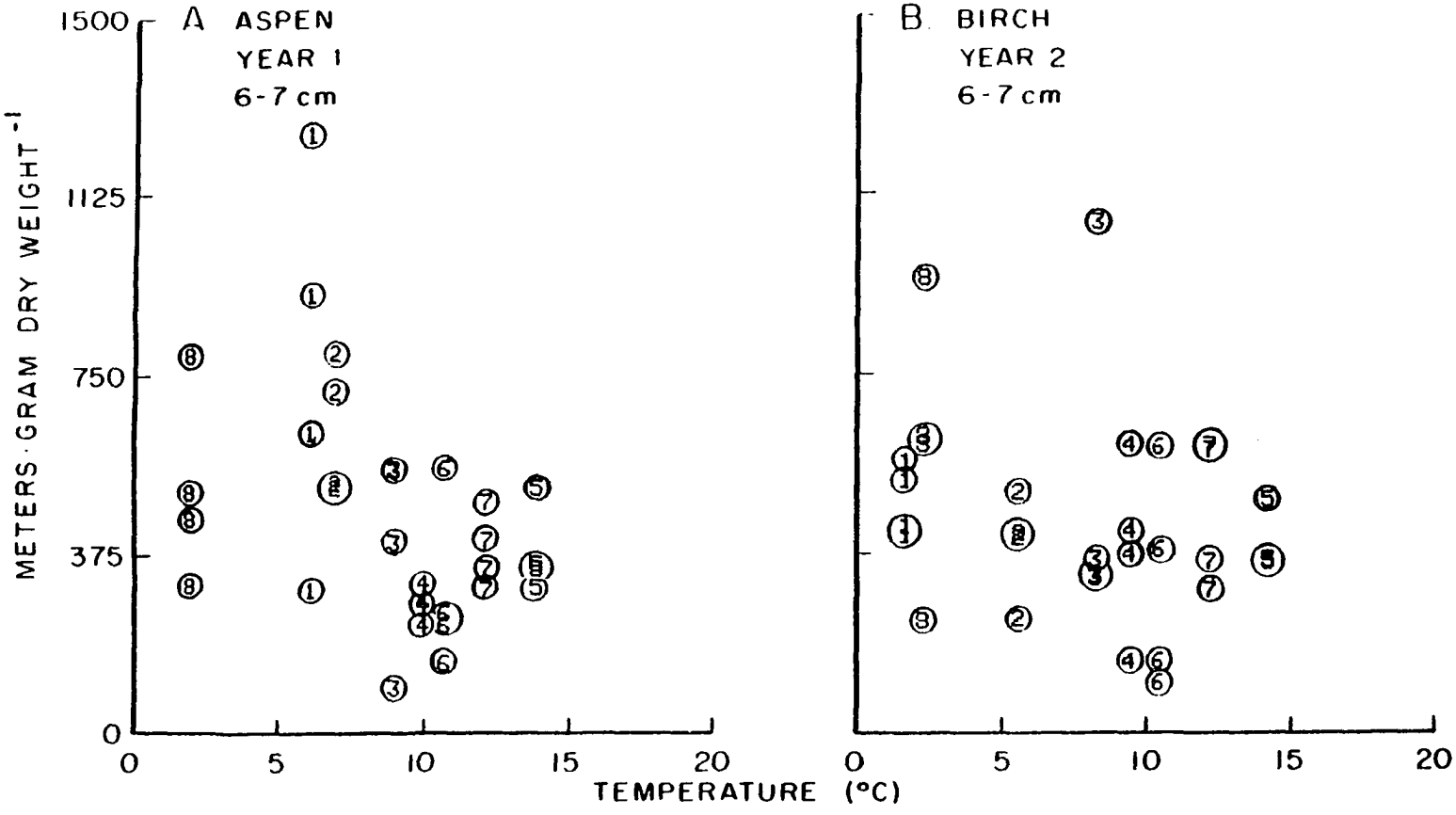


Figure 44. Fungal biomass and soil temperature: Circled data points 1-8 = sample dates 1 - 8.

Table 15. Fungal biomass (meters mycelium · gram day soil^{-1}), soil moisture (dry weight %) and bulk density (g · cc^{-1}) means.

Description	Sample N	DWT %	$S\bar{x}$	Bulk Density	$S\bar{x}$	Biomass	$S\bar{x}$
(A) By Year							
1974	224	66.0	3.5	.7300	.0310	1091	64
1975	224	94.7	3.5	.6620	.0310	1237	77
(B) By Depth							
1-2 cm	224	81.9	6.3	.2835	.0146	1821	77
6-7 cm	224	13.4	1.0	1.1217	.0200	508	16
(C) Site by Depth by Year							
1974 AC 1-2 cm	40	108.7	5.9	.2656	.0205	1836	154
AF 1-2 cm	40	114.5	8.2	.2386	.0816	1431	121
BC 1-2 cm	40	62.6	5.7	.6563	.0727	1190	160
BF 1-2 cm	40	95.7	7.2	.3075	.0202	1851	168
AC 6-7 cm	40	22.1	1.7	1.2076	.0260	450	33
AF 6-7 cm	40	21.0	1.5	1.1100	.0277	473	30
BC 6-7 cm	40	26.9	2.7	.9917	.0500	520	43
BF 6-7 cm	40	22.0	1.5	1.1133	.0216	481	26
1975 AC 1-2 cm	32	185.5	13.3	.2055	.0123	2208	238
AF 1-2 cm	32	193.2	13.0	.1889	.0057	1814	212
BC 1-2 cm	32	149.0	11.7	.2158	.0090	1529	240
BF 1-2 cm	32	175.2	12.8	.1982	.0087	2142	205
AC 6-7 cm	32	24.6	2.0	1.1151	.0229	440	43
AF 6-7 cm	32	32.9	1.7	.9852	.0429	530	42
BC 6-7 cm	32	28.1	2.2	1.1293	.0409	459	45
BF 6-7 cm	32	29.4	1.4	1.0630	.0272	581	50
(D) Site by Year							
AC-74	56	75.6	7.4	.738	.0691	1278	143
AC-75	56	98.8	12.4	.676	.0636	1303	165
AF-74	56	74.7	8.4	.734	.0649	994	100
AF-75	56	106.9	12.4	.620	.0603	1232	151
BC-74	56	50.4	4.5	.803	.0552	946	117
BC-75	56	81.9	9.7	.703	.0666	1082	159
BF-74	56	63.1	7.1	.727	.0587	1147	147
BF-75	56	91.3	9.6	.650	.0611	1331	140
(E) By Plot							
AC	112	49.8	7.7	.707	.047	1291	109
AF	112	53.8	8.0	.662	.044	1113	91
BC	112	41.1	6.2	.753	.043	1014	98
BF	112	46.0	6.4	.689	.042	1239	101
(F) Plot by Depth							
AC 1-2 cm	56	88.6	13.5	.230	.013	2111	143
AF 1-2 cm	56	92.1	14.0	.214	.008	1713	165
BC 1-2 cm	56	69.4	11.0	.428	.050	1517	100
BF 1-2 cm	56	77.6	11.3	.263	.016	1941	151
AC 6-7 cm	56	11.0	1.7	1.185	.020	470	117
AF 6-7 cm	56	15.5	2.2	1.109	.024	512	159
BC 6-7 cm	56	12.7	1.8	1.108	.036	511	147
BF 6-7 cm	56	14.3	2.5	1.115	.020	537	140

a negative correlation of biomass and temperature (Figures 42 and 44). Overall regression of biomass with temperature for 1974 (Table 16) gives a P-value of (.6056). The trend is approximately the same for 1975 (Table 17 non-significant P-value = .9711) although the partial T-test does not show a negative relationship.

These observations could be explained by any of the following:

(A) In the forest floor (O1, O21 and O22 horizons) early and end of season biomass was inversely related to soil temperature. Temperature decreases corresponded with biomass increases. From Figure 42, mineral soils for season 1 showed this relationship across the sample season: increasing temperature was correlated with decreasing biomass. The trend in mineral soils was similar but less pronounced in 1975.

(B) What appears to be a negative relationship between temperature and biomass, as noted in (A) above, is the result of lack of turnover of dead but undecomposed hyphae (the biomass method used did not distinguish viability status) at low soil temperatures so that biomass measurements made during low temperature periods contained a disproportionately large amount of dead but undecayed hyphae. In mineral soils there was a large amount of dead but undecayed hyphae at the beginning of the field season (post ground thaw) and the decomposition of this pool over time to a steady state yielded the negative relationship shown in Figure 42.

Table 16. Season One: Linear Regression

A. By Vegetation (Aspen and Birch)

Independent Variable	Seq. Prob. $\hat{Y}_2$ =	Dependent Variable estimates	Partial T-Test	P-Value
Bulk Desity	.0001	Meters Mycelium•gm^{-1}	-473.86	(.0414)
Moisture Percent	.0001	Meters Mycelium•gm^{-1}	1224.19	(.0014)
Soil Temperature	.2618	Meters Mycelium•gm^{-1}	-12.45	(.6056)
B.D. * DWT%	.9811	Meters Mycelium•gm^{-1}	25.39	(.9634)
DWT% * Soil Temp.	.8947	Meters Mycelium•gm^{-1}	-4.30	(.8947)

Total R^2 = .61

B. All Sites (AC, AF, BC, BF)

$\hat{Y}_2 = 743.27 - 472.37X_1 + 1009.36X_2 + 139.60X_4$

(.0001) (.0031) (.0001) (.7206) R^2 = .59

C. Biomass with soil moisture only (X)

1. All sites, all depths

   (Q) Log (m•gm^{-1}) = 5.950 (.0001) + 1.280 (.0001)X R^2 = .74

2. AC + AF (1-2 cm & 6-7 cm)

   (Q) Long ($\hat{m}$•gm^{-1}) = 5.919 (.0001) + 1.184 (.0001)X R^2 = .75

3. BC + BF (1-2 cm + 6-7 cm)

   $\hat{m}$•gm^{-1} = 88.494 (.2014) + 1770.157 (.0001)X R^2 = .88

4. By site by depth

   AC (1-2 cm): $\hat{m}$•gm^{-1} = 2.06.511 (.8122) + 1499.230

   (.0792)X R^2 = .34

AC (6-7 cm): $m \cdot gm^{-1} = 139.523\ (.1112) + 1404.560$
$(.0024)X$ $R^2 = .70$

AF (1-2 cm): $m \cdot gm^{-1} = 894.760\ (.0290 + 468.120$
$(.1278)X$ $R^2 = .27$

AF (6-7 cm): $m \cdot gm^{-1} = 299.983\ (.0036) + 825.370$
$(.0334)X$ $R^2 = .80$

BC (1-2 cm): $m \cdot gm^{-1} = 358.818\ (.2624) + 1328.059$
$(.0200)X$ $R^2 =$

BC (6-7 cm): $\hat{m} \cdot gm^{-1} = 187.275\ (.1005) + 1234.504$
$(.0066)X$ $R^2 = .62$

BF (1-2 cm): $\hat{m} \cdot gm^{-1} = 175.805\ (.6367) + 1749.786$
$(.0011)X$ $R^2 = .76$

BF (6-7 cm) $\hat{m} \cdot gm^{-1} = 415.992\ (.0038) + 296.065$
$(.5168)X$ $R^2 = .05$

All sites, all depths: (Q) Log $(\hat{m} \cdot gm^{-1}) = 5.950$
$(.0001) + 1.280\ (.0001)X$ $R^2 = .74$

Table 17. Season Two: Linear Regression

A. By Vegetation (Aspen and Birch)

Independent Variable	Seq. Prob.	Dependent Variable $\hat{Y}_2$ =	Partial T-Test estimates	P-Value
Bulk Density	(.0001)	Meters Mycelium·gm^{-1}	-597.13	(.1650)
Moisture Percent	(.0034)	Meters Mycelium·gm^{-1}	12.57	(.0588)
Soil Temperature	(.4067)	Meters Mycelium·gm^{-1}	2.05	(.9711)
B.C. * DWT%	(.5441)	Meters Mycelium·gm^{-1}	-4.83	(.7766)
DWT% * Soil Temp.	(.3660)	Meters Mycelium·gm^{-1}	-0.41	(.3660)

Total R^2 = .44

B. All Sites (AC, AF, BC, BF)

$\hat{Y}_2 = 1382.31 - 1053.39X_1 + 2.591X_2 + 7.798X_3$

(.0001) (.0001) (.0942) (.3244) R^2 = .38

C. Biomass with soil moisture only (X)

1. All sites, all depths

(Q) Log ($\hat{m}$·gm^{-1}) = 6.118 (.0001) + .0068 (.0001)X R^2 = .59

2. AC + AF (1-2 cm + 6-7 cm)

(Q) Log ($\hat{m}$·gm^{-1}) = 6.038 (.0001) + 00.71 (.0001)X R^2 = .66

3. BC + BF (1-2 cm + 6-7 cm)

Log ($\hat{m}$·gm^{-1}) = 6.193) (.0001) + .0066 (.0001)X R^2 = .52

4. By site by depth

AC (1-2 cm): $\hat{m}$·gm^{-1} = 253.17 (.7937) + 10.54

(.0692)X R^2 = .45

AC (6-7 cm): $\hat{m} \cdot gm^{-1}$ = 143.72 (.2446) + 12.04 (.0281)X R^2 = .58

AF (1-2 cm): $\hat{m} \cdot gm^{-1}$ = 894.76 (.0290) + 468.12 (.1278)X R^2 = .27

AF (6-7 cm): $\hat{m} \cdot gm^{-1}$ = 179.56 (.3461) + 10.66 (.0852)X R^2 = .41

BC (1-2 cm): $\hat{m} \cdot gm^{-1}$ = 2552.29 (.0278) - 6.44 (.2903)X R^2 = .18

BC (6-7 cm): $\hat{m} \cdot gm^{-1}$ = 276.32 (.0214) + 6.48 (.0725)X R^2 = .44

BF (1-2 cm): $\hat{m} \cdot gm^{-1}$ = 1269.16 (.1427) + 4.98 (.2638)X R^2 = .20

BF (6-7 cm): $\hat{m} \cdot gm^{-1}$ = 488.09 (.1811) + 3.16 (.7787)X R^2 = .01

All sites, all depths: (Q) Long ($m \cdot gm^{-1}$) = 6.118 (.0001) + .0068 (.0001)X R^2 = .59

(C) Fungal biomass was more closely correlated with some other environmental parameter, namely soil moisture, and within the confines of temperatures recorded during the field experiment, biomass responded to soil moisture fluctuations much more strongly than to fluctuations in soil temperature.

(D) A combination of conditions (A) & (C) was responsible for the temperature/biomass relationships shown in Figures 41-44.

It is not possible to assess the relative merits of any of these four statements without addressing the soil moisture status of the sites over time. Figures 45-49 are scatter plots of fungal biomass means at 1-2 cm and 6-7 cm soil depth for 1974 and 1975, plotted against soil moisture.

The relationship of fungal biomass and soil moisture percent is essentially linear for 1974 (Figures 45-A, 46-A, 47-A and 49-A). The composite soil moisture/biomass for 1975 (Figure 45-B) shows a non-linear scatter of points due, in part, to biomass observations of low magnitude at a soil moisture of 150% to 320% (the maximum soil moisture for 1974 was approximately 200%), and a broader scatter of biomass values between 75% and 150%. It was noted in the main effects discussion of soil moisture (Tables 9 - 13) that 1975 was significantly greater (α = .0010) than 1974 in overall soil moisture.

The trend of a more linear relationship of biomass and soil moisture for 1974 in comparison to 1975 is pointed out in Figure 45 through 49 for all vegetation types and treatments by sample depth. Site AF

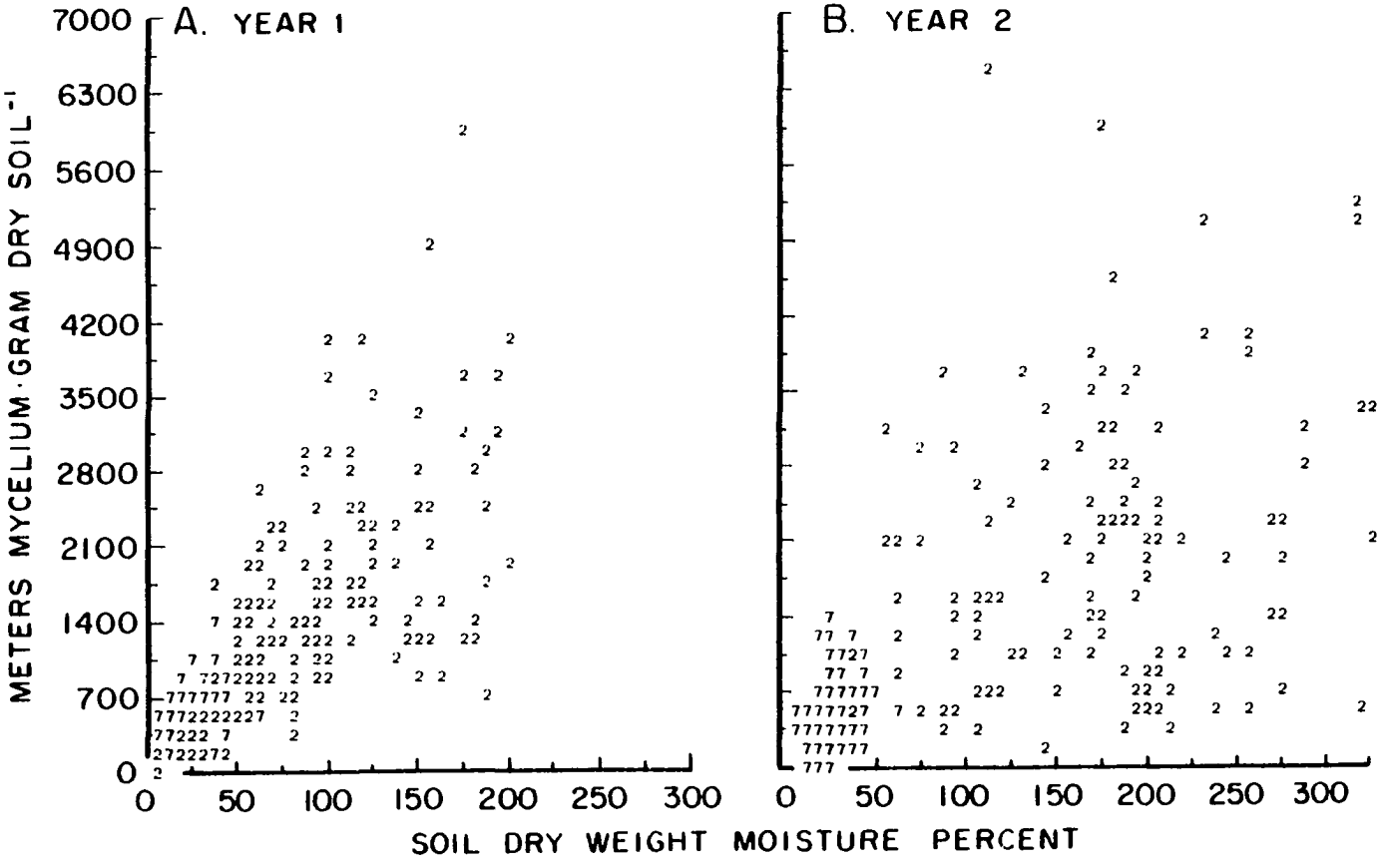


Figure 45. Fungal biomass and soil moisture by year: 2 = 1-2 cm below forest floor surface (01 - 021 horizon interface), 7 = 6-7 cm below forest floor surface (022 - A horizon interface).

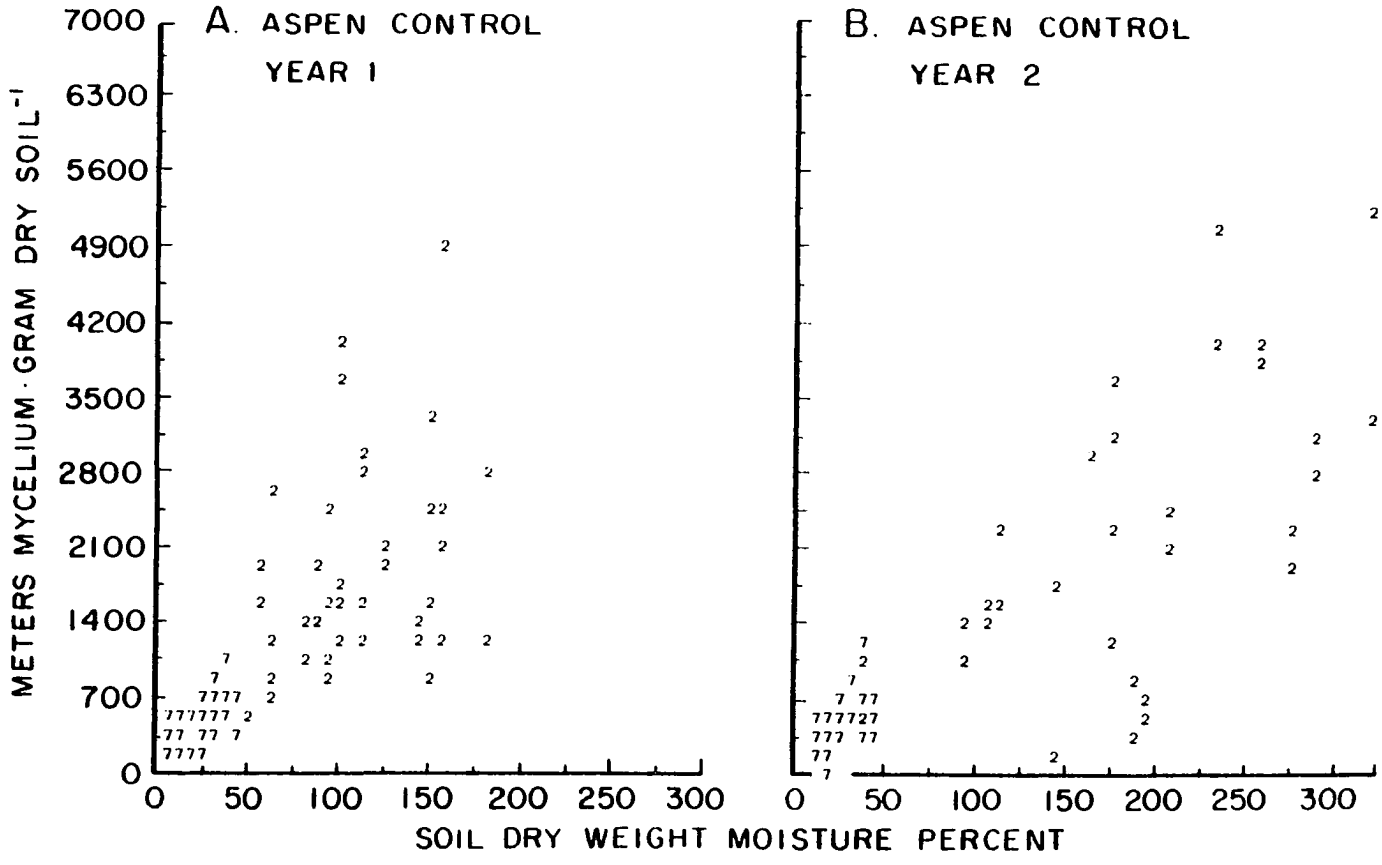


Figure 46. Fungal biomass and soil moisture by site: 2 = 1-2 cm below forest floor surface (01 - 021 interface), 7 = 6-7 cm below forest floor surface (022 - A interface).

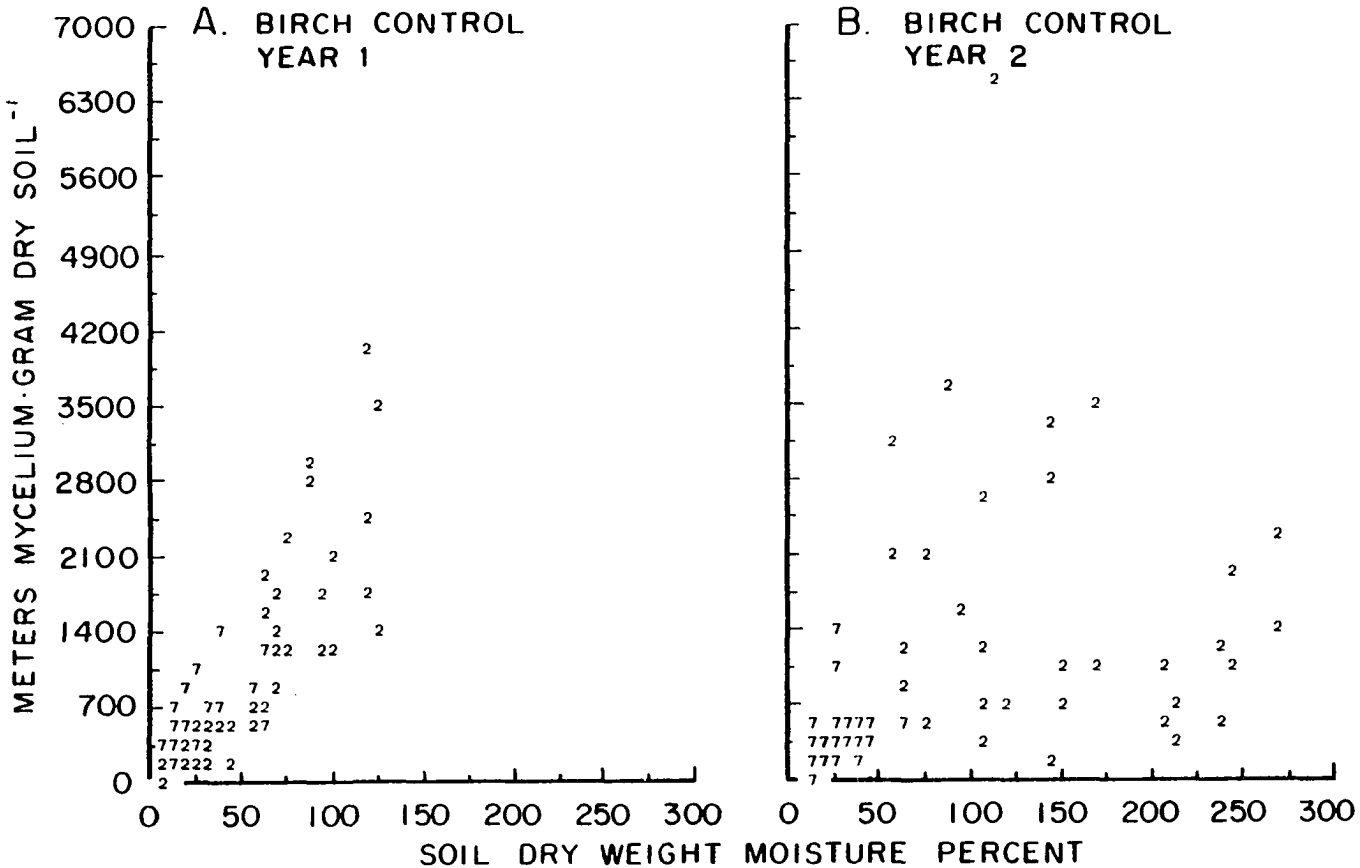


Figure 47. Fungal biomass and soil moisture by site: 2 = 1-2 cm below forest floor surface (01 - 021 horizon interface), 7 = 6-7 cm below soil surface (022 - A horizon interface).

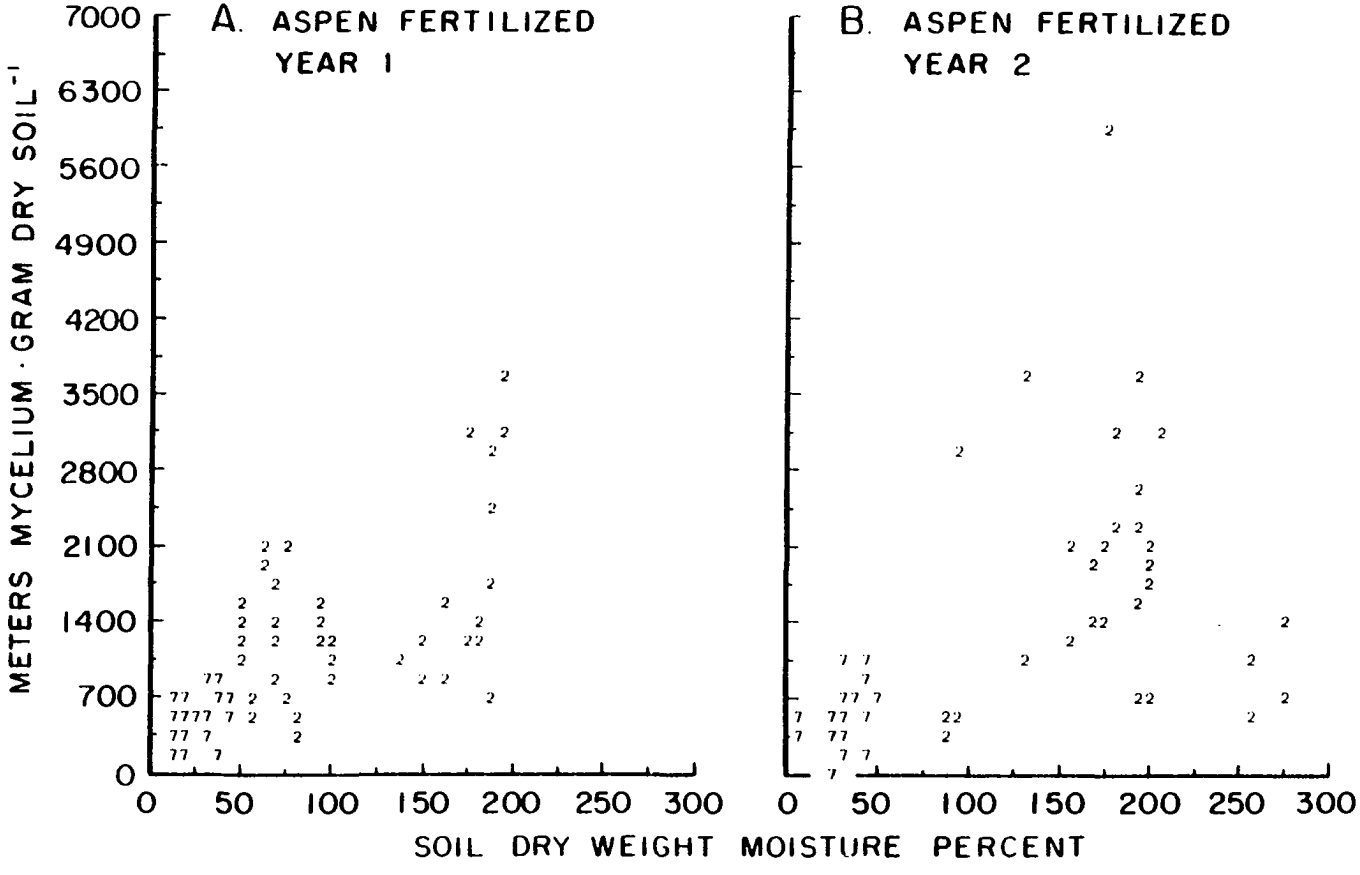


Figure 48. Fungal biomass and soil moisture by site: 2 = 1-2 cm below forest floor surface (01 - 021 horizon interface), 7 = 6-7 cm below forest floor surface (022 - A horizon interface).

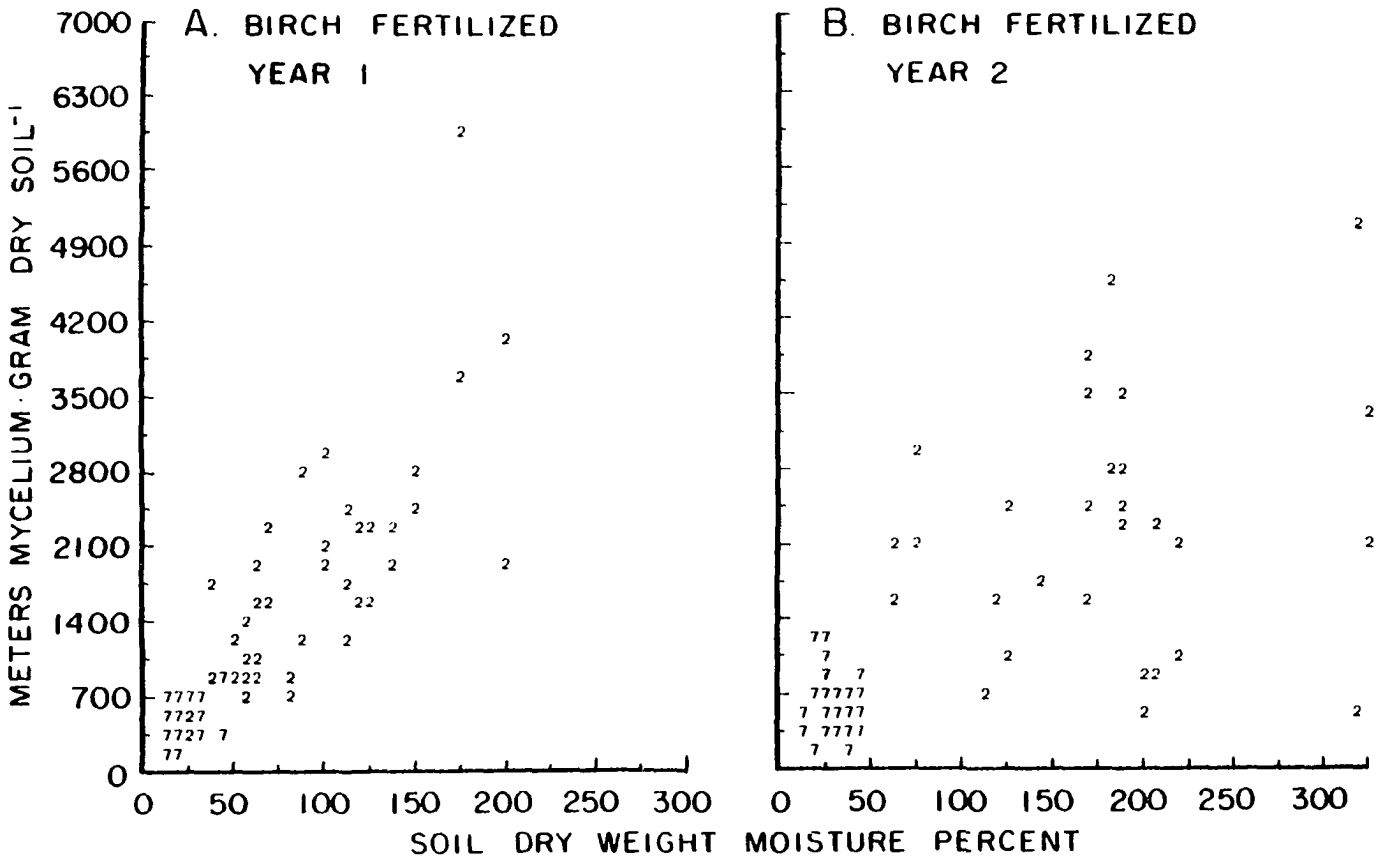


Figure 49. Fungal biomass and soil moisture by site: 2 = 1-2 cm below forest floor surface (01 - 021 horizon interface), 7 = 6-7 cm below forest floor surface (022 - A horizon interface).

(Figure 48) shows the greatest spread of points for any site in 1974 and site AC (Figure 46) shows the strongest linear relationship of any site in 1975. Some insight into these specific site differences can be gained by comparing Figures 46-B (AC-1975), 48-A (AF-1974) with Table 15, section C. Site AF-1974 was greatest in soil moisture of any site (114.5%) at the 1-2 cm soil depth and ranked third of the 4 sites (less than AC and BF) in biomass with several low biomass/high soil moisture points contributing to the spread. From Table 16 (Season 1 Regression) part C.4, site AF shows the lowest R^2 (.27) of any site at the 1-2 cm soil depth. Conversely, site AC for 1975 is lowest of all sites in soil moisture and biomass at the 6-7 cm soil depth, intermediate in soil moisture at the 1-2 cm soil depth and greatest in fungal biomass. Table 17 (Season 2 Regression) shows that site AC has the highest R^2 values (R^2 = .45 for 1-2 cm; R^2 = .58 for 6-7 cm) for both depths of any site. Table 18 gives R^2 values and significance levels for moisture and bulk density regression with biomass by sample date.

A comparison of Figures 46-A and 47-A (aspen and birch for 1974, respectively) shows that aspen site values for the 1-2 cm soil depth in the moisture range of 130% to 180% contribute to the scatter of the overall year figure (Figure 45-A). There were no comparable values from birch sites for this range. Figures 50 through 54 illustrate the relationship between biomass and bulk density by depth, Figures 55 and 56 give soil moisture ranges for biomass means plotted against bulk density. Comparison of Figure 51-A and 52-A, biomass vs bulk density for aspen control and birch control, respectively, show that for aspen

Table 18. Fungal biomass: Bulk density ($g \cdot cc^{-1}$) and soil moisture (DWT %) regression by sample date

	Sample No.	P Statistic For		
A	Season One	Bulk Density	Moisture %	R^2
	1	(.3220)	(.2113)	.49
	2	(.9963)	(.2365)	.50
	3	(.8113)	(.0624)	.62
	4	(.2004)	(.0001)	.80
	5	(.6526)	(.0078)	.67
	6	(.8883)	(.0060)	.65
	7	(.0874)	(.3249)	.78
	8	(.4709)	(.0223)	.67
	9	(.4076)	(.0878)	.69
	10	(.3382)	(.1050)	.66
B	Season Two			
	1	.9290	.0373	.66
	2	.5093	.6792	.36
	3	.1176	.9699	.52
	4	.0645	.6427	.21
	5	.5491	.3594	.46
	6	.3680	.3252	.42
	7	.0616	.5831	.88
	8	.0236	.0005	.50

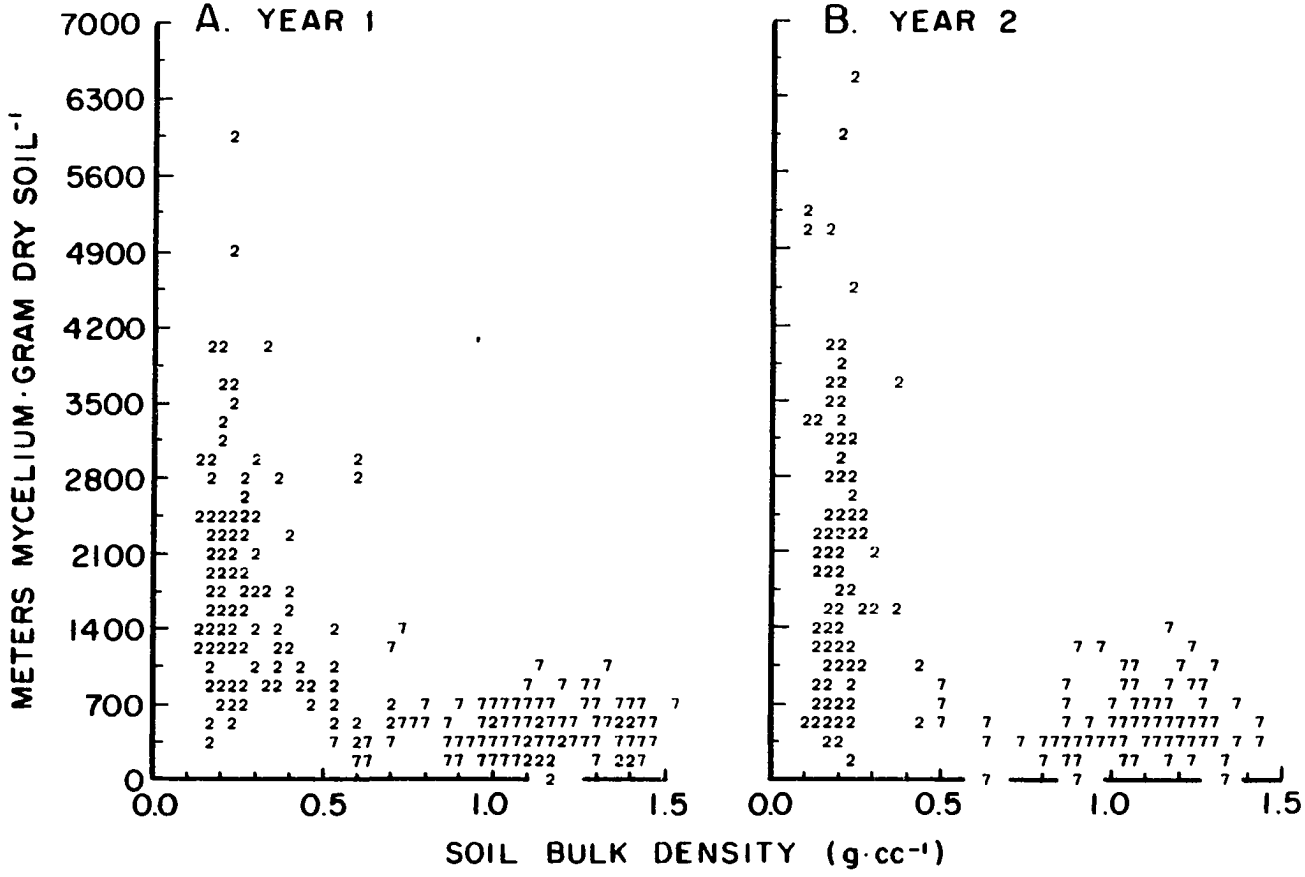


Figure 50. Fungal biomass and soil bulk density: Overall relationship by year; 2 = 1-2 cm below forest floor surface (01 - 021 horizon interface), 7 = 6-7 cm below forest floor surface (022 - A horizon interface).

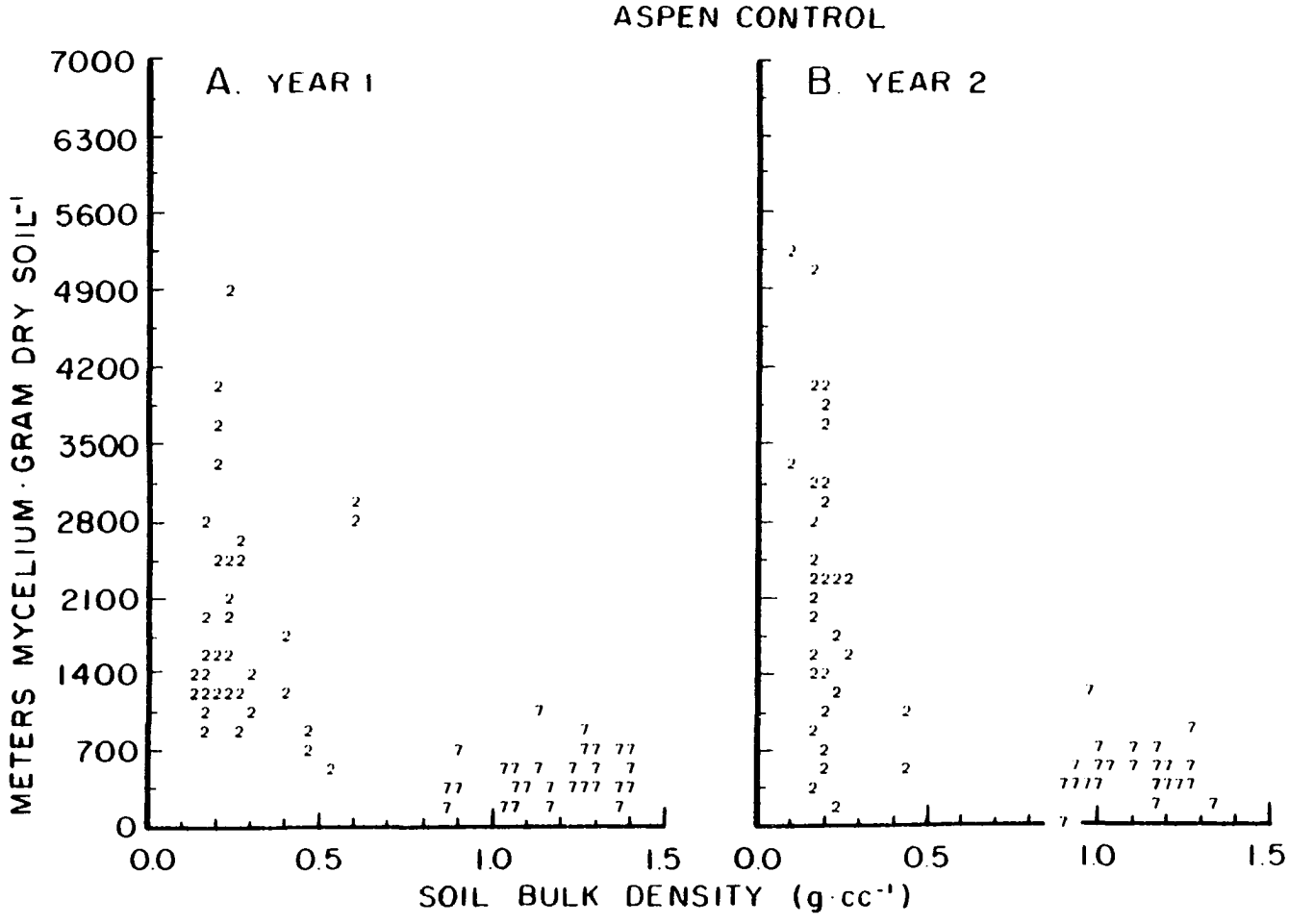


Figure 51. Fungal biomass and soil bulk density by site: 2 = 1-2 cm below forest floor surface (01 - 021 horizon interface), 7 = 6-7 cm forest floor surface (022 - A horizon interface).

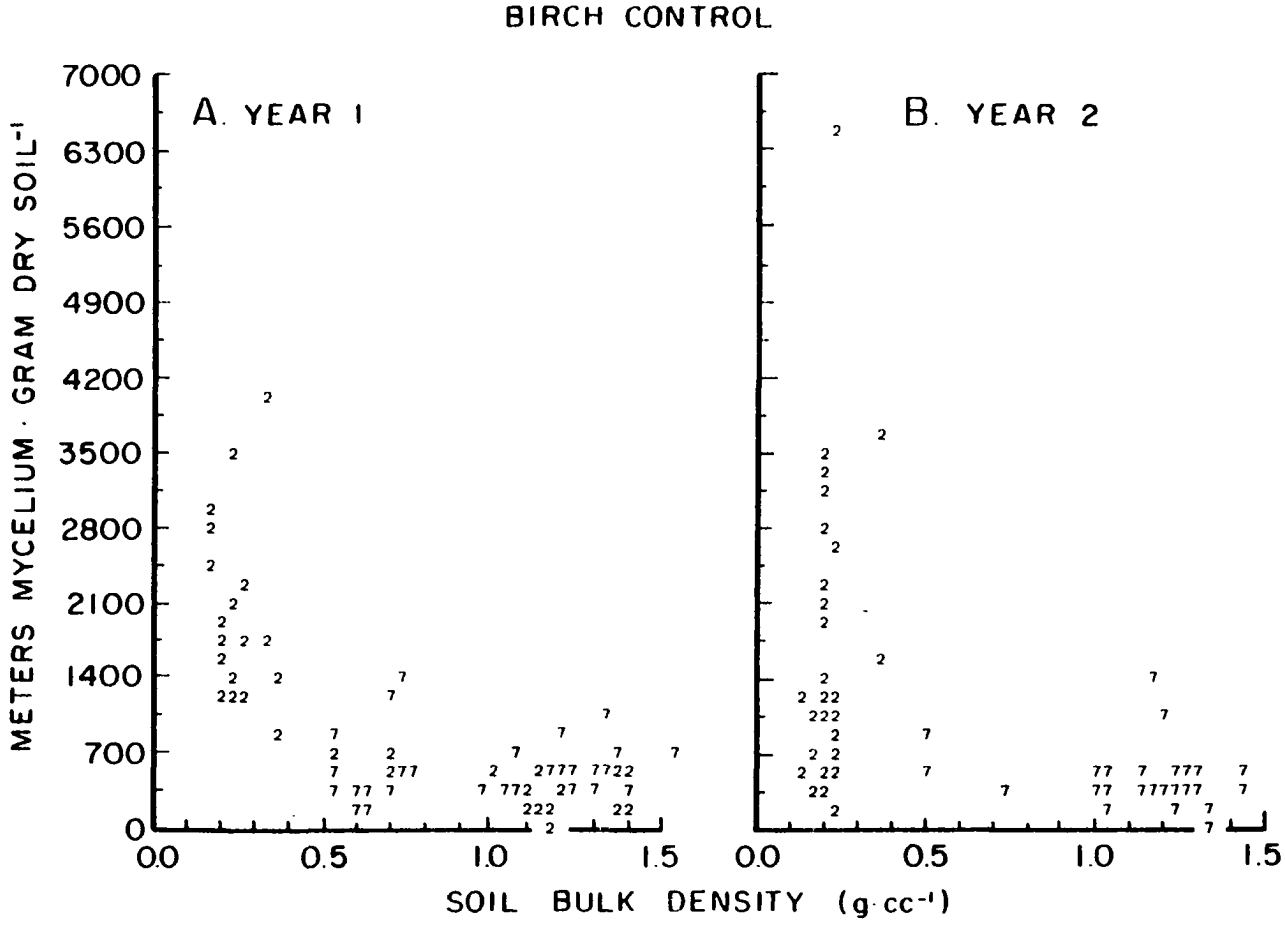


Figure 52. Fungal biomass and soil bulk density by site: 2 = 1-2 cm below forest floor surface (01 - 021 horizon interface), 7 = 6-7 cm below forest floor surface (022 - A horizon interface).

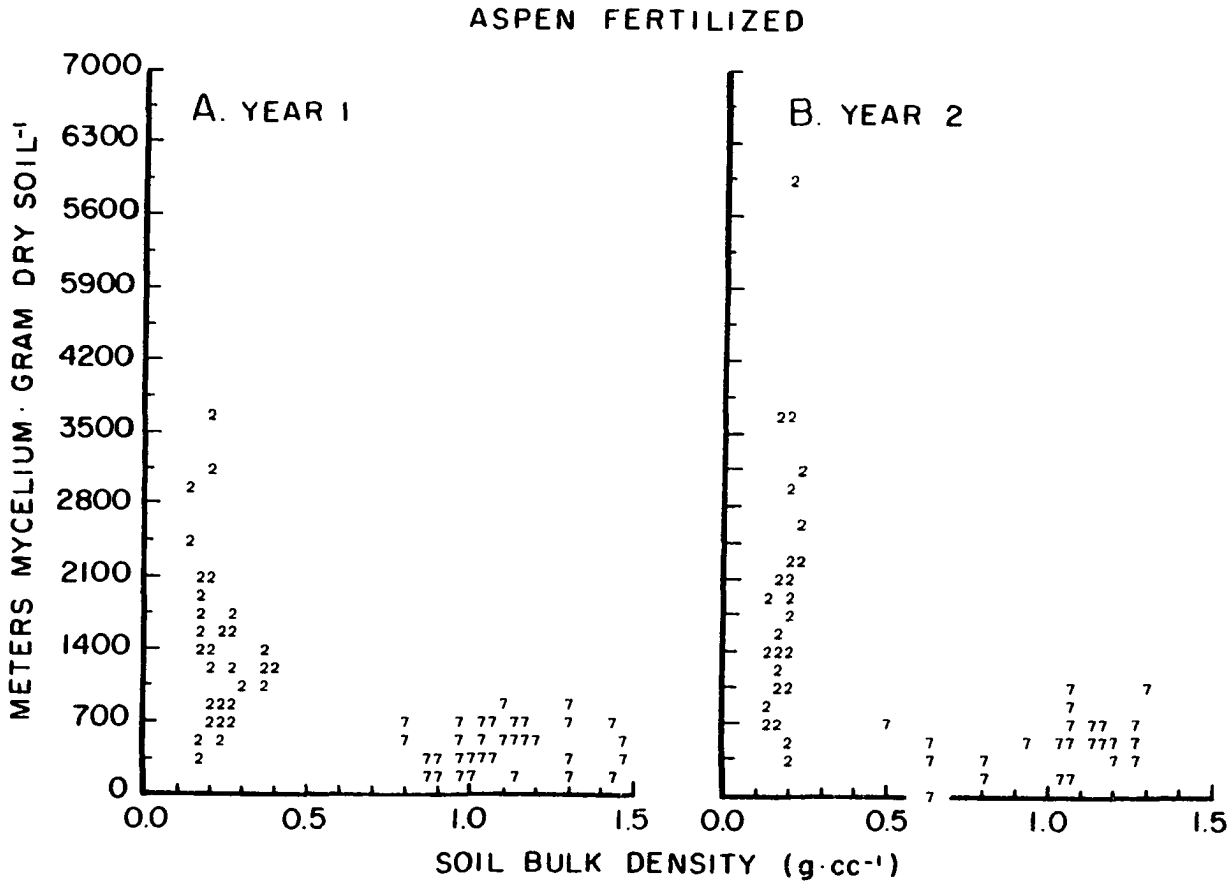


Figure 53. Fungal biomass and soil bulk density by site: 2 = 1-2 cm below forest floor surface (01 - 021 horizon interface), 7 = 6-7 cm below forest floor surface (022 - A horizon interface).

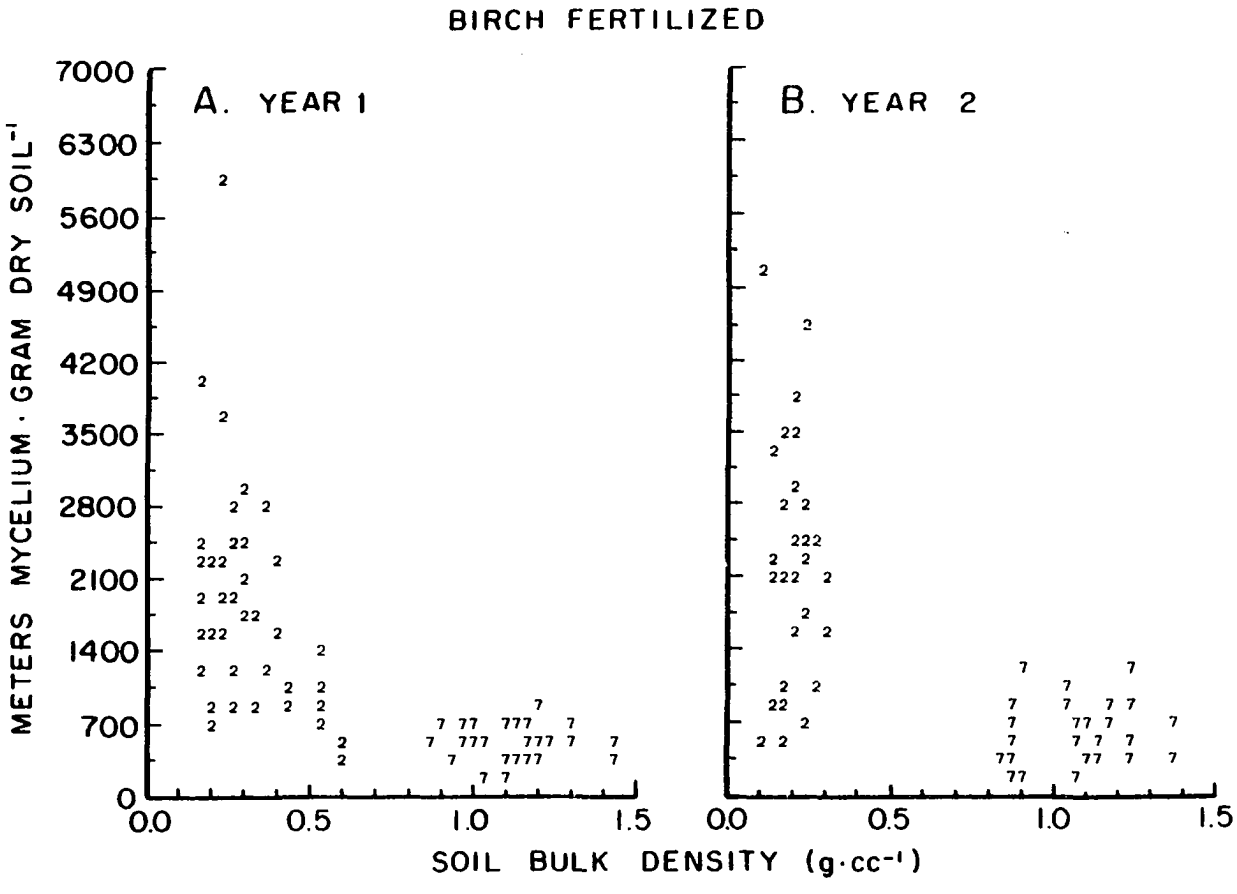


Figure 54. Fungal biomass and soil bulk density by site: 2 = 1-2 cm below forest floor surface (01 - 021 horizon interface), 7 = 6-7 cm below forest floor surface (022 - A horizon interface).

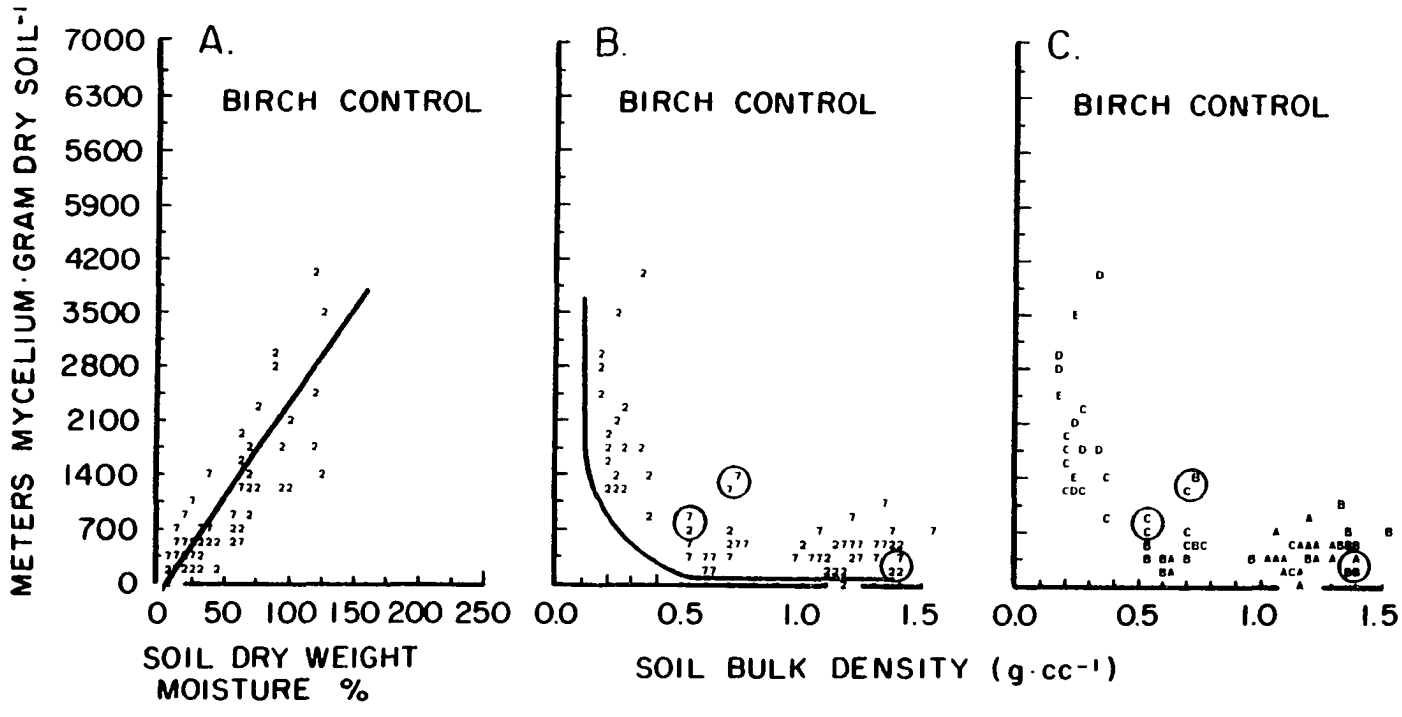


Figure 55. Birch Control Fungal Biomass (2 = 1-2 cm soil depth, 7 = 6-7 cm soil depth): (A.) vs soil moisture; (B.) vs soil bulk density; (C.) vs soil bulk density with corresponding soil moisture class for each biomass data point. Soil moisture classes: A = 0-20%, B = 21-40%, C = 41-80%, D = 81-120%, E = 121-160%, F = 161-200%, G = 201-240% and H = 241-405%.

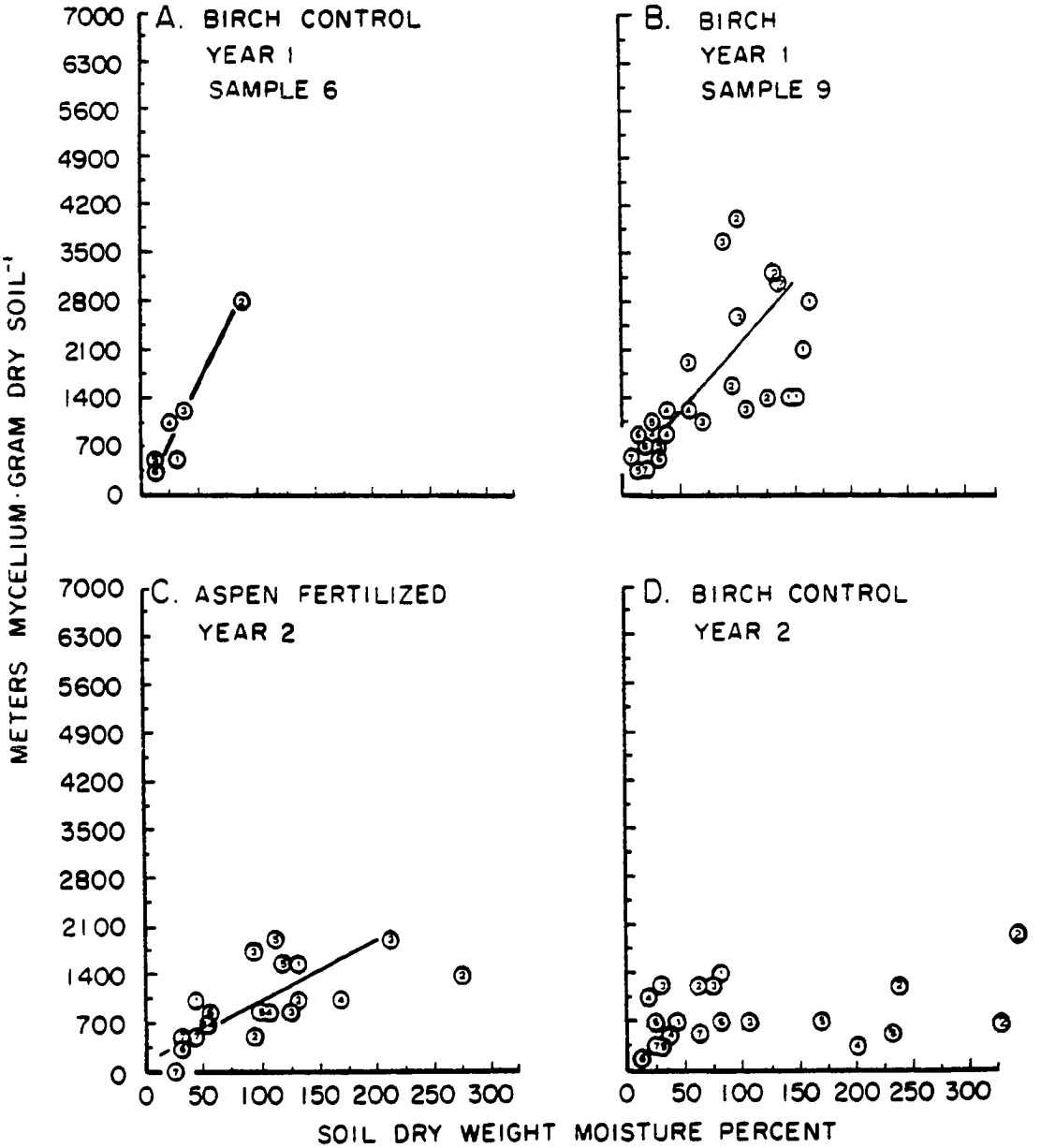


Figure 56. Fungal biomass vs soil moisture: Level II Profile samples by site, by date; Data points 1 = soil depth 0-1 cm, 2 = 1-2 cm, 3 = 2-3 cm, 4 = 3-4 cm, 5 = 4-5 cm, 6 = 5-6 cm, 7 = 6-7 cm, (measurements in 1 cm increments from forest floor surface through 7 cm depth).

sites at a bulk density of .55 to .80 there were no biomass observations. However, birch for the same rank shows a group of points attributable to birch 1-2 cm and 6-7 cm means (the previously discussed anomalous plots). This group of means with a bulk density of .50 to .80 and a fungal biomass of 280 to 1500 $m \cdot gm^{-1}$, shown in Figure 55, have a moisture range of < 20% to 80%. In plotting mean biomass values against soil moisture percent, this group of low to intermediate biomass points - at a low moisture percent - tightens the spread of birch biomass points (Figure 46-A) in comparison to aspen (Figure 47-A).

From Figure 50 (A and B) it can be noted that fungal biomass means for the 1-2 cm soil depth show less spread in bulk density for 1975 (Table 15). Individual by-site comparisons (Figures 51-54) confirm this observation for all sites. The difference is due to greater variation of 01-021 soil horizon bulk densities in 1974, with a marginally significant year effect (P = .0570) of: 1974 ($\overline{X}$ = .7300 $g \cdot m^2$) greater than 1975 ($\overline{X}$ = .6620 $g \cdot m^2$, Table 16). The reason for the narrowing of bulk density reanges for 1975 1-2 cm soil depth remains unclear.

Soil Profile (Forest Floor Surface - 7 cm depth) Biomass

The degree of relative linearity of the relationship between biomass and soil moisture for 1974 (Figures 45-A; R^2 = .74, Table 16) and low biomass/moisture correlation for 1975 (Firgure 45-B; R^2 = .38, Table 17) is further illustrated by profile sample data for both seasons (Figure 56). 1974 profile biomass means, charted by vegetation type, treatment or sample data (Figure 56A-B, are consistent with the trends noted in Figure 45-A and Table 16. Although inclusion of data from 01,

O22 and A horizons for 1975, strengthened the correlation of biomass and moisture in some cases (Figure 56-C), the overall trend reflected low correlation due to relatively low biomass means from samples high (in comparison to 1974 figures) soil moisture (Figure 56-D).

Plotting biomass against soil bulk density gives a sine wave pattern characteristic of all sites and sample dates for 1974 (Figures 57-60). In all cases, soil depth 1-2 cm or 2-3 cm below the soil surface (O21 horizon) were greatest in biomass.

Although the characteristic sine wave pattern of biomass vs bulk density was evident in isolated cases for 1975 (Figure 61), the overall trend for the profile samples did not show an increase in biomass for the O21 layer as in 1974. For 1975, with more favorable O1 horizon soil moisture, the forest floor litter layer was greatest in biomass in a number of cases, illustrated by Figures 62 and 63. Figure 64, profile biomass for day 315 (November 12) taken after snowfall and ground freeze shows a rapid decline in biomass (and bulk density) for depths 2 through 5 in contrast to a more typical (late August) distribution of biomass and bulk density (Figure 65).

Composite Comparisons: Fungal Biomass, Temperature and Moisture

Figures 66-73 are comparisons of seasonal standing crop fungal biomass and seasonal temperature and moisture cycles by site (AC, AF, BC, BF) for soil depth 1-2 cm for 1974 and 1975, respectively. In seven of eight cases (all comparisons excluding 1974 aspen fertilized, Figure 71) initial biomass measurements are followed by a drop in biomass over

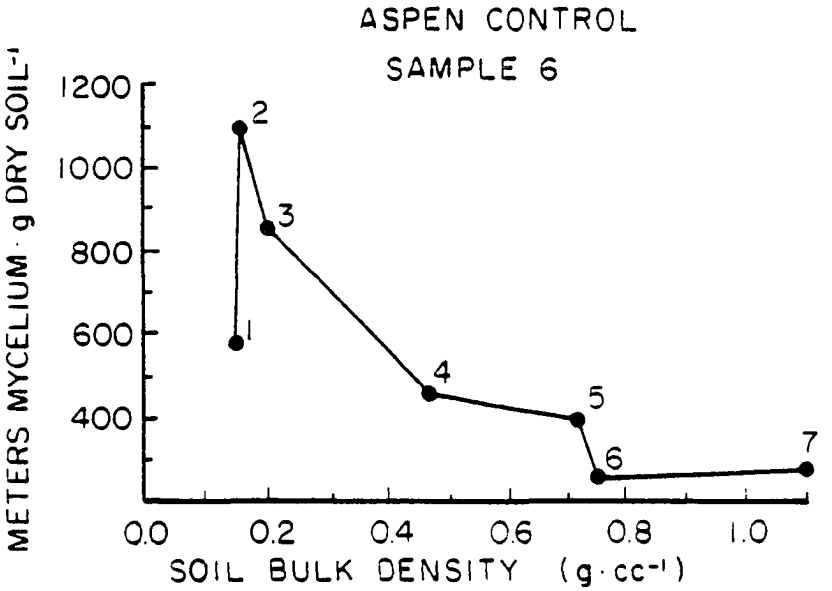


Figure 57. Level II biomass profile: 1 = soil depth 0-1 cm, 2 = 1-2 cm, 3 = 2-3 cm, 4 = 3-4 cm, 5 = 4-5 cm, 6 = 5-6 cm, 7 =6-7 cm.

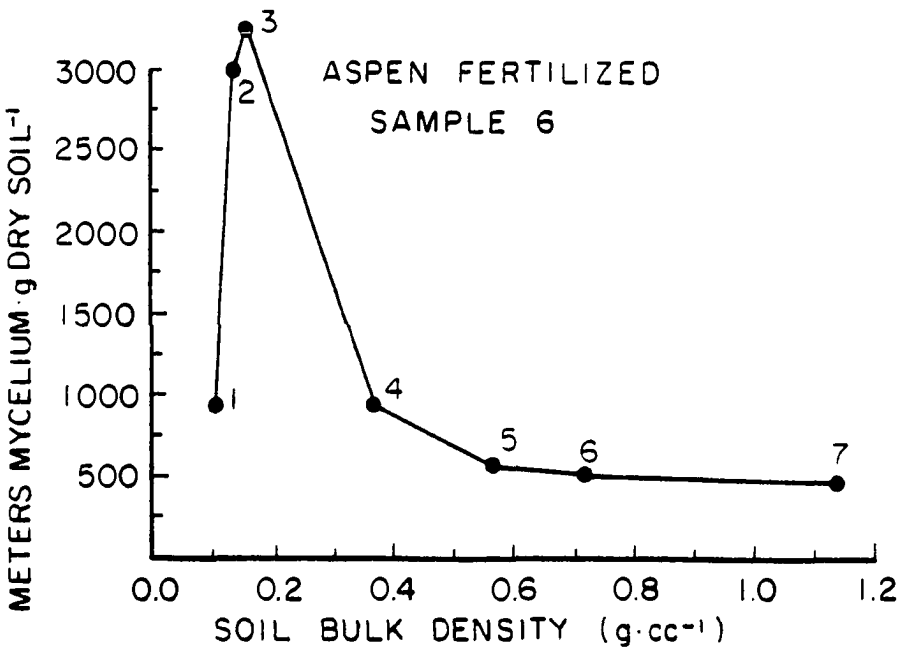


Figure 58. Level II biomass profile: Forest floor surface through 7 cm in 1 cm increments (1-7).

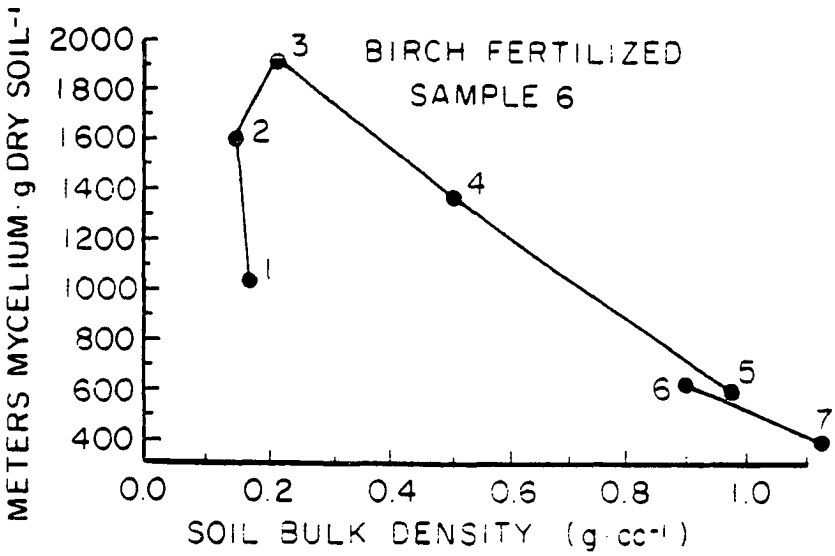


Figure 59. Level II biomass profile. Forest floor surface through 7 cm in 1 cm increments (1-7).

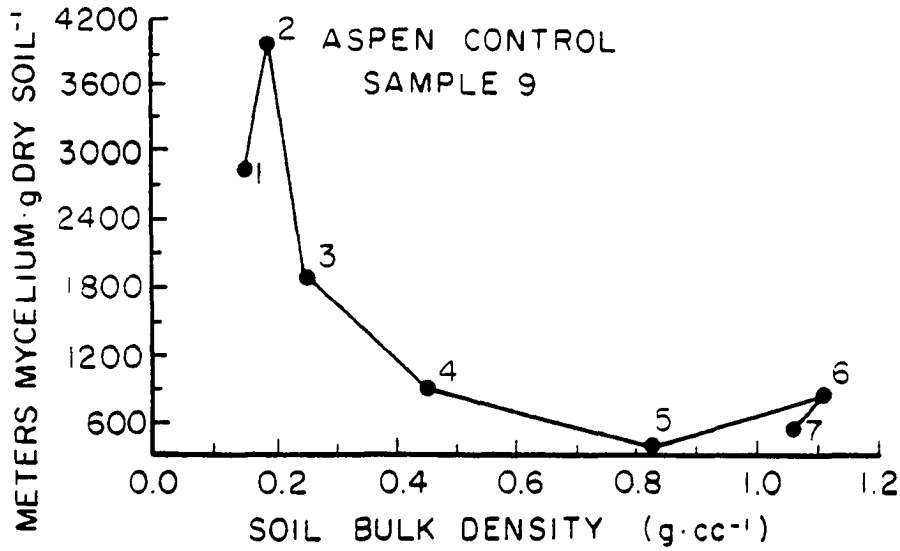


Figure 60. Level II biomass profile: Forest floor surface through 7 cm in 1 cm increments (1-7).

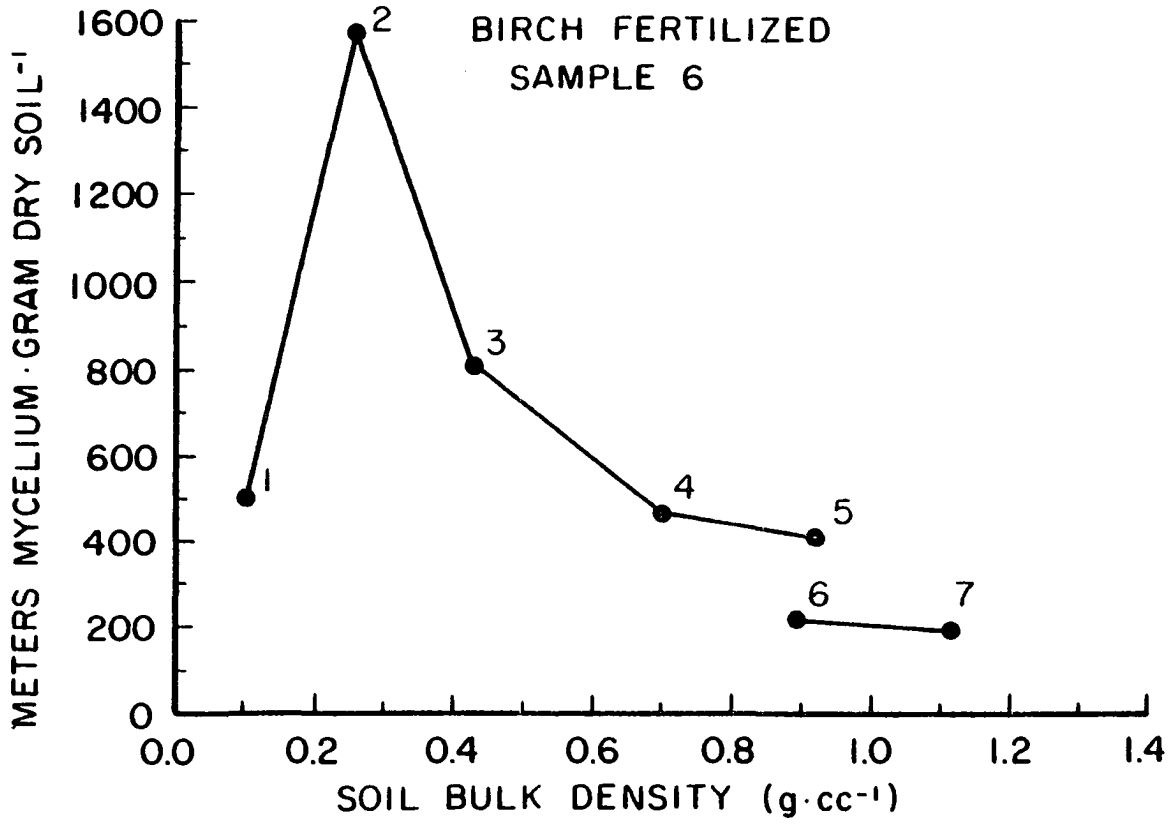


Figure 61. Level II biomass profile: Forest floor surface through 7 cm in 1 cm increments (1-7).

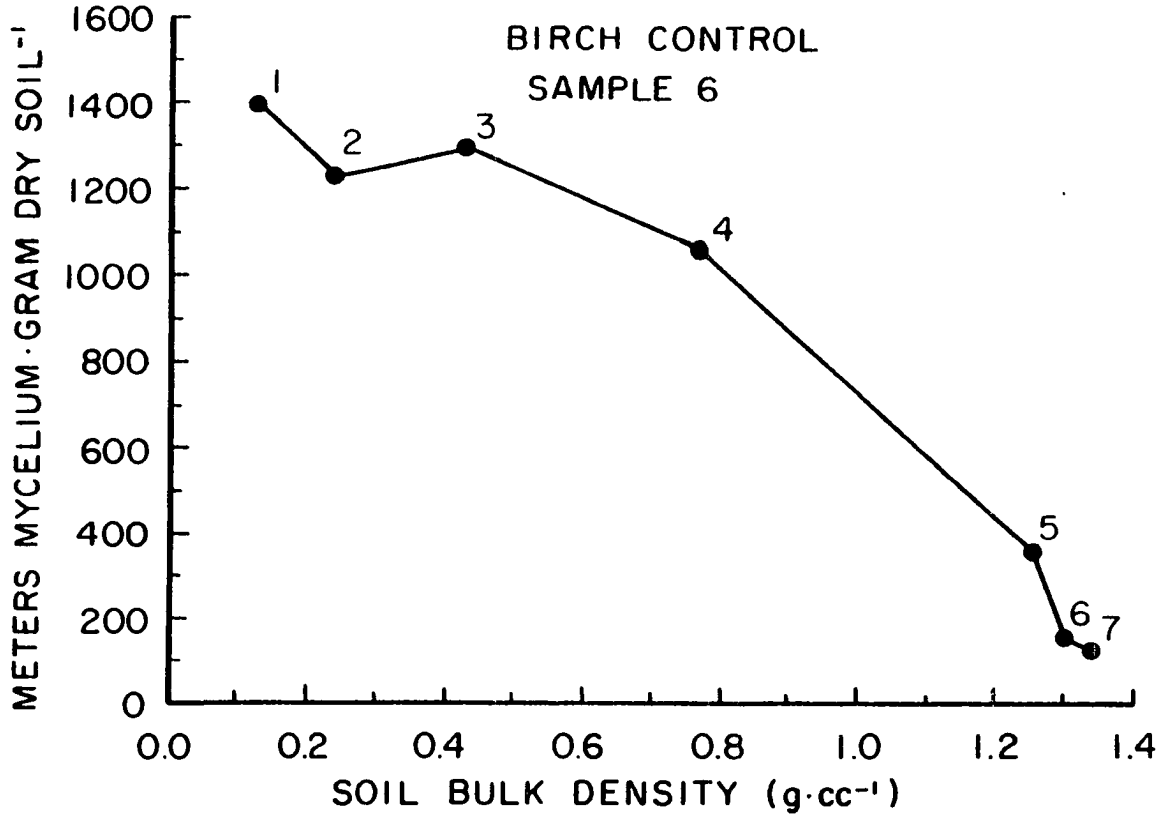


Figure 62. Level II biomass profile: Forest floor surface through 7 cm in 1 cm increments (1-7).

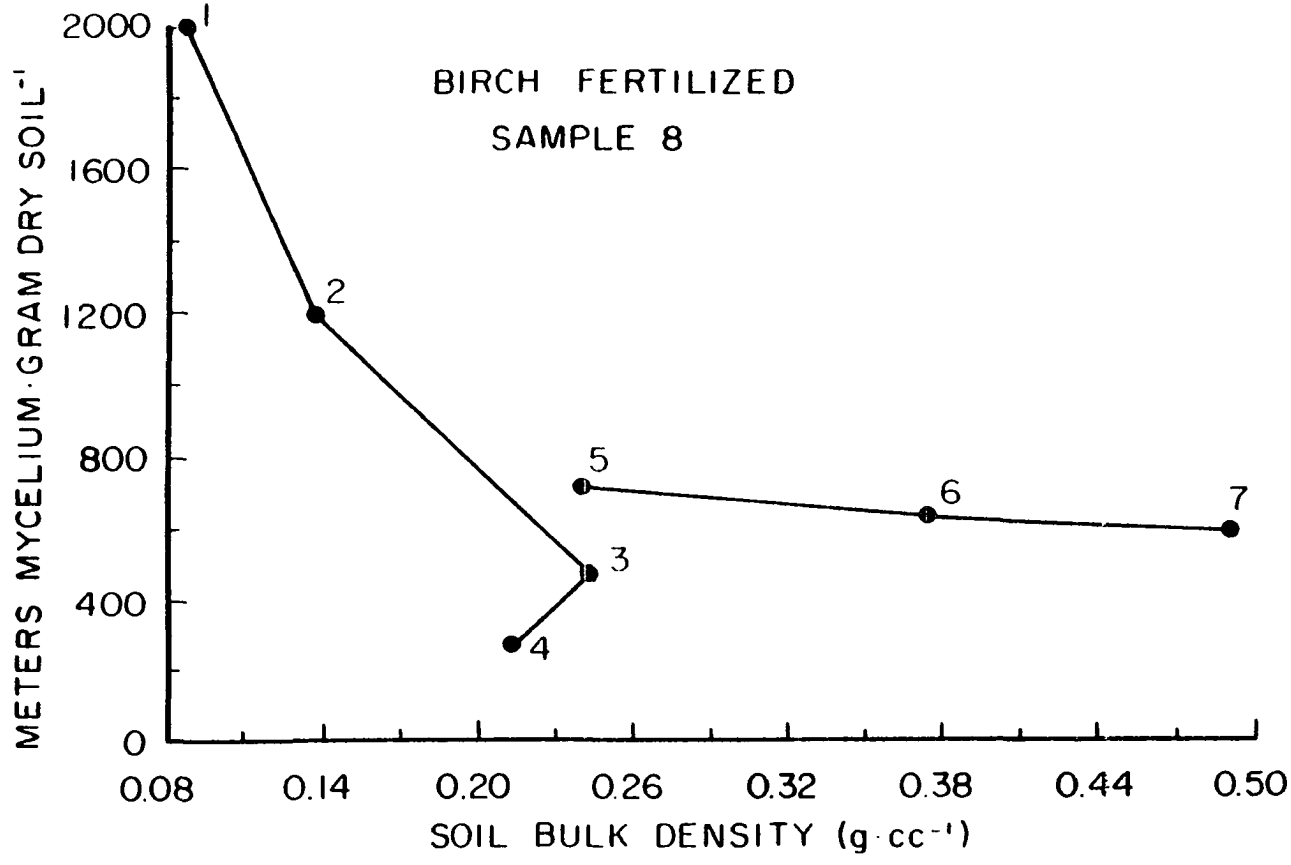


Figure 63. Level II biomass profile: Forest floor surface through 7 cm in 1 cm increments (1-7).

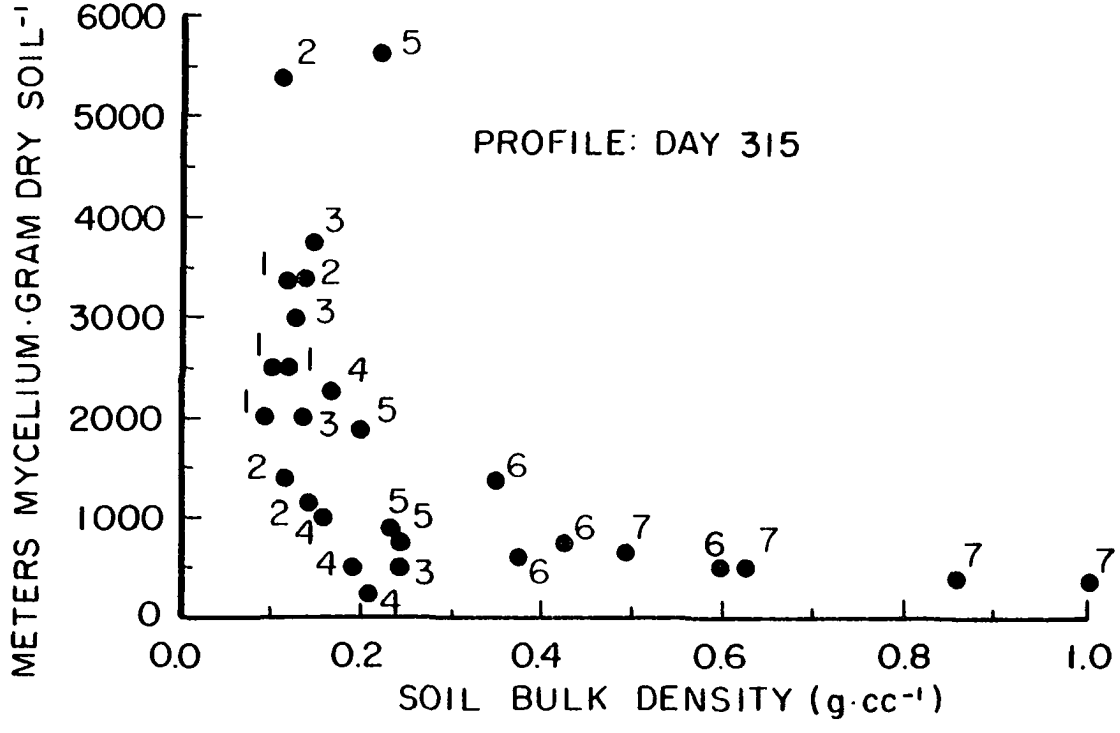


Figure 64. Level II fungal biomass profile for day 315, season 2: All sites (AC, AF, BC, BF), soil surface through 7 cm in 1 cm increments (1-7).

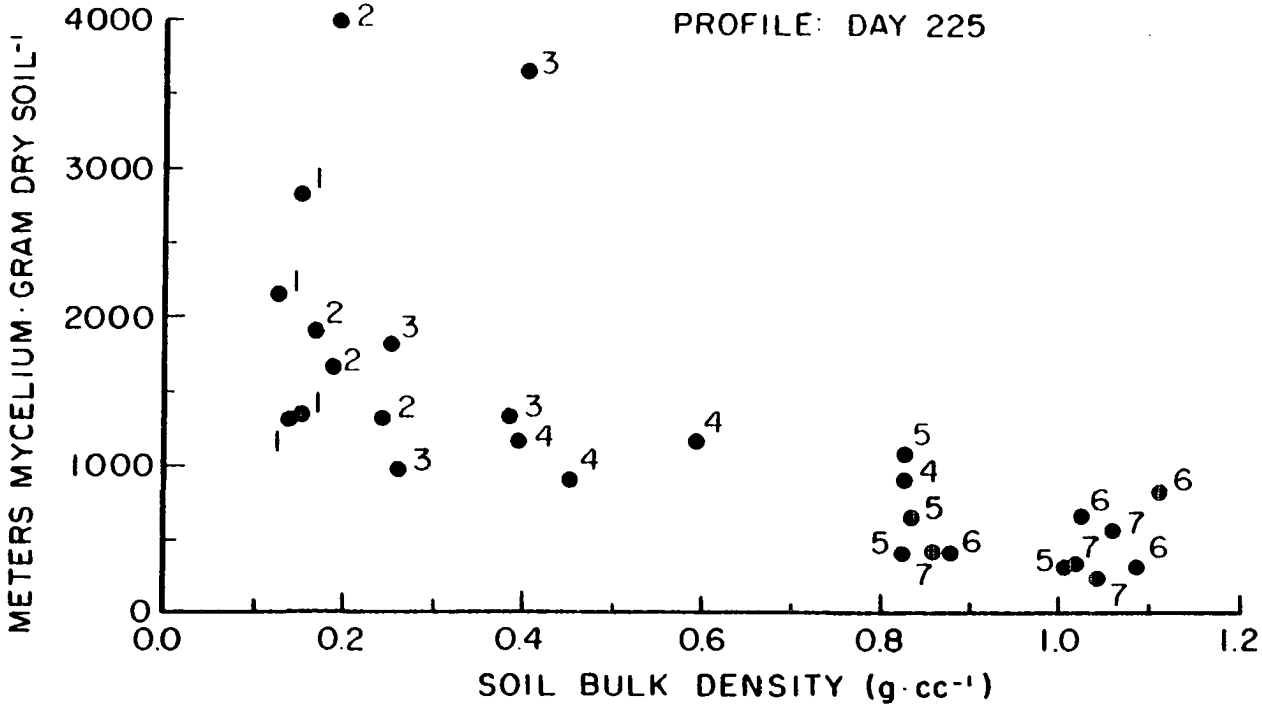


Figure 65. Level II fungal biomass profile for day 225, season 2: All sites (AC, AF, BC, BF), soil surface through 7 cm in 1 cm increments (1-7).

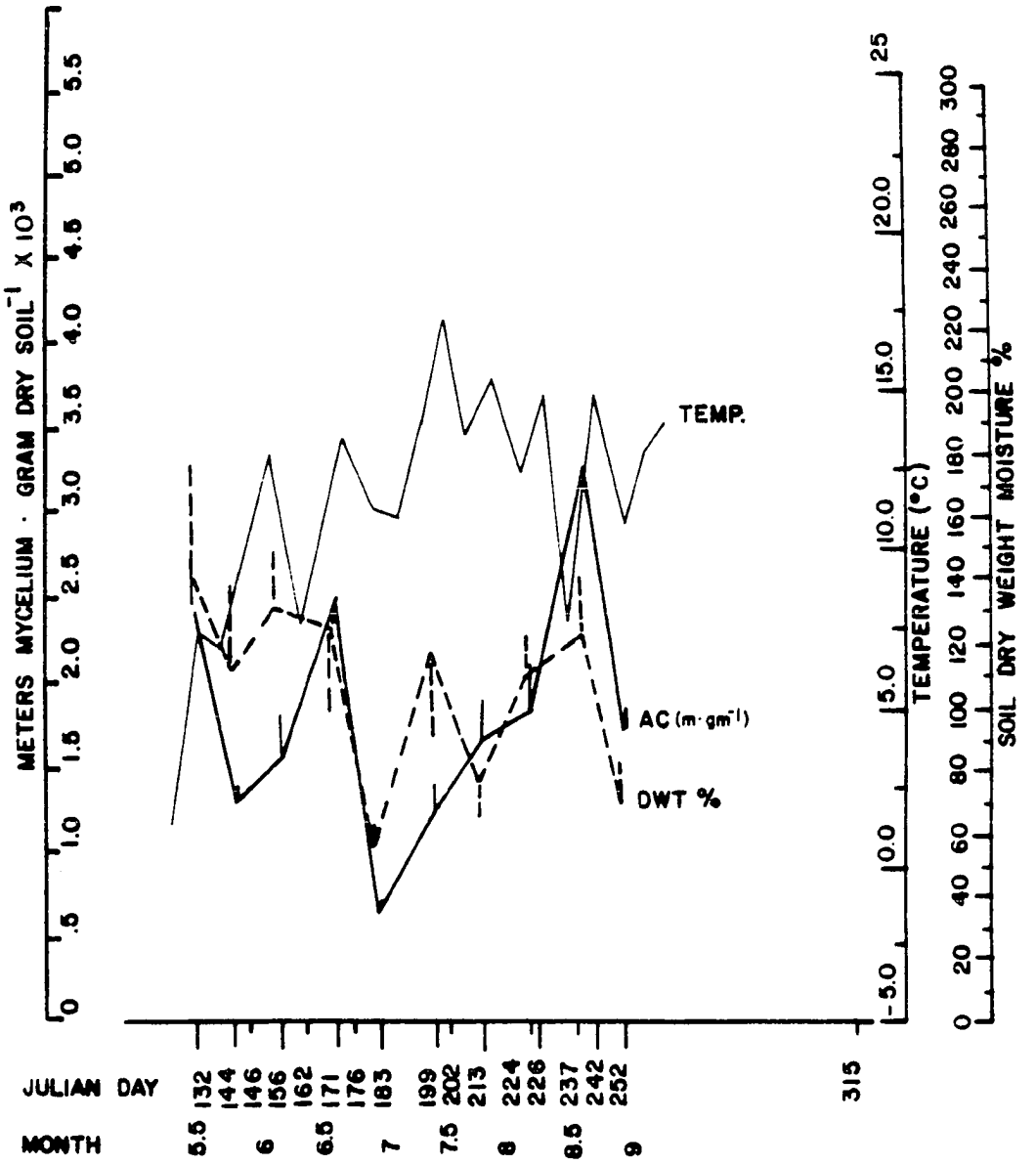


Figure 66. Fungal biomass, soil moisture and soil temperature at 1-2 cm soil depth: Season 1, site Aspen Control (AC).

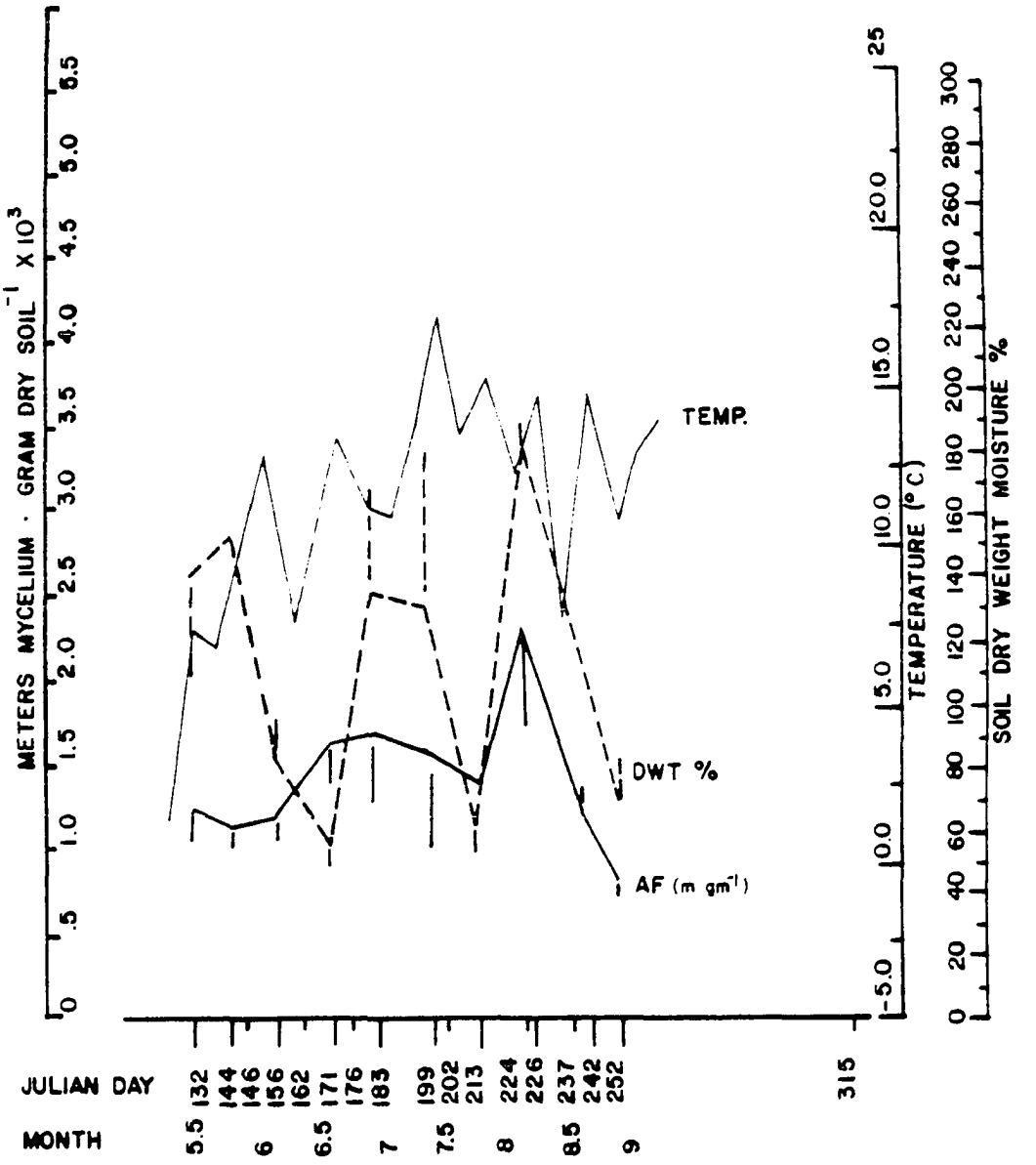


Figure 67. Fungal biomass, soil moisture and soil temperature at 1-2 cm soil depth: Season 1, site Aspen Fertilized (AF).

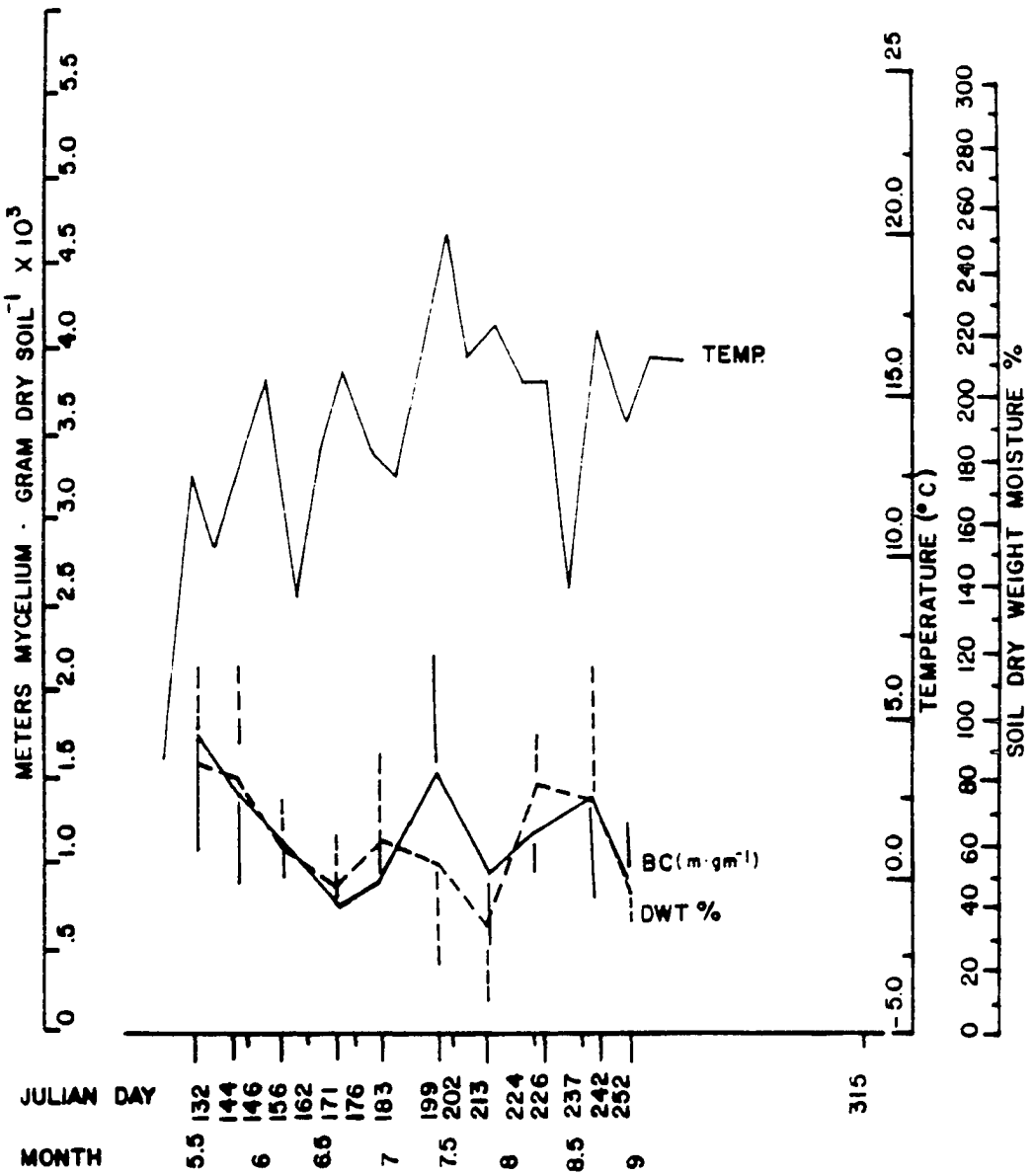


Figure 68. Fungal biomass, soil moisture and soil temperature at 1-2 cm soil depth: Season 1, site Birch Control (BC).

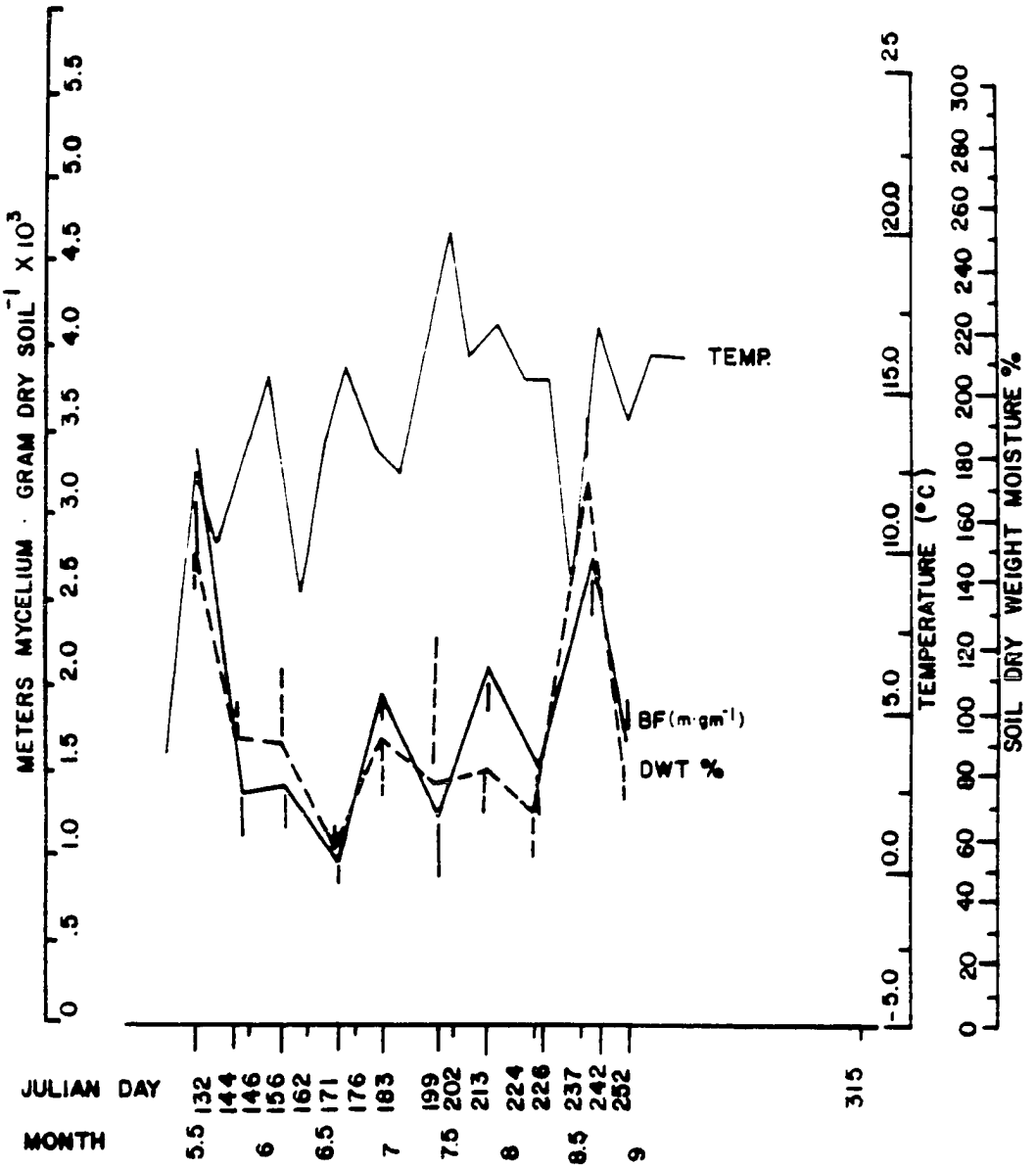


Figure 69. Fungal biomass, soil moisture and soil temperature at 1-2 cm soil depth: Season 1, site Birch Fertilized (BF).

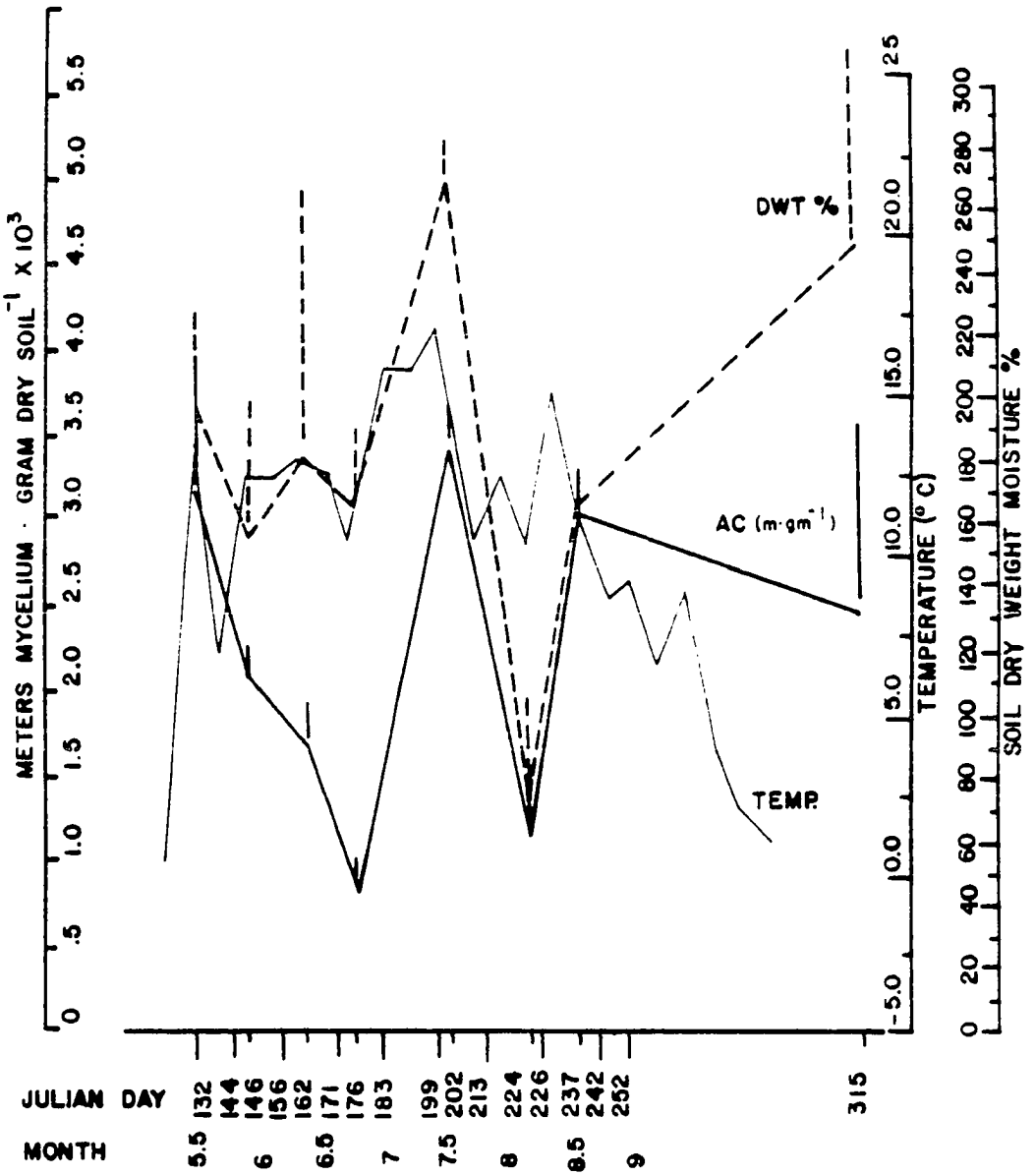


Figure 70. Fungal biomass, soil moisture and soil temperature at 1-2 cm soil depth: Season 2, site Aspen Control (AC).

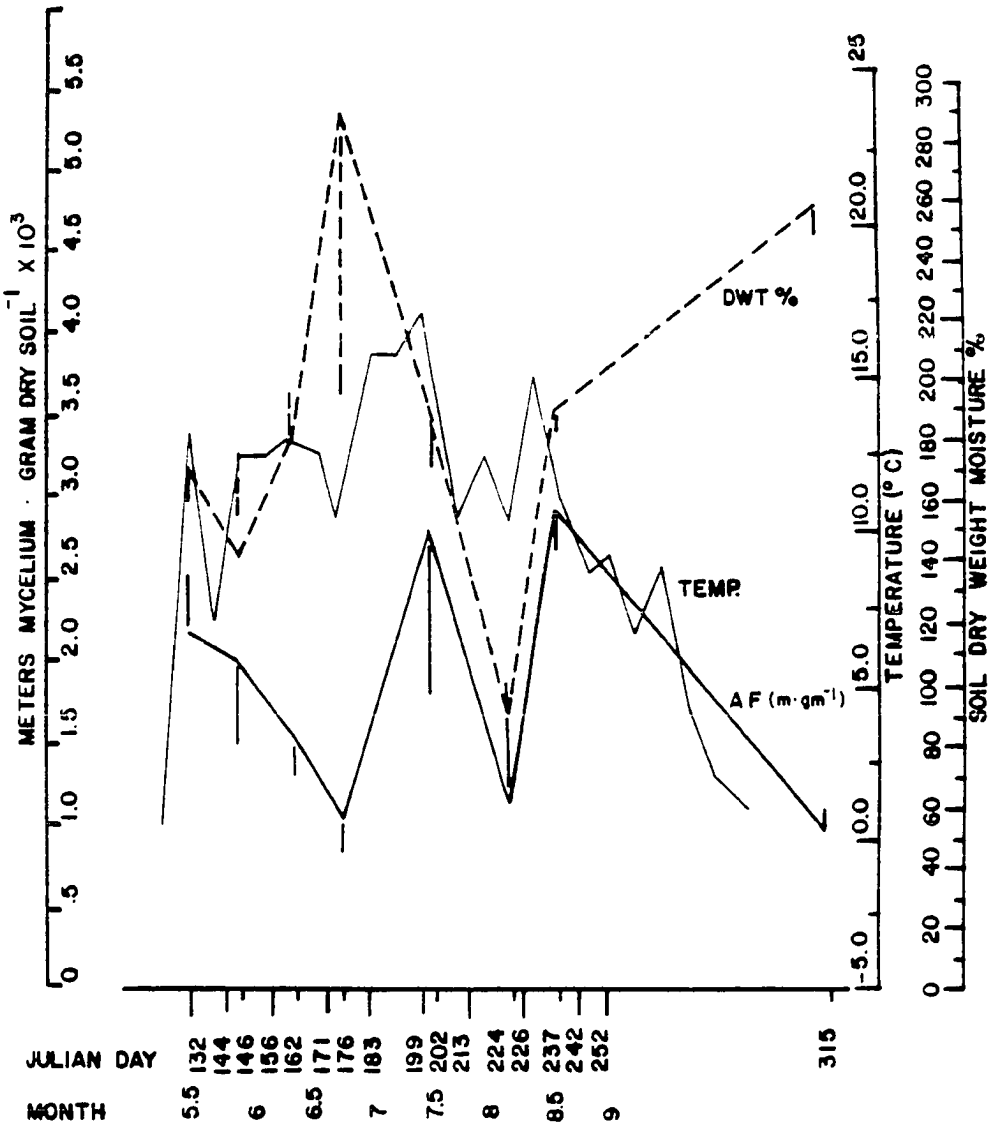


Figure 71. Fungal biomass, soil moisture and soil temperature at 1-2 cm soil depth: Season 2, site Aspen Fertilized (AF).

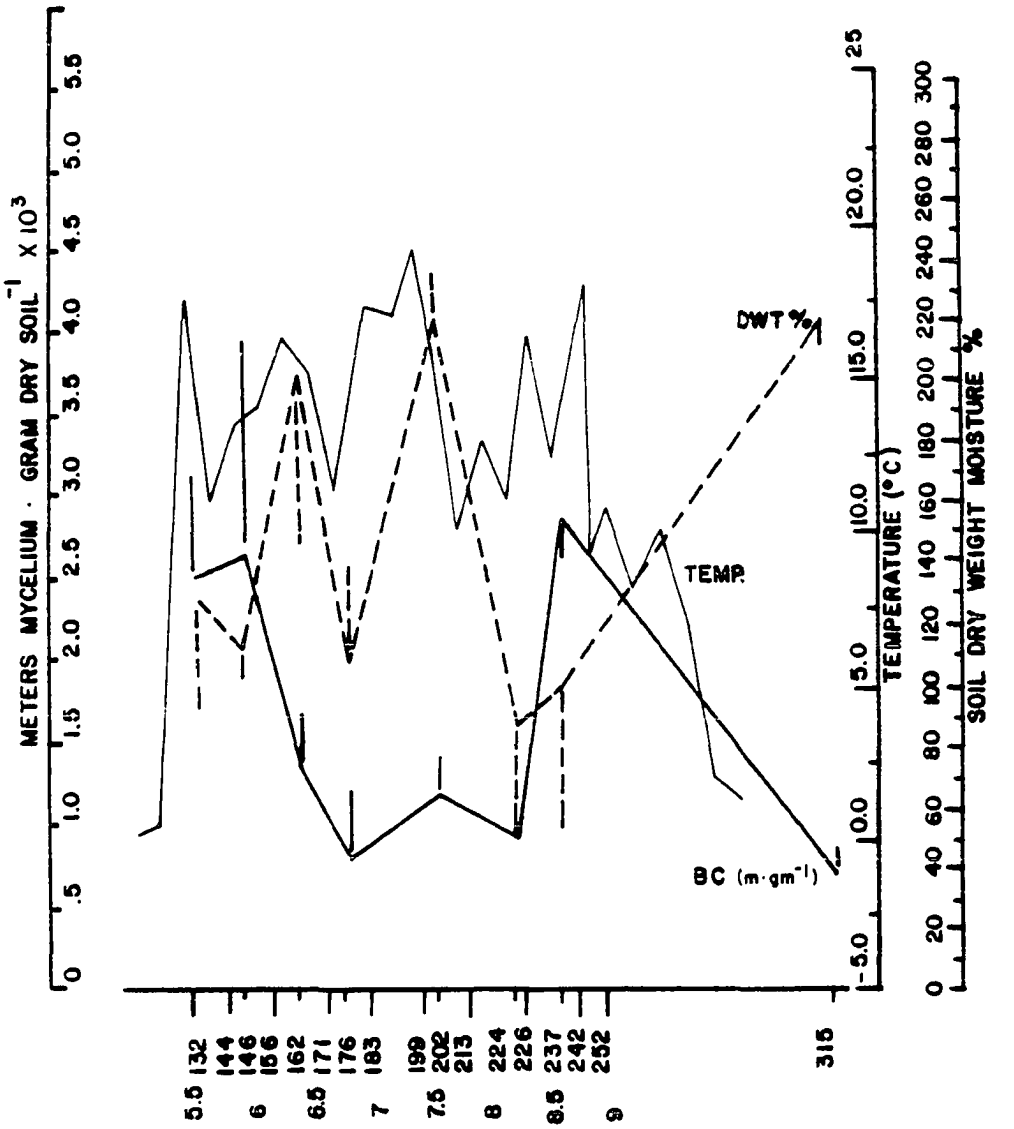


Figure 72. Fungal biomass, soil moisture and soil temperature at 1-2 cm soil depth: Season 2, site Birch Control (BC).

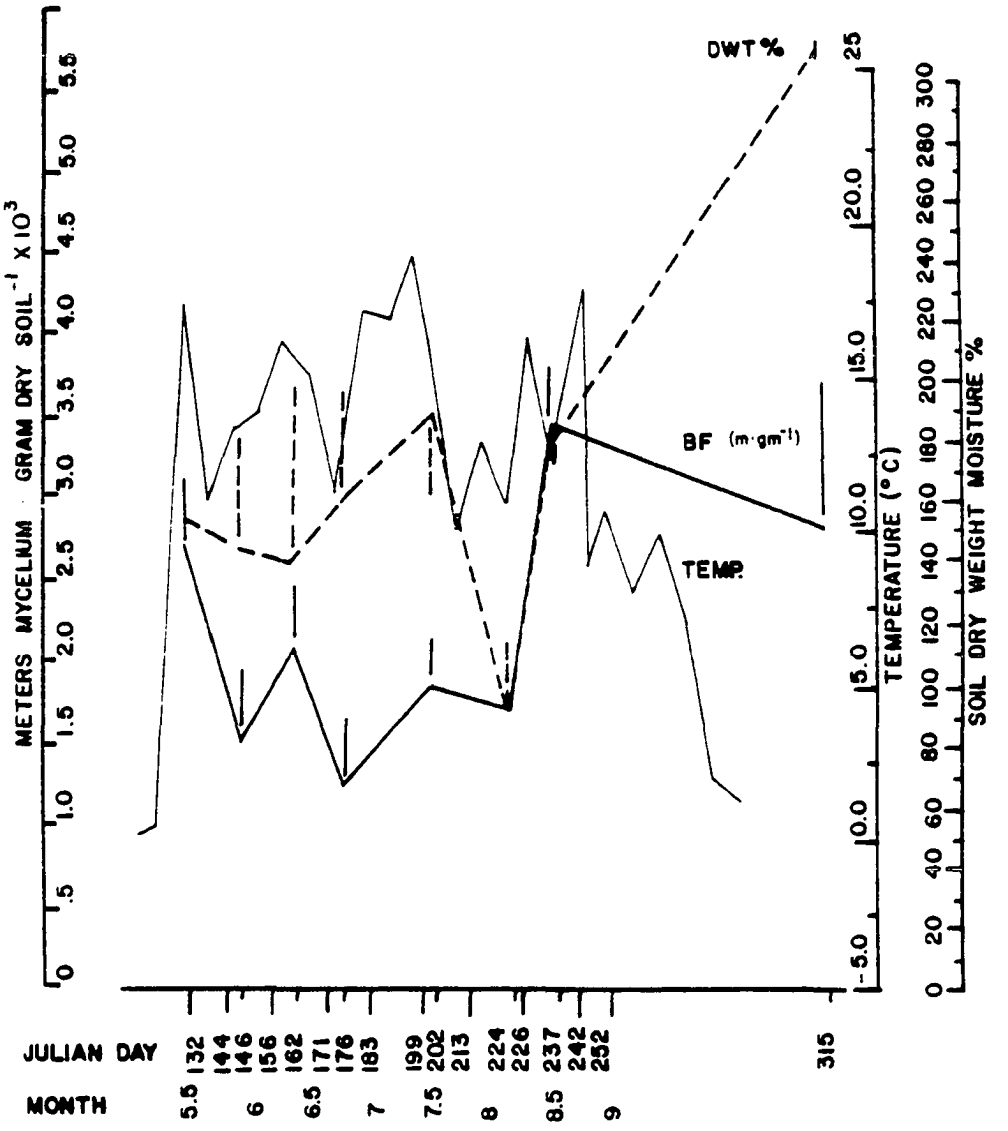


Figure 73. Fungal biomass, soil moisture and soil temperature at 1-2 cm soil depth: Season 2, site Birch Fertilized (BF).

the first two to four sample periods. In all of these cases initial biomass measurements are significantly greater (α = .05) than those recorded for the first season biomass 'troughs' as follows:

Figure	Sample #	>	Sample #
66	1	>	2
67	1	>	4
68			
69	1	>	2
70	1	>	2
71	1	>	4
72	1	>	4
73	1	>	2

For both field seasons these net biomass decreases correspond with steady soil temperature increases. In some cases the early season biomass decreases and temperature increases are paralleled by soil moisture decreases (Figures 68, 69). However, figures from 1975, an overall wetter year, (Figures 70-73) show that with a maintenance of, or increase in soil moisture over the first 1-4 sample periods, there is still a significant decrease in fungal biomass for all sites.

The decreased correlation of biomass with moisture for season two vs season one is supported by a comparison of Tables 19 and 20. For 1974 at 1-2 cm soil depth the correlation of biomass and moisture over the season was significant at α .01 for 4 of 10 sample dates (correlation coefficient of .68 to .79), and at the α = .05 level for an

Table 19. Season 1: Correlation Coefficients

	Variable	Description	Depth	P-Value	Corr. Coeff.
1.	DWT%	Day May 12	1-2 cm	0.1655	0.36417
2.	DWT%	May 24	1-2 cm	0.1458	0.38062
3.	DWT%	June 5	1-2 cm	0.0275	0.54928
4.	DWT%	June 20	1-2 cm	0.0003	0.79021
5.	DWT%	July 2	1-2 cm	0.0025	0.70078
6.	DWT%	July 18	1-2 cm	0.0039	0.67746
7.	DWT%	Aug 1	1-2 cm	0.0040	0.67715
8.	DWT%	Aug 14	1-2 cm	0.0172	0.58542
9.	DWT%	Aug 30	1-2 cm	0.0563	0.48608
10.	DWT%	Sept 9	1-2 cm	0.0145	0.59737
1.	DWT%	May 12	6-7 cm	0.0249	0.59571
2.	DWT%	May 24	6-7 cm	0.6298	-0.13058
3.	DWT%	June 5	6-7 cm	0.1552	0.37259
4.	DWT%	June 20	6-7 cm	0.0622	0.47618
5.	DWT%	July 2	6-7 cm	0.1761	0.35589
6.	DWT%	July 18	6-7 cm	0.8240	-0.06044
7.	DWT%	Aug 1	6-7 cm	0.1888	0.34632
8.	DWT%	Aug 14	6-7 cm	0.1777	0.35466
9.	DWT%	Aug 30	6-7 cm	0.6900	0.10819
10.	DWT%	Sept 9	6-7 cm	0.7827	-0.07492

Table 20. Season Two: Correlation Coefficients

	Variable	Description	Depth	P-Value	Corr. Coeff.
1.	DWT%	Day 132	1-2 cm	0.1340	0.39127
2.	DWT%	146	1-2 cm	0.8147	0.0638
3.	DWT%	162	1-2 cm	0.8538	0.05010
4.	DWT%	176	1-2 cm	0.5671	-0.1547
5.	DWT%	202	1-2 cm	0.5887	0.14631
6.	DWT%	224	1-2 cm	0.5854	0.1476
7.	DWT%	237	1-2 cm	0.2931	0.28026
8.	DWT%	315	1-2 cm	0.0029	0.69308
1.	DWT%	Day 132	6-7 cm	0.2703	0.29326
2.	DWT%	146	6-7 cm	0.8009	-0.06855
3.	DWT%	162	6-7 cm	0.7492	-0.08682
4.	DWT%	176	6-7 cm	0.3634	0.24355
5.	DWT%	202	6-7 cm	0.3996	0.22620
6.	DWT%	224	6-7 cm	0.5305	-0.16950
7.	DWT%	237	6-7 cm	0.1046	0.42075
8.	DWT%	315	6-7 cm	0.0067	0.64707

additional 4 dates (including sample #9, α = .0563) with correlation coefficients of .54 to .59. For 1974 80% of the sample dates for organic soils show a significant correlation with soil moisture percent. For 1975 (Table 20) only a single sample (sample 8, day 315) shows a significant correlation with moisture (P - value = 0.0029, correlation coefficient = .69). This sample was taken after forest floor surface temperatures had fallen below 0^0C and after snowfall.

At the 1-2 cm soil depth for 1975 a negative correlation is evident, though not significant, for sample 4 (Table 20) which occurred at a seasonal soil moisture high.

Measurements of independent environmental factors of temperature and moisture cannot be expected to correlate on a point to point basis with biomass; biomass is a function of the influence of environmental parameters preceding the single point measurement of the biotic variable; however, a number of cases show that, given favorable moisture conditions, a seasonal temperature low is followed in several days by a biomass peak, this is illustrated in Figure 66 where the biomass peak for sample number 9 (August 30) is 3320 $m \cdot gm^{-1}$, significantly greater than the biomass mean ($\overline{X}$ = 1834 $m \cdot gm^{-1}$) for the preceding sample (number 8, August 14) and concurrent with a temperature drop of approximately 7^0C of two day duration (from 15.80^0C to 8.9^0C). Similar trends can be seen in figures 67 and 69. From Figure 67 there is a steady biomass increase from 924 $m \cdot gm^{-1}$ to 1395 $m \cdot gm^{-1}$ correlated with a soil moisture increase from 35.5% to 80.4% at the same temperature decrease noted for Figure 67.

wetter year (20-40% > year 1) and showed a significant increase in active fungal biomass with a slight decrease in correlation of biomass and soil moisture, as do Tables 16 through 20 of this study.

It must also be assumed, from the data showing an increase in standing crop biomass with a decrease in temperature, that temperature fluctuations of the magnitude recorded (± 8-10^{0}C) for short durations (1-3 days) were not sufficient to either stimulate or limit fungal biomass (McGill et al., 1975). These results are consistent with those of Baath and Soderstrom (1982) and Soderstrom (1978 and 1979a) which showed little or no fluctuation of active fungal biomass with soil temperature fluctuations of ± 10^{0}C over snow-free summer months and no correlation or negative correlation of biomass with temperature and positive correlation with soil moisture. These figures are in contrast with those of Flanagan and Van Cleve (1977) who showed that for an interior Alaska black spruce ecosystem (nutrient limited and permafrost dominated) temperature was the dominant influence in control of forest floor respiration and microbial biomass.

The effects of interaction of soil moisture and soil temperature are most likely to be of significance at the critical extremes of each variable, i.e., low soil moisture is thought to be most limiting to biological processes at elevated temperatures (Flanagan and Veum, 1974; Rahno et al., 1978 and Van Cleve et al., 1981). Rahno et al., (1978) suggests that although temperature, and secondarily moisture, have historically been shown to be the driving forces behind growth and respiration of microorganisms under laboratory conditions, field studies

1975 biomass moisture and temperature comparisons do show correspondence of biomass and temperature peaks. The two major temperature peak periods (roughly days 171-202 and 224-230) corresponded with both soil moisture peaks and fungal biomass peaks for the year (Figures 70-73) making the assessment of the individual importance of temperature and of moisture more difficult than for 1974.

CONCLUSIONS

For both field seasons soil temperature shows little correlation with fungal biomass, and is negatively correlated in some instances. Soil moisture is positively correlated with biomass and in the overall regression for 1974 shows an R^2 value of .74 and from 1975 an R^2 of .59. The correlation and regression equations indicate that sample season two, significantly (α = .0560) greater in soil moisture than season one, showed less dependence (correlation) of biomass on soil moisture, i.e., soil moisture for 1975 did not act as the limiting factor in biomass fluctuations. Baath and Soderstrom (1982), in monitoring seasonal and spatial variations in live fungal biomass of forests in central Sweden, arrived at similar conclusions. Their study indicated that significant (α = .05 to .01) seasonal variations in soil moisture was strongly correlated with FDA active biomass fluctuations, with biomass and moisture peaks in early spring and autumn. Soderstrom (1977, 1979a) shows similar results. The two year study of Baath and Soderstrom (1982) shows between year moisture and biomass correlations analogous to findings of this study. Year two of their study was a

showed temperature and other soil physical factors (addition of organic matter and mineral fertilizers) to be of secondary importance to soil moisture. They conclude that for soils of the Estonian Region, Harku, U.S.S.R. winter conditions of 0^0C to -5^0C did not reduce the number of fungi; not as a consequence of decreased temperature but as a consequence of an improved (elevated) soil moisture regime during the winter months. Their work shows a constant rise in numbers of soil fungi with a rise in soil moisture concommitant with a decrease in soil temperature as follows:

Season	N	$\bar{X}$ Soil Temp. ^0C	Soil Moist. %	Av. No. Fungi*
Autumn	403	6.9	19.0	14.3
Winter	392	1.4	23.3	21.0
Spring	368	2.4	22.4	17.3
Summer	252	15.4	16.7	17.4

*Thousands per gram dry soil by dilution plate method.

This scenario of overriding effect of soil moisture in relation to soil temperature would account for the decreased fungal biomass recorded for birch sites for year 1 of this study (momentarily ignoring any substrate quality differences between aspen and birch vegetation types). The birch sites showed an increased soil temperature at the O1 layer coupled with decreased soil moisture and lower standing crop fungal biomass in comparison to aspen soils. This argument can be pursued a step further in addressing a possible cause for elevated birch O1 soil temperature (in addition to decreased canopy solar intercept already mentioned) and decreased O21/A temperature in comparison with aspen

soils. I have stated from the bulk density main effects ANOVA that birch soils show a higher bulk density in the O1-O21 layer and a lower bulk density in the O22/A layer in comparison to aspen soils. An increase in bulk density lowers total soil porosity and thus improves thermal contact between soil particles improving overall thermal conductivity. A bulk density increase from 1.1 to 1.5 could increase the thermal conductivity of the soil as much as 100% with a decrease in total porosity. This could explain the bracketing effect noted for birch and aspen soils under the same general thermal regime (Temperature section of this work).

With the main effects and interactions of soil moisture and soil temperature defined, it is now possible to assess the relative merits of explanations of temperature/moisture interactions presented earlier in this chapter.

(A) As already noted, the negative relationship between temperature and biomass is most probably a function of increased moisture availability as opposed to an actual causal relationship confined to temperature and biomass. The trend is most pronounced for mineral soils for 1974 because it was at this depth that soil moisture approached its limiting minimum values (Van Cleve and Sprague, 1971). 1975, a wetter year with increased soil moisture in both organic and mineral soils would, following the argument presented, show less negative relationship to temperature and less correlation with soil moisture; as has already been shown.

(B) The validity of supposition two cannot be ascertained from this experiment since no viability status of fungal biomass was possible with the method used. However, some comments can be made regarding the status of fungal biomass over the period (mid-November to mid-May) not sampled in this study.

It is generally accepted that significant respiration, decomposition and fluctuations in fungal biomass occur at temperatures less than 0°C. A number of workers have monitored some combination of these processes in vivo at temperatures of +5°C to -10°C (Gams and Domsch, 1969; Latter and Heal, 1971; Van Cleve and Sprague, 1971; Ivarson, 1973; Van Cleve, 1972; Flanagan and Veum, 1974; Toth and Hammer, 1977; and Winn-Williams, 1982).

Figure 74 adapted from Soderstrom (1979a) and Baath and Soderstom (1982) show FDA-active biomass fluctuations during winter months with temperatures of +2°C to -3°C, these fluctuations in metabolically active biomass indicate that there was turnover of dead fungal tissue at sub-zero °C temperatures. Flanagan and Van Cleve (1977) reported that for a black spruce ecosyste, live fungal hyphae accounted for approximately 90% of total standing crop fungal biomass and that with a decline in live hyphae there was not a significant increase in dead hyphae. Soderstrom (1979a) reports that for soils in central Sweden, first winter freezing of soil is followed by a drastic reduction in active biomass, followed by a gradual recovery during winter months.

(C-D) Even though this study attempted to intersect the soil fungal biomass cycle at a time when activity could be most success-

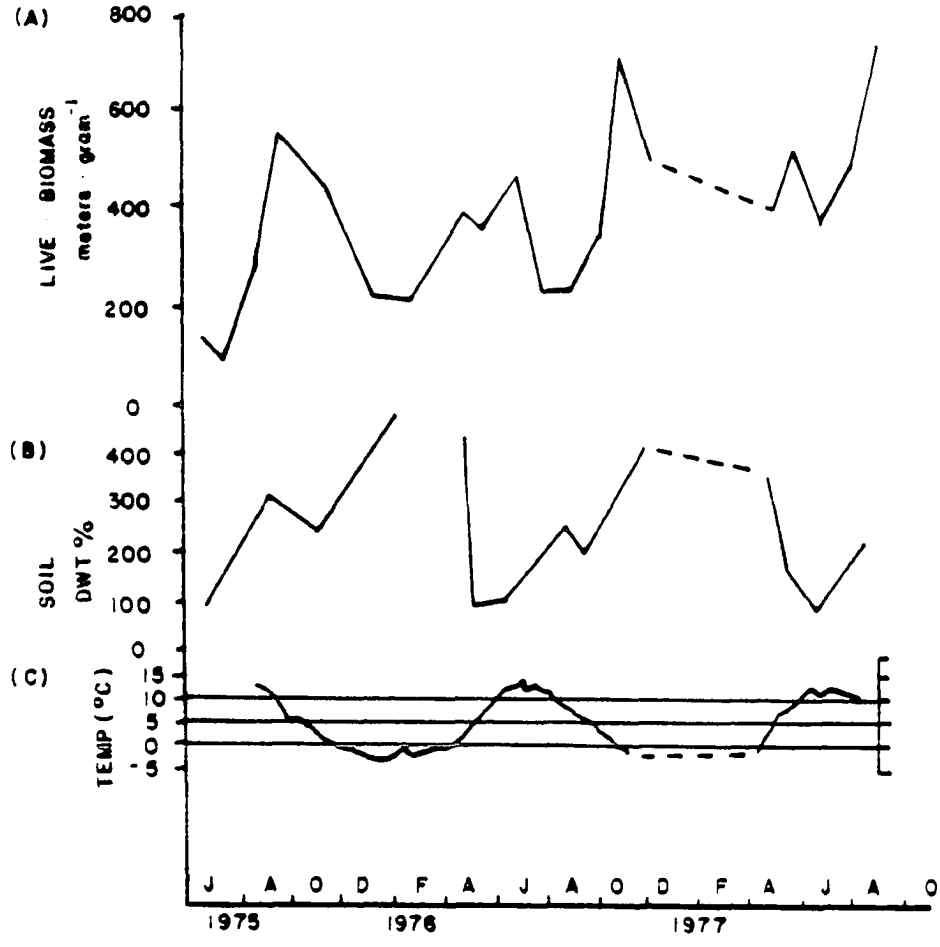


Figure 74. Fungal biomass ($m \cdot g^{-1}$), temperature, moisture and time (seasonality), adapted from Soderstrom (1979a).

fully related to soil microclimatic factors, it is now obvious that significant fluctuations in the fungal biomass cycle most probably continued throughout some portion of the winter months (post November - pre mid-May). Figures 66 and 67 show that for both vegetation types for both field seasons sample 1 (mid-May) biomass means are significantly (α = .05) greater than the last season sample mean. Comparison of 1974 end of season (last sample) means with 1975 first sample date means shows that in all cases there has been a net increase in standing crop fungal biomass during the unsampled portion of the 1974-1975 winter. In addition, for 1975 the field sample season was extended into what was assumed to be the winter quiescent period - post snowfall and ground freeze (November 12). For 50% of these samples biomass means are significantly elevated (α = .05) over means recorded for June and August. All evidence indicates that the date, mid-May (average time of spring breakup and snow melt for the study sites) did not represent the starting point for a hypothetical early spring biomass increase in response to favorable soil temperature and moisture regimes.

I assume conjectures (C) and (D) to be correct; fungal biomass, within the dates comprising the field season for this study, is most closely correlated with soil moisture and not soil temperature - mediated at the period encompassed by ground freeze and ground thaw by temperature and temperature-moisture interactions.

D. II. DATA PRESENTATION: EFFECTS OF VEGETATION TYPE AND LONG-TERM FERTILIZATION ON FUNGAL BIOMASS

Overview

1. Combined years ANOVA indicates a significant effect of vegetation type on fungal biomass at the 1-2 cm soil level: aspen > birch.
2. Longterm addition on N-P-K fertilizers reduced fungal biomass in aspen soils and increased fungal biomass in birch soils.
3. The addition of fertilizers significantly decreased the relative abundance of hyphae of higher fungi (basidiomycetes) in both aspen and birch soils.

Table 21, two year combined ANOVA, shows a significant site effect on fungal biomass (P value = .0007). However, the significant interactions of all other main effect variables: Plot within Site, Site by Depth, Plot within Site by Depth and Year (marginally), make interpretation of the overall site effect questionable from the pooled data ANOVA alone. It was necessary to partition the ANOVA by year, by sample period within year and by depth within sample period to arrive at meaningful comparisons.

Table 22 indicates that the main effect of site is significant for 1974 and nonsignificant for 1975. However, all main effect error source interactions are significant for the 1974 data and are limited to depth, day and depth by day for 1975. Only 2 of the 10 sample periods (samples 9 and 10) in 1974 show a significant main effect of site, although P-values of 0.10 or less on 3 other dates (samples 132, 171 and 183)

Table 21. Fungal Biomass*ANOVA: Combined Seasons

Source of Variability	P-Statistic Meters$\cdot g^{-1}$
Site	.0007
Plot (Site)	.0006
Depth	.0001
Site * Depth	.0015
Plot (Site) * Depth	.007
Year	.0768
Site * Year	.7580
Plot (Site) * Year	.0624
Depth * Year	.0183
Site * Depth * Year	.4518
Plot (Site) * Depth * Year	.0163
Day	.0001
Site * Day	.3090
Plot (Site) * Day	.2531
Depth * Day	.0001
Site * Depth * Day	.0278
Plot (Site) * Depth * Day	.0522
Day * Year	.0009
Site * Day * Year	.0834
Plot (Site) * Day * Year	.0615
Depth * Day * Year	.0078
Site * Depth * Day * Year	.0666
Plot (Site) * Depth * Day * Year	.1116

*$m\cdot g^{-1}$

Table 22. Fungal Biomass* ANOVA: By Sample Season

Source of Variability	P-Statistic Season 1	Season 2
Site	.0173	.1688
Plot (Site)	.0014	.6658
Depth	.0001	.0001
Site * Depth	.0070	.0775
Depth * Plot (Site)	.0008	.2475
Day	.0001	.0001
Site * Day	.0001	.6128
Plot (Site) * Day	.0038	.1800
Depth * Day	.0001	.0001
Site * Depth * Day	.0001	.1733
Depth * Day * Plot (Site)	.0005	.1737

*$m \cdot g^{-1}$

contributed to the overall main effect (Table 23-A). No sample date in 1975 showed a significant site effect (Table 23-B).

1974 Biomass: Vegetation Type and Fertilization

The specific instances of significant differences among site biomass means at depth 1-2 cm show that birch fertilized sites and aspen control sites are approximately equal and rank highest in biomass in 85% of the significant cases (Table 23) and account for 70% of all first and second place means overall (Table 24-A). Arrangement of 1-2 cm depth biomass means, in order of magnitude (Table 15-C) BF(1851*) > AC(1836) > AF(1431) > BC(1190) yields a hierarchy in agreement with conclusions drawn from Tables 23 and 24. Using Duncan's Multiple Range Test the means are grouped:

Site	Depth	Mean*	Grouping
AC	1-2 cm	1851	|
BF	1-2 cm	1836	|
AF	1-2 cm	1431	|
BC	1-2 cm	1190	|

On the basis of this single season, single soil depth data:

1. There was a significant main effect of vegetation type on fungal biomass: aspen control > birch control.
2. There was a significant main effect of fertilization. Long-term fertilization increased fungal biomass in birch soils and decreased fungal biomass in aspen soils.

However, the significant interactions of site, plot and depth (Table 21) indicates that these relationships are not the same at both soil depths sampled. Rank of biomass means for 6-7 cm soil depth fungal biomass is:

*All biomass means expresses as $m \cdot gm^{-1}$.

Table 23. Fungal biomass (meters·g^{-1}) ANOVA by sample period (day) within year; S = Site, P = Plot, D = Depth.

Error Source	A 1974 Day	P-Value	B 1975 Day	P-Value
S	132	.0768	133	.3975
P (S)		.1387		.0506
D		.0001		.0001
S * D		.0307		.6624
D * P (S)		.0325		.0696
S	144	.6198	147	.8220
P (S)		.0002		.6487
D		.0001		.0071
S * D		.0688		.8186
D * P (S)		.0001		.6585
S	156	.8823	163	.6245
P (S)		.1879		.3113
D		.0005		.0001
S * D		.2321		.2518
D * P (S)		.0457		.1076
S	171	.0914	177	.3939
P (S)		.1229		.3447
D		.0003		.0138
S * D		.0121		.9325
D * P (S)		.0901		.3821
S	183	.0748		
P (S)		.4241		
D		.0002		
S * D		.0133		
D * P (S)		.0539		
S	199	.6491	203	.3019
P (S)		.0001		.6406
D		.0001		.0001
S * D		.2317		.0253
D * P (S)		.0001		.3868
S	213	.1172		
P (S)		.1616		
D		.0001		
S * D		.0688		
D * P (S)		.0860		
S	226	.1158	225	.3559
P (S)		.0316		.4923
D		.0001		.0008
S * D		.1921		.5705
D * P (S)		.0623		.2330
S	242	.0107	238	.6199
P (S)		.1600		.8494
D		.0001		.0001
S * D		.0231		.7445
D * P (S)		.2097		.8533
S	252	.0222	315	.1920
P (S)		.1054		.1772
D		.0001		.0077
S * D		.0929		.0976
D * P (S)		.2729		.2350

Table 24. Fungal biomass ($m \cdot g^{-1}$) means by: year, site, depth and day. Means within a single sample date and depth differing at $\alpha = .05$ noted by *. Means sharing a common bridge * do not differ significantly from each other but differ individually and as a group from other '*' marked mean(s) within a sample date.

I. 1974

Sample Date & Number		A: 1-2 cm. Biomass Ranked > to < by site				B: 6-7 cm Biomass			
132	1	BF-3450*	AC-2486	BC-1779	AF-1246*	BC-850*	AC-730	BF-519	AF-431*
144	2	BC-1423	BF-1371	AC-1309	AF-1135	AF-668	AC-664	BC-588	BF-446*
156	3	AC-1580	BF-1412	AF-1194	BC-1129	BC-842	BF-629	AF-613	AC-514
171	4	AC-2534*	AF-1631	BF- 987	BC- 738*	BC-616*	AF-468	BF-385	AC-296*
183	5	BF-1996*	AF-1689	BC- 891	AC- 651	BF-598	BC-538	AC-480	AF-305
199	6	AF-1582	BC-1525	AC-1268	BF-1235	BF-465	BC-423	AC-396	AF-326
213	7	BF-2124	AC-1685	AF-1404	BC- 924	AF-520	BC-339	BF-302	AC-200
226	8	AF-2334	AC-1834	BF-1529	BC-1180	AF-474	BC-429	AC-420	BF-400
242	9	AC-3320	BF-2807	BC-1395	AF-1226	AF-542	AC-515	BF-422	BC-322
261	10	AC-1689	BF-1630	BC- 918	AF- 823*	BF-648*	AF-389	AC-254	BC-252

II. 1975

Sample Date & Number		A: 1-2 cm. Biomass Ranked > to < by Site				B: 6-7 Biomass			
133	1	AC 3140	BF 2692	BC 2461	AF 2168	AC 757	AF 684	BF 599	BC 470
147	2	BC 2616	AC 2079	AF 2006	BF 1488	AC 620	AF 493	BF 416	BC 377
163	3	BF 2053	AC 2616	AF 1555	BC 1346	AF 581	BF 574	BC 504	AC 383
177	4	BF 1230	AF 1047	AC 801	BC 768	BF 574	BC 372	AF 325	AC 255
203	5	AC 3432*	AF 2784	BF 1822	BC 1155*	BF 866	BC 618	AF 593	AC 363
225	6	BF 1678	AC 1097	AF 1088	BC 894	BF 410	AF 305	BC 294	AC 277
238	7	BF 3412	AC 3015	AF 2940	BC 2830	BF 687	AF 668	BC 447	AC 367
315	8	BF 2764	AC 2443	AF 910	BC 666	AF 595	BC 586	AC 496	BF 396

AC = Aspen Control, AF = Aspen Fertilized, BC = Birch Control, BF = Birch Fertilized

BC(520) > BF(481) > AF(473) > AC(450)

Whereas, 1-2 cm biomass means ranked by magnitude are:

AC = BF > AF > BC.

Duncan's Multiple Range Test (α = .05) groups the 6-7 cm means:

Site	Depth	Mean ($m \cdot gm^{-1}$)	Grouping
BC	6-7 cm	520	|
BF	6-7 cm	581	|
AF	6-7 cm	473	|
AC	6-7 cm	450	|

Although not significantly different the means offer some interesting comparisons. At the 1-2 cm soil depth site birch control had the least biomass, but at the 6-7 cm soil depth BC had the greatest biomass in comparison with all sites. This lack of continuity between depths within site can be accounted for in terms of soil moisture and organic matter content (inferred from bulk density measurements). Birch control means include data from a plot (previously discussed) with a displaced mineral soil layer at 1-2 cm below the soil surface. Consequently, this site-depth combination has the greatest bulk density (1.13 to 1.80 orders of magnitude) and the lowest soil moisture (33.1 soil moisture percent to 51.9 soil moisture percent less) of all sites. This set of conditions is reversed at the 6-7 cm soil depth where there is a buried layer high in organic matter, yielding the highest soil moisture values and lowest bulk density figures (high organic matter content) of all sites at this depth (Table 15-C, 15-F). This 'reversal' of the usual order of soil layers and the resulting soil moisture, bulk density and biomass means:

	(AC, AF, BF)	BC
1-2 cm	High moisture Low bulk density High fungal biomass	Lower moisture Higher bulk density Lower fungal biomass
6-7 cm	Low moisture Higher bulk density Low fungal biomass	Higher moisture Lower bulk density Higher fungal biomass

illustrates the controlling/limiting effect of moisture and available substrate on fungal biomass.

1975 Biomass: Vegetation Type and Fertilization

Ranking of biomass means by magnitude yields the same patterns as 1974 means ranking for 1-2 cm soil depth.

AC(2208) > BF(2142) > AF(1814) > (1529).

Aspen control and birch fertilized sites are responsible for 81% of first and second place means ranked by magnitude (Table 24-II). Duncan's Multiple Range Test (α = .05) shows:

Site	Depth	Mean Biomass	Grouping
AC	1-2 cm	2208	
BF	1-2 cm	2142	
AF	1-2 cm	1814	
BC	1-2 cm	1529	
BF	6-7 cm	581	
AF	6-7 cm	530	
BC	6-7 cm	459	
AC	6-7 cm	440	

Although the 1-2 cm rankings are of the same order as 1974 means rankings, the 6-7 cm ranking is dissimilar from both the 1975 1-2 cm means and the 1975 6-7 cm means order, the one notable exception is that aspen

control 6-7 cm consistently shows the lowest biomass for both seasons. Table 25-B, combined depths by year, indicates that although there is overlap in significance of means for 1975, two distinct groups continue to stand out:

AC and BF > AF and BC for 1-2 cm.

Combined years - Combined depths

Table 25-C (N = 144, α = .05) shows that over both sample seasons there was both a significant vegetation effect:

Aspen > birch in fungal biomass

and a significant effect of fertilization

Aspen control > aspen fertilized

Birch fertilized > birch control.

In essence, the sequence of partitioned ANOVAs and Duncan's Multiple Range Tests have confirmed Table 21 (Combined ANOVA). The comparative ranking of means for both sample seasons on the basis of the combined and partitioned ANOVA and Duncan's Multiple Range Tests:

1974 AC(1278) = BF(1147) > AF(994) > BC(946)

1975 BF(1331) = AC(1303) > AF(1232) > BC(1082)

reinforces the literal interpretation of the combined ANOVA even in light of the significant interactions.

With predictable consistency (summarized in Table 26) aspen control and birch fertilized sites (at 1-2 cm or 1-2 cm combined with 6-7 cm soil depth) were approximately equal in terms of fungal biomass and significantly greater (α = .05) than aspen fertilized and birch control sites (which show an overall trend of aspen fertilized > birch control).

Table 25. Duncan's Multiple Range Test. N = 56. α = 0.05. Those means sharing a common line do not differ significantly.

		Fungal Biomass by Site and Year		
	Sample Season	Site	Biomass ($m \cdot g^{-1}$)	Grouping
A	1	AC	1278	
	1	BF	1147	
	1	AF	994	
	1	BC	946	
B	2	BF	1331	
	2	AC	1303	
	2	AF	1232	
	2	BC	1082	
C	1 + 2	AC	1290	
		BF	1238	
		AF	1113	
		BC	1014	

Table 26. Duncan's Multiple Range Test. N = 28. α = .05. Those biomass means ($m \cdot g^{-1}$) sharing a common line are not significantly different.

Fungal biomass ($m \cdot g^{-1}$) by year, site and depth.

Site	Depth	Biomass ($m \cdot g^{-1}$) Year 1	Group	Site	Biomass ($m \cdot g^{-1}$) Year 2	Grouping
AC	1-2 cm	1851	|	AC	2208	|
BF	1-2 cm	1836	|	BF	2141	|
AF	1-2 cm	1431		AF	1814	
BC	1-2 cm	1190	|	BC	1529	
BC	6-7 cm	520		BF	581	|
BF	6-7 cm	581	|	AF	530	|
AF	6-7 cm	473	|	BC	459	|
AC	6-7 cm	450	|	AC	440	|

D. III. DISCUSSION: Effect of Dominant Overstory Vegetation on Fungal Biomass in Soils

Howard and Howard (1980) in their work on microbial decomposition of birch and oak litter, state that the rate of decomposition is influenced by differing substrate quality of the two vegetation types. Van Cleve (1974) notes that, in any attempt to interpret the role of organic matter quality in decomposition, a distinction must be made between primary and secondary substrate quality. He defines primary substrate quality as the potential for decomposition of introduced organic matter, i.e., the physical, chemical and biological properties of the soil and its associated organic matter and secondary substrate quality as the potential decomposability (physical and chemical properties) of introduced organic matter. In order to address Corollary 2 of this study:

> Fungal biomass dynamics which are dependent, in part, upon substrate availability and quality, may be expected to differ between dominant overstory vegetation types aspen and birch)

it is necessary review primary and secondary substrate quality of the aspen and birch sites and relate the fungal biomass data to these parameters. It must be noted that no measurements (soil respiration, weight loss of substrate, etc.) were made which could tie the fungal biomass data to any differences in decomposition between aspen and birch sites. Additionally, the method used does not allow distinction between living, quiescent and dead fungal biomass. Elevated or depressed biomass may

not be correlated with increased or reduced decomposition for these sites so that conclusions drawn from these comparisons are conjecture. However, from studies comparing some index of fungal biomass (dilution plate counts, standing crop biomass and/or live biomass) with one or more measurements of decomposition (respiration and/or substrate weight loss), a case can be made for the comparison of fungal biomass as measured in this study and site organic matter quality.

Stotzky and Norman (1961) showed a positive correlation (R^2 = .69) of fungal biomass as determined by the dilution plate method (generally thought to be a less accurate method of determining fungal biomass than direct measurement) and CO^2 evolution over a study period of 48 days, as did Witkamp (1966). Sing and Shukla (1977) in studies of tropical dry deciduous forests showed a positive correlation of micrbial biomass as measured by the dilution plate method and total soil respiration over a period of 6 months. Flanagan and Van Cleve (1977), for an interior Alaskan black spruce ecosystem, found a positive correlation of fungal biomass as measured by the Jones and Mollison technique (1948), and *in situ* soil respiration measurements (R^2 = .61). From this work, Flanagan notes that rapid turnover of dead fungal tissue lessens the objection to using standing crop vs active fungal biomass figures. Nannipieri et al. (1978) in a study of criteria for measurement of microbial growth in soil by methods of:

1. Direct microscopic measurement
2. Soil ATP analysis
3. CO^2 evolution (respiration studies)

showed a positive correlation of direct measurements of fungal biomass with ATP analysis and CO^2 evolution, although CO^2 evolution peaks in response to carbohydrate addition preceded peaks in biomass measurements by 12 to 24 hours. Berg and Soderstrom (1979) using the Jones and Mollison technique in assaying decay rates for Scots pine needle litter found a positive correlation of standing crop fungal biomass and loss in needle litter weight over a period of 600 days which corresponded to a 35-40% initial weight loss. Baath (1980) found that live biomass (FDA active) and total biomass (Jones and Mollison, 1948), were positively correlated in a study of microbial response to clear cutting of a Scots pine forest in central Sweden. Ineson and Anderson (1982) in soil microcosm experiments found that from time 0 through 35 days direct biomass measurement and CO^2 evolution were correlated (R^2 = .69).

As noted in the Site Description and Climate section of this work, many of the problems encountered by other workers attempting to correlate microbial biomass and site characteristics: differing soil genesis, parent material, slope, aspect, stand age and climatic regimes (Baath and Soderstrom, 1982; Howard and Howard, 1980; Bissett and Parkinson, 1979a) were not encountered in this study, consequently emphasis can be placed on differing substrate quality and conditioning of the soil by dominant overstory vegetation.

Tables 27 through 30 include data compiled from Van Cleve and Noonan (1971), Van Cleve and Sprague (1971), Van Cleve (1972), Van Cleve (1974), Van Cleve and Noonan (1975) and Van Cleve (unpublished data). In all cases, data was collected from the same aspen and birch sites

Table 27. Summary of variables measured at weekly intervals (summer 1972) to assess impact of fertilization on nutrients and organic matter decomposition on aspen and birch sites. Adapted from Van Cleve (1974).

Aspen Layer	Live Mycelia ($g \cdot g^{-1}$)		Resp. ($ml \cdot g^{-1} \cdot hr^{-1}$)		Temp °C		H_2O %		Mineral N ($mg \cdot g^{-1}$)		Soluble (organic) ($mg \cdot g^{-1}$) N		Lipid ($mg \cdot g^{-1}$)		Starch ($mg \cdot g^{-1}$)		CHO ($mg \cdot g^{-1}$)	
	Cont.	Fert.	Cont.	Fert.	Cont.	Fert.	Cont.	Fert.	Cont.	Fert.	Cont.	Fert.	Cont.	Fert.	Cont.	Fert.	Cont.	Fert.
L	.00083	.00063	114.8	125.2	14.9	13.8	92.4	100.9	20.7	300.6	.1667	.6967	.0381	.0487	2.698	3.570	24.8	13.0
F	.00297	.00207	75.0	44.8	12.3	12.1	129.2	122.4	47.1	274.6	.2157	.3382	.0316	.0392	1.960	1.483	9.42	6.36
H	.00195	.00117	47.6	20.9	10.2	10.1	124.4	118.5	36.6	111.8	.2738	.3263	.0291	.0266	1.530	.763	7.36	5.30
Birch																		
L	.00059	.00065	125.7	130.2	12.8	16.3	103.1	105.3	18.7	1127.9	.1429	.2578	.0562	.0555	2.579	2.646	17.20	12.90
F	.00227	.00210	101.8	47.9	10.4	14.4	126.0	138.4	32.6	747.7	.2130	.4543	.0550	.0438	2.086	1.988	9.88	7.83
H	.00114	.00096	42.6	19.3	8.8	12.5	126.2	107.0	19.2	294.1	.1803	.2756	.0289	.0216	1.136	.780	7.13	3.51

Table 28. Means for seasonal respiration and nutrient data for aspen and birch control and fertilized study sties. Data adapted from Van Cleve (1972).

Layer	Fungi (Number·gdwt^{-1})* Cont.	Fungi (Number·gdwt^{-1})* Fert.	Resp ml·g^{-1}·hr^{-1} Cont.	Resp ml·g^{-1}·hr^{-1} Fert.	Moisture % Cont.	Moisture % Fert.	Temp. °C Cont.	Temp. °C Fert.	Glucose mg·g^{-1} Cont.	Glucose mg·g^{-1} Fert.	Nitrate mg·g^{-1} Cont.	Nitrate mg·g^{-1} Fert.	Phosphate mg·g^{-1} Cont.	Phosphate mg·g^{-1} Fert.	Mass organic matte g·m^{-2} Cont.	Mass organic matte g·m^{-2} Fert.
Aspen																
L	1.04^{7}	1.15^{7}	195.6	241.0	106.0	115.5	22.2	22.2	5.47	4.01	.033	.054	1.12	1.14	191.6	178.8
F	6.03^{6}	8.89^{6}	69.2	46.3	152.0	156.1	16.8	16.8	1.21	0.24	.022	.069	0.12	0.27	2076.0	1731.3
H	5.06^{6}	7.07^{6}	34.5	19.6	118.9	131.0	11.8	11.8	0.61	0.12	.008	.015	0.03	0.11	3353.2	3117.3
Birch																
L	5.35^{6}	1.04^{7}	153.1	229.0	116.8	132.7	18.7	18.7	7.58	5.06	.033	.032	1.41	1.71	268.1	264.5
F	7.46^{6}	1.55^{7}	80.3	67.7	128.9	170.1	15.2	15.2	3.23	0.64	.024	.048	0.32	0.38	1407.9	1524.2
H	6.66^{6}	9.37^{6}	30.8	17.1	105.5	105.1	11.7	11.7	0.54	0.16	.008	.015	0.04	0.12	3924.1	3160.5

*number of fingal colonies isolated per gram dry soil

Table 29. Selected soil chemical and biotic data. Adapted from Van Cleve and Noonan (1971), Van Cleve and Sprague (1971), Van Cleve (1972), Van Cleve (1974), Van Cleve and Noonan (1975).

	Mineral N ($mg \cdot g^{-1}$	Soluble N (organic) ($mg \cdot g^{-1}$	P (Conc. % DWT)	K (Conc. % DWT)	CHO ($mg \cdot g^{-1}$)	Starch ($mg \cdot g^{-1}$)	Live Mycelia ($g \cdot g^{-1}$)	Fungi (Number• gram dry wt)
ASPEN								
$\bar{x}$ L & F	33.88	.1912	0.135	0.180	17.12	2.4289	.00190	8.22×10^6*
H	36.55	.2738*	0.150	0.210	7.36	1.5293	.00195	5.06×10^6
BIRCH								
$\bar{x}$ L & F	25.64	.1780	0.120	0.170	13.56*	2.3320	.00143	6.41×10^6*
H	19.24	.1803	0.130	0.160	7.13	1.1363	.00114	6.66×10^6

* means significantly different at $\alpha = .05$

Table 30. Selected soil chemical and stemflow data. Adapted from Van Cleve (1974 and unpublished data).

Seasonal Averages	pH	CEC*	% Base* Sat.	Exch.* H+	Stemflow Volume	Stemflow pH
$\bar{x}$ L & F	5.55	113.3	77.3	32.1		
					43.6	7.37
H	5.10	143.0	62.4	50.1		
$\bar{x}$ L & F	5.05	103.7	65.7	21.7		
					13.0	4.48
H	4.60	129.1	47.1	37.7		

* = meq·g^{-1}

used in this study. Mean values for variables most likely to influence fungal biomass and previous fungal biomass determinations are given. Values for litter (L) and fermentation (F) layers were averaged since measurements for this study were made at a static soil depth (1-2 cm below the soil surface) which corresponds, in most cases, to the interface of the L and F layers.

A more favorable nitrogen status is evident for aspen sites for both mineral and soluble organic nitrogen fractions. The larger mineral nitrogen pool and greater organic matter biomass in aspen L and F soils (Van Cleve and Noonan, 1971) would represent a greater potential pool for increased net mineralization. From the higher concentration of readily metabolizable substances (CHO and starch) it can be inferred that organic matter produced on the aspen sites would have a narrower C/N ratio, reflecting increased potential decomposibility or accelerated decomposition rates. Van Cleve and Noonan (1973) showed that for these sites the average yearly soil organic fraction biomass turnover was 30% greater for aspen than birch. Both previous measurements of microbial biomass (Tables 27 and 28) show aspen greater than birch (significant at $\alpha = .05$ for measurement 2). The slightly increased soluble organic nitrogen and elevated CHO and starch levels could be important in increased response of opportunistic decomposers (fast growth and large number of spores/reproductive propagules), organisms for which population cycles are often delimited by optimum soil moisture conditions and easily decomposable carbon sources.

Table 29 and 30 list selected soil chemical and stemflow data from the sites. Although both sites are within the range of pH tolerance for

a large number of soil fungi, aspen sites show a higher pH, greater overall cation exchange capacity, less exchangeable hydrogen and higher base status (greater mass of base elements in aspen (1094 $kg \cdot ha^{-1}$) vs 857 $kg \cdot ha^{-1}$ birch (Van Cleve and Noonan, 1971)) which, acting in concert, indicate a better buffered chemical environment in aspen soils. The pH effect is most noticeable in stemflow from the two sites, pH of 7.37 for aspen stemflow and pH of 4.48 for birch. Howard and Howard (1980) note that in comparison of birch and oak litter decomposition those sites with elevated pH (5.0-5.7 vs sites with pH of 4.7-5.0) showed increased decomposition rates over a period of 100 days.

As Van Cleve and Sprague (1971) point out, these factors could constitute a more favorable chemical environment for microbial activity in aspen organic soils and acting in concert with the improved moisture status of aspen soils, account for significantly increased fungal biomass over that of birch soils.

D.IV. DISCUSSION: EFFECTS OF LONG TERM FERTILIZATION ON BELOW GROUND FUNGAL BIOMASS

In addressing Corollary 3:

> A manipulation of within site primary and secondary substrate quality by long term (9 years application) addition of N-P-K fertilizers may alter the magnitude of fungal biomass, in comparison with untreated sites

it is helpful to restate some of the conclusions drawn from earlier sections of this work, as they apply to manipulation of organic matter quality.

OVERVIEW:

1. The combined years ANOVA has shown a significant (α = .05) effect of fertilization on fungal biomass in the two vegetation types sampled.
2. The fertilization effect was not consistent between vegetation types. Below ground standing crop fungal biomass was decreased in aspen organic soils (01/021 horizons) and increased in birch organic soils by yearly applications, 1967 through 1975, of N-P-K fertilizers (111 $kg \cdot ha^{-1}$ nitrogen as NH_4NO_3, 55 $kg \cdot ha^{-1}$ phosphorus as treble superphosphate and 111 $kg \cdot ha^{-1}$ potassium as KCl.
3. There was no statistically significant effect of fertilization on fungal biomass in mineral soils for either vegetation type for either sample season.

4. Fertilization had no statistically significant effect on soil bulk density for either vegetation type. However, the overall trend for by-year means comparisons and the main effect for combined years (Table 14) indicates that bulk density is decreased in fertilized sites for both vegetation types at both soil levels sampled.
5. Aspen organic soils consistently had greater soil moisture content than birch. Although the difference in soil moisture regimes was not statistically significant it was of sufficient magnitude (approximately 25% greater) to be of biologic importance.
6. A point of possible importance in the explination of lack of continuity of fertilization effect between sites is that for aspen organic soil layers there is little difference in soil moisture between control and fertilized sites, however moisture means from birch fertilized sites are 25% to 30% greater than birch control sites for the 2 seasons. Combined means are:

1-2 soil depth

AC = 151%
AF = 154%
BC = 104%
BF = 128%

IV.A. Decrease of below ground fungal biomass in aspen soils

Lack of stimulation or inhibition of microbial activity in forest or agricultural soils after treatment with inorganic fertilizers is well

documented (Sing and Gupta, 1977; Sing and Shykla, 1977); Sandhu and Moraghan, 1972; Ryan and Sims, 1974; Salonius, 1972; Van Cleve and Moore, 1978; Baath et al., 1981. Baath et al. (1981) comment that:

> "...mechanisms behind the effects of (inorganic) nitrogen addition (and other inorganic nutrients) on soil microorganisms are obscure...with quite different effects in different soil systems."

They state in their studies of response to application of (NH_4NO_3) to Pinus sylvestris L. forests in central Sweden, that most indices of microbial activity decreased proportionally to the amount of fertilizer applied, as shown by the following table adapted from their work (1981).

		(NH_4NO_3) kg·ha^{-1}		
Activity Index	Control	150	300	600
1. Respiration at 15°C α g·CO^2 (h·gdwt)$^{-1}$	103	126	105	80
2. Acid phosphatase μ mole phenol released (h·gdwt)$^{-1}$ (20°C)	41	38	37	32
3. FDA active mycelium m·gdwt^{-1}	390	290	340	220
4. Total fungal mycelium m·gdwt^{-1}	9800	7000	7200	9300

They note that NH_4NO_3 or other forms of ammonium salts have historically been shown to decrease microbial activity in humus with up to 50% decrease in soil respiration and hypothesize that the decline in microbial biomass was more or less an immediate response to fertilizer

application and that the response lasted throughout the five year duration of their study. Their speculations regarding the mechanism of decrease in microbial activity include the possibility of depletion of essential nutrients other than those added and the possibility of altered root status by:

1. decreased root production rate
2. decreased root exudates mass and rate
3. decreased frequency of mycorrhizal root infection.

Other workers including Bjorkman (1970) and Menge and Grand (1978) have shown decreased occurrence of mycorrhizal root tips in fertilized forests. A decrease in mycorrhizal infection would result in less carbohydrate transported from the vascular plant to its fungal symbiont and consequently less turnover of mineralized nitrogen and other nutrients in the rizosphere. This observation is particularly germain to this study since there is indication that occurrence of basidiomycete hyphae was significantly depressed by fertilization for both vegetation types (Section D V).

Bopaiah and Bhat (1981) showed that the application of inorganic forms of nitrogen, phosphorus and potassium to cultivated lateritic soils significantly decreased biomass (number of culture colonies) of bacteria, actinomycetes and fungi in comparison to sites amended with organic manures as follows:

	Bacteria (10^4)	Actinomycetes (10^4)	Fungi (10^3)
Organic manure	129	29	10.5
Inorganic N-P-K	18	22	5.0

Taha et al. (1967) and Foster et al. (1980) report similar findings in which applications of inorganic nitrogen salts depressed soil respiration while applications of urea or manure increased respiration. Their conclusions indicate that available carbon rather than nitrogen was limiting to decomposition and that once microbial demand for carbon was satisfied a further increase in activity, as measured by respiration, was produced by finorganic nitrogen additions. Kelly and Henderson (1978) arrived at similar conclusions.

The results of this study are consistent with those of Van Cleve (1974) in which he reported that N-P-K fertilizer additions to the aspen site used for this study resulted in the main effects of:

1. Decreased forest floor respiration
   (88.72 vs 66.32 $\mu l \cdot g \cdot hr^{-1}$)
2. Decrease in fungal biomass by soil layer (C=control, F=fertilizer)
   L $8.3^{C} \times 10^{-4}$ vs $6.0^{F} \times 10^{-4}$ $g \cdot gdwt^{-1}$
   F 3.0×10^{-3} vs 2.1×10^{-3} $g \cdot gdwt^{-1}$
   H 2.0×10^{-3} vs 1.2×10^{-3} $g \cdot gdwt^{-1}$

and noted that fermentation and humus layers represent an increased cation exchange capacity, in relation to litter, and may accumulate nutrients to toxic levels, decreasing microbial activity. Van Cleve and Moore (1978), in a study of N-P-K application to a 15 year old aspen stand, concluded that increased soil salt concentration from the introduction of nitrogen and/or chloride salts could reduce soil water availability to microbes by osmotic imbalances, an important point in

that fungal biomass in this study was closely correlated with soil moisture fluctuations. They also note that a second important change in substrate quality differences between control and fertilized sites was decreased soil pH, reflecting a combination of higher plant and microbial metabolic activities which include microbial oxidation of NH_4^+ to NO_3^- with the associated increase in acidity. Although most fungi are capable of utilization of both ammonia and nitrate, ammonia is preferred for reasons of energy expenditure. In fungi, nitrate utilization is dependent upon the induction of nitrate reductase. Nitrate reductase is inhibited by the presence of ammonia (feedback repression) causing preferential uptake of ammonia, further decreasing soil pH (Nicholas, 1965; Griffin, 1972; Moore-Landecker, 1982).

IV.B. Increase in fungal biomass in fertilized birch soils

The increase in fungal biomass in birch fertilized soils at 1-2 cm below the soil surface is statistically significant and predictable over the two year field study. Although Van Cleve (1972, 1974) showed a similar increase in fungal biomass in birch fertilized litter (O1) layers it is important to note that the soil organic layer sampled for this study was at a static soil depth, 1 cm below the forest floor surface and represents, in the great majority of cases, the interface of the O1 and O21 layer with a preponderance of O21 organic material. Additionally, fertilized sites at the 6-7 cm soil layer (O21/A horizon(s)) shows an increase (non-significant) in fungal biomass.

It has been noted in the soil moisture presentation that birch fertilized soils show a mean moisture elevation of approximately 25% over unfertilized sites at the 1-2 cm soil layer. This soil moisture increase corresponds with a bulk density decrease (increased organic matter content). The improved bulk density/soil moisture carbon regime could present a more favorable environment for fungal growth.

D.V. EFFECT OF VEGETATION TYPE AND FERTILIZATION ON BIOMASS OF HIGHER FUNGI (BASIDIOMYCETES)

OVERVIEW

1. There was no significant difference in quantity of hyphae of basidiomycete fungi in aspen and birch soils; i.e., no vegetation effect.
2. Fertilization significantly decreased biomass of basidimycete hyphae in both vegetation types for both years of this study.

Baath et al., (1978) found that additions of nitrogen (unspecified form) to soil microcosms increased in relative number of yeast cells. Oliver and Van Cleve (1981) found that factorial applications of N-P-K fertilizers (112 $kg \cdot ha^{-1}$ NH_4NO_3, 56 $kg \cdot ha^{-1}$ P_2O_5, 112 $kg \cdot ha^{-1}$ KCL) to a 15 year old aspen stand did not significantly affect the number of isolates but did cause a shift in percent composition of several species of Penicillium and imperfect forms. Bharat and Srivastava (1982) found that additions of nitrogen, phosphorus and potassium decreased the number of fungal species isolated from soil microcosms and altered the ratio of species present, showing mainly a net decrease in imperfect forms with an increase in relative abundance of several Aspergillus species and the occurrence of Chaetomium sp., Curvuliaia sp. and Fuasrium sp. Joffe (1963), in a rather exhaustive study of the effects of N-P-K fertilization of alluvial clay loam soils found that fertilization doubled the quantity of isolates from soil dilution plates. Although there was no significant change in the number of species present a change in relative abundance of several species accounted for the

increased number of isolates.

All fore mentioned studies depended upon soil dilution plate determination of species composition, effectively excluding detection of presence and speciation change in higher fungi (basidiomycetes).

The sparse work addressing the effect of fertilization on basidiomycetes does so indirectly by counting mycorrhizal root tips in control and treated sites. This literature is relevant to this work only in that the Jones and Mollison (1948) technique, as used for measuring biomass in this study, dislodges and fragments ectomycorrhizal sheaths in the soils sampled so that fragments of basidiomycete mycorrhizal hyphae as well as nonsymbiotic soil inhabiting basidiomycete hyphae are measured.

Conflicting data is presented for those studies assessing the effect of fertilizers on mycorrhizal formation. Menge et al. (1977) notes that fertilization with NH_4NO_3 at 56 and 112 $kg \cdot ha^{-1}$ resulted in 40% fewer mycorrhizal root tips in the first 6 months after fertilization. Two years after fertilization the treated site showed 20% fewer mycorrhizal root tips than control sites. Fertilization with 25 $kg \cdot ha^{-1}$ phosphorus ($Ca(H_2PO_4)_2$) did not affect numbers of root tips while applications of N + P decreased mycorrhizal root tips by 13-15%. Applications of N + P + K showed no significant effect on mycorrhizal infection. Baath et al. (1981) noted that increasing rates of NH_4NO_3 from control to 150, 300 and 600 $kg \cdot ha^{-1}$ drastically reduced the percent occurrence of the basidiomycete Piloderma bicolor, a non-mycorrhizal cellulose decomposer, from 100% occurrence in soil isolates to 20% occurrence.

For this study, fungal lengths were designated as clamped or unclamped during measurement. Although the presence of clamp connections, a hyphal outgrowth or branch for passage of one of the two nucleii formed during bi-nucleate cell division, can be used as an identifying characteristic of basidiomycetes, not all basidiomycetes have clamp connections and basidiomycete mycelium in a monocaryotic stage lack them. These factors, coupled with the fact that fragmentation of basidiomycete mycelium during analysis most probably results in sections occurring without clamps, indicates that 'clamped' biomass represents an underestimate of the percent composition of total biomass attributable to higher fungi. However, the method is adequate for comparative studies. Laursen (1976) reports mean values for tundra soils ranging from 28% to 7.5% basidiomycete contribution to total fungal biomass with an overall mean of 10.8%. Frankland (1981) indicates that for the L horizon of a temperate woodland, basidiomycete mycelium comprises approximately 60% of all living fungal biomass.

Figure 75 shows that for this study approximately 12.2% of the total biomass for control sites 1-2 cm below the soil surface (01-021 horizons) is attributable to basidiomycetes. Individual means contributing to this overall average show that the percentage of total standing crop fungal biomass attributable to basidiomycete hyphae rose as high as 50% during the course of the field season.

There is a significant fertilization effect on clamped biomass for both sample seasons; fertilization significantly decreased (α = .0010, N = 40) the percent of total fungal biomass attributable to basidiomycetes in both vegetation types.

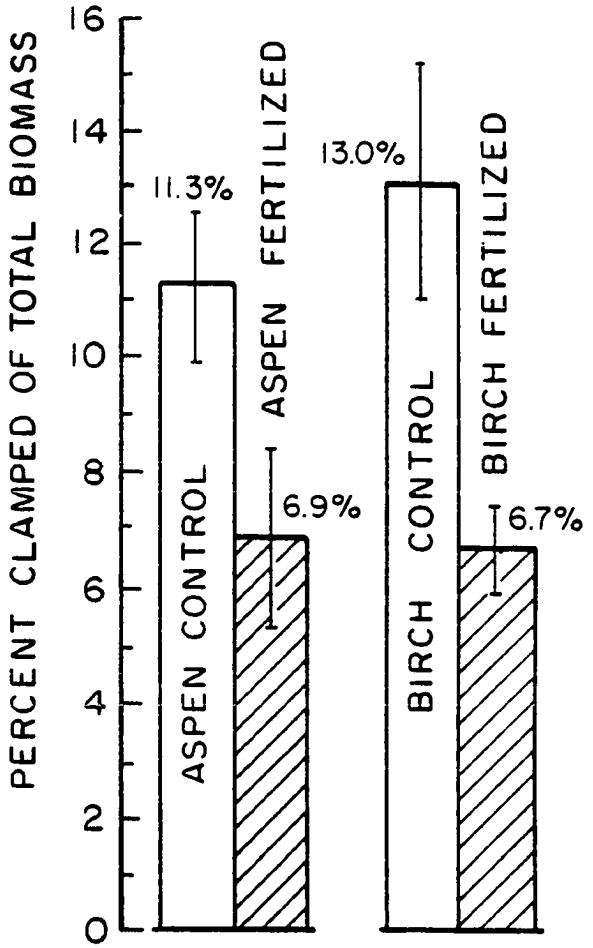


Figure 75. Fungal biomass ($m \cdot g^{-1}$). Effect of vegetation type and fertilization on occurrence of basidiomycete (clamped) hyphae.

SUMMARY AND PROSPECTUS FOR FURTHER RESEARCH

SUMMARY

The central hypothesis:

> Below ground standing crop fungal biomass in upland, permafrost-free interior Alaskan paper birch (*Betula papyrifera*) and quaking aspen (*Populus tremuloides*) forests exhibit within season population changes which may be accounted for by changes in microclimatic conditions; specifically, soil temperature and soil moisture. Within the confines of dates comprising the field season for this study, soil moisture is thought to be the overriding causative factor for 'seasonal' fluctuations in fungal biomass,

is substantiated from the data. Correlation and regression analysis indicate that soil moisture is significantly correlated with fungal biomass. The relationship is pronounced for field season one when soil moisture may have acted as a limiting factor in fungal biomass development. Fluctuations of soil temperature ($\pm 10^{\circ}C$) encountered during mid-May through mid-September sample dates show little correlation with fluctuations in fungal biomass and in isolated cases show negative correlation, possibly due to increased moisture availability (at decreased soil temperatures) to soil fungi under moisture stress. There is indication, from elevated biomass encountered at the first sample data for most sites for both seasons and elevated biomass for one sample taken after snowfall and ground freeze, that the time frame selected for

this study did not encompass all periods of significant fluctuation in fungal biomass.

Corollary 1:

The magnitude of fungal biomass is affected by localized differences in soil bulk density, used here as a comparative index of organic matter (substrate) content, was shown to be correct. Bulk density variations and the concommitant increase in soil moisture and organic matter content associated with decreased soil bulk density in horizons not subject to rapid drying affected the magnitude of fungal biomass for both single point and seasonal means.

Corollary 2:

Fungal biomass dynamics which are dependent, in part, upon substrate availability and quality, may be expected to differ between dominant overstory vegetation types (aspen and birch) which have been shown to produce organic materials of different quality,

was substantiated by the data from this study. Aspen soils with a more favorable chemical environment for microbial activity (increased cation exchange capacity/increased exchangeable base, elevated soil pH and a consistently greater soil moisture content, in organic layers) showed significantly greater fungal biomass than birch sites.

Corollary 3:

> Investigations aimed at testing corollary three: A manipulation of within site primary and secondary substrate quality by long term (nine years) additions of N, P and K fertilizers may alter the magnitude of fungal biomass, in comparison with untreated sites,

produced conflicting results for the two vegetation types. Biomass was decreased in aspen soils and increased in birch soils by long-term inorganic N-P-K fertilization. Van Cleve (1974) showed similar results on the same sites; however, other work in the same or similar taiga vegetation has produced conflicting results (Van Cleve, 1972; Van Cleve and Moore, 1978; Van Cleve and Oliver, 1982), an indication that data from this study is probably tied to a specific set of soil chemical, physical and biotic conditions acting in concert within the temporal and spatial confines of this study and conclusions drawn may not be applicable over the range of similar taiga vegetation.

FURTHER RESEARCH

It has become evident during the course of this work that a more integrated approach to the study of population cycles of soil fungi is necessary to explain biotic phenomena in terms of physical, chemical and climatic state factors. Traditionally, mycologists have treated the soil system as a somewhat inert carrier for fungi under study, in contrast to the meticulous chemical monitoring of artificial media used for *in vitro* studies of fungal response to substrate form and composition, temperature, pH, competition, etc. Since a great many mycologists

trained in North America have a limited background in forestry, soil physics, general soil science, biometeorology and biochemistry of decomposition, this static treatment of the soil complex is understandable. However, an ecosystem approach to decomposition cycles makes it necessary that the mycologist interact in each of these areas. Figure 76 is a grossly simplified view of factors which must be considered in hypothesis testing and experimental design for *in vivo* studies of soil fungal dynamics. If P = the population of soil fungi extant at T_1 (Time of commencement of study) it must be considered that this population (PT_1) is composed of metabolically active and dead components as well as live but metabolically inactive (Pmi_1) fungi and a potential for both short term and long term fluxes in the form of vegetative and sexual reproductive propagules (Pp_1). This balance is dependent upon fluxes in the soil matrix, conditions under constant change in the form of temperature and moisture input (with consideration given to stemflow and through fall) input of litter, root biomass, root exudates, changes in moisture availability and the interactions of temperature and moisture cycles. Of equal consideration are effects of successional sequences and stand maturity (organic matter quality) of vascular plant vegetation associated with the soil system under study. These factors act to modify the soil fungal population, in terms of mass and composition along a time gradient (P_{Ti}). In order to draw conclusions concerning the change in PT_1 and P_{Ti} it is imperative that any experimental design contain provisions for defining the soil matrix over time with particular emphasis on a high resolution of microclimate monitoring.

The soil matrix should be described in terms of substrate quality for soil horizons sampled with aprticular emphasis on measurements of organic matter content, C/N ratio and nitrogen content and form for individual soil samples used for biomass measurement.

Fungal biomass measurements should ideally provide indices of total standing crop, living tissue and an index of population potential for increased biomass or increased metabolic activity (as measured by enzyme activity or respiration) over changes in microclimate, nutrient and carbon source input likely to be encountered in the field. Provisions for monitoring change in size of vegetative hyphae over:

(1) Time (successional sequences often show population shifts to vegetative hyphae of significantly different hyphal diameter); and

(2) Soil depth (from this study there is a significant and predictable decrease in mean hyphal diameter in mineral soils)

must be made for accurate extrapolation of data from hyphal length per gram dry soil to mass per unit area figures.

Consideration of these factors would allow more accurate integration of fungal population parameters into studies concerned with nutrient cycling and turnover of forest floor biomass and would provide the mycologist with more accurate qualitative and quantitative data, allowing the formulation of successively more sophisticated hypotheses and conclusions regarding the interaction of fungi in ecosystem processes.

Figure 76. Interactions of climate, vegetation, soil matrix and below-ground fungal biomass over time: Pt_1 = total population (biomass) measured at time 1, Pmi = porportion of Pt_1 attributable to live but metabolically inactive fungi, Pp_1 = population potential for growth fluxes (reproductive propagules, etc.); Pti, Pmi and Ppi = population component fluxes over time.

APPENDIX 1

SAMPLE FUNGAL BIOMASS CALCULATIONS FOR:

(1.) Meters Mycelium per gram dry soil

(2.) Grams fungal biomass per gram dry soil

(3.) Meters Mycelium per unit area

(4.) Grams dry wt. biomass per unit area

(1.) METERS MYCELIUM PER GRAM DRY SOIL

A. Volume of measurement grid

Modified whipple disc measurement grid superimposed on microscope visual field = 117 um x 0.0117 cm x 0.010 cm = 1.3689×10^{-6} cc

B. Total number of cubic cm. sampled = Total number of visual field counted x CC's per field

= 1.3689×10^{-6} cc x 50 (visual fields) - 68.445×10^{-6}

= 6.8445×10^{-5} cc

C. Fraction of Initial suspension actually measured. Total initial soil/water suspension = 50 cc

so $\underline{6.8445 \times 10^{-5}}$ cc = 1.3689×10^{-6} or 1.3689×10^{-4} %

D. Fraction of Dry Soil in Suspension

For Example:

Soil wet wt. = 14.8334 grams

Soil dry wt. = 6.7634 grams

so: $\frac{6.7634}{14.8334} = .4560$ or 45.6% of soil wet weight is attributable to dry soil

Therefore of 2.5 gram wet wt. of soil in the 50 cc suspension the actual wt. of dry soil = 2.50 x .4560 = 1.1399 grams dry soil

E. Actual amount of dry soil observed in 50 fields

From "C" above we noted that 1.3689×10^{-4}% of soil was sampled. Therefore $1.3689 \times 10^{-6} \times 1.1399$ (the total grams dry soil in suspension) = 1.5606×10^{-6} grams dry soil

1.5605×10^{-6} grams dry soil actually measured for biomass

F. Length of Hyphae measured in sample

For this example, figure = 6326.95 μm hyphae measured in 1.5065×10^{-6} grams dry soil or 0.00632695 meters per 1.5605×10^{-6} grams dry soil (or per 50 microscope fields)

Length hyphae = 6.32965×10^{-3} meters

Using the figures in this example:

6.32695×10^{-3} meters in 1.5606×10^{-6} grams dry soil =

$$\frac{6.32695 \times 10^{-3} \text{ meters}}{1.5605 \times 10^{-6} \text{ gms}} = 4.054438 \times 10^{3} \text{ meters} \cdot g^{-1} =$$

4054.4 meters mycelium per gram dry soil

Measurements for meters mycelium per gram dry soil =

1. Grid volume = 1.3689×10^{-6} cc
2. 50 grids per slide counted

3. Total volume of suspension per slide counted = 6.8445×10^{-5} cc
4. Percent of 50cc suspension actually counted = 1.3689×10^{-4}%
5. Fraction of dry soil in suspension = 45.6% of initial wt. For all samples wet wt. = 2.5 gm.
6. Example: Amt. of dry soil in suspension = 1.1399 grams
7. Amount of dry soil observed in 50 fields = 1.5605×10^{-6} gms
8. Length of hyphae measured in 50 fields = 6326.95 um or 6.32695 meters per 1.5605×10^{-6} gms dry soil
9. Meters per gram dry soil = 4054.4

Now that the baseline variable Meters Mycelium per Gram Dry Soil is calculated the remaining variables may be calculated as follows:

(2) GRAMS MYCELIUM per GRAM DRY SOIL

Necessary for the calculation of $g \cdot g^{-1}$ are: Hyphal diameter ($\bar{X}$ = 2.75μm, N = 600) and specific gravity of X length of hyphae. Specific gravity was arrived at by flotation (displacement of H_2O in a column, assuming 1 cc displacement = 1 g i.e., mass per unit volume.

Given: 1. Hyphal diameter = 2.75μm
2. Specific gravity = 1.10
3. Hyphal length = 1.00 meters

Weight of 1 meter mycelium in wet wt = 6.534×10^{-6} gm wet wt.

.115 = experimentally derived fract. of wet wt that is dry wt or 11.5% = dry wt

Therefore:

6.534×10^{-6} (wet wt. of 1 meter mycelium) x 0.115 (mycelial dry wt fraction)

$= 7.510 \times 10^{-7}$ grams dry wt. · meter mycelium^{-1}

so for the example given of 4054.4 meters of mycelium per gram of dry soil:

$$4054.4\ m \cdot g^{-1} \times 7.510 \times 10^{-7} = 3.044883 \times 10^{-3}$$

grams dry fungal tissue per gram dry soil = 3.0449×10^{-3}

In order to figure biomass weight on a Unit Area Basis the following measurements are necessary:

1. Bulk Density: for this example BD = .334 g·cc^{-1}

(3) Grams Dry Wt. Fungal Biomass per Meter^2 to Dpth of 1 cm.

3.04483×10^{-3} (see 2 above) x 0.334 g·cc^{-1}

$= 1.01699 \times 10^{-3}$ grams biomass per cc

x 10,,000 (1 meter sq to dpth of 1 cm)

= 10.16991 grams dry wt. biomass per 10,000 cc^3

(4) Lengths of Mycelium per unit area =

meters mycelium per gram dry soil x B.D. x (1×10^4)

= (in this ex.) 13,5441,700 m·m^{-2} to 1 cm or

1.354×10^8 meters mycelium per 10,000 cc

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