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DATE: 1985

CARBOHYDRATE RESERVES AND PHENOLOGY OF
FOUR WESTERN MONTANA
UNDERSTORY FORAGE SPECIES

by

Janice K. Krueger

B.S., University of Montana, 1980

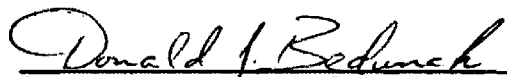
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Master of Science

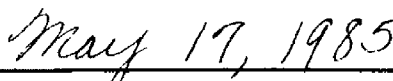
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Krueger, Janice K., M.S., June 1985

Forestry

Carbohydrate Reserves and Phenology of Four
Western Montana Understory Forage Species (60 pp.)

Director: Donald J. Bedunah ^{DTB}

The objectives of this research were: 1) To describe the seasonal carbohydrate reserve cycles of four western Montana understory forage species and the relationships of these cycles to phenological growth stages, 2) to study the effects of different forest habitat types on the species' carbohydrate reserves and phenology, and 3) to study the effects of canopy cover on the species' carbohydrate reserves and phenology.

The four study species were elk sedge (Carex geyeri), snowberry (Symphoricarpos albus), serviceberry (Amelanchier alnifolia) and pinegrass (Calamagrostis rubescens). Plants were collected from four forest sites on Lubrecht Experimental Forest at approximate two-week intervals in 1983. Pinegrass was also collected on 10 dates in 1984. The sites were comprised of a clearcut and forested area within two different habitat types. Total nonstructural carbohydrates (TNC) were determined using an enzyme digestion technique. Data were analyzed to compare TNC for each species by site and date.

It was concluded that site and date were significant factors affecting TNC in all four species. Site by date interactions were also significant for all species but serviceberry. In general, TNC in elk sedge, snowberry and serviceberry were higher on forested sites than clearcut sites (within the same habitat type) while the opposite was found for TNC in pinegrass. Comparisons across habitat types (and within the same canopy cover) gave inconsistent results; although, significant differences were found in all species. Differences between dates and site by date interactions were closely related to differences in the phenological development of the plants.

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CHAPTER I

INTRODUCTION

The majority of western Montana's publicly owned land is forested. Many of these areas provide an important forage resource for both livestock and wildlife. In northwestern and west-central portions of the state some of the most open, low-elevation forests (i.e. Pinus ponderosa series and drier habitat types in the Pseudotsuga series) and streamside areas have been moderately to heavily grazed by cattle, horses and sheep. Clearcuts and other logged areas are also often used by cattle. Production of forage varies considerably between habitat types depending on the density and nature of the tree cover and composition of understory plants.

A primary concern of rangeland managers is the maintenance of desirable forage species for grazing animals. Proper frequency, intensity and season of forage use will ultimately depend upon the physiological state or condition of the plants within various sites of the forest ecosystem. For perennial plants adequate carbohydrate reserves is the determining factor in the maintenance of healthy and productive plants. Severe depletion of a plant's carbohydrate reserves may result in decreased vigor and productivity and a possible shift in competitive balance toward nonpalatable species resulting in a change in community composition. Significant damage to the plant will occur only if reserves fall below a certain critical level. This critical point can vary among species and varieties and is probably affected by environment, season or phenological stage of development and management.

Knowledge of a plant's seasonal carbohydrate reserve cycle and the relationships of that cycle to the plant's environment can be used by range managers to establish grazing guidelines that will maintain high yields of desirable species and control of less desirable ones. The present study was developed to provide data for the establishment of management criteria for the use of forage in western Montana's forested ecosystems. Specific objectives were:

1. To describe the seasonal carbohydrate reserve cycles of four western Montana understory forage species and the relationships of these cycles to phenological growth stages,
2. to study the effects of different forest habitat types on the species carbohydrate reserves and phenology, and
3. to study the effects of canopy cover on the species carbohydrate reserves and phenology.

CHAPTER II

LITERATURE REVIEW

Carbohydrate reserves in plants have received much attention from plant physiologists and range researchers. This section includes a general discussion of carbohydrate reserves describing the different types found in plants, where they are stored and how they are used by the plants. Internal and external factors affecting carbohydrate levels and research related to these topics are also reviewed.

Through the process of photosynthesis green plants are able to assimilate carbon dioxide into complex carbon compounds. Of the carbon compounds produced carbohydrates are considered to be the most important in terms of supplying energy to the plant (McIlvanie 1942, Weinmann 1948, Cook 1966, Smith and Silva 1969). Energy is produced as the carbohydrates are oxidized to CO_2 during respiration. It is then used by the plants to synthesize the large molecules required for growth. Carbohydrate substances used most commonly by green plants as sources of energy are: monosaccharides (glucose and fructose), oligosaccharides (sucrose and maltose) and polysaccharides (starch and fructosans).

The monosaccharides consist of a single chain of carbon atoms, the most abundant being hexoses and pentoses. They are usually present only in small amounts and may be regarded as metabolic intermediates; i.e., they combine with other simple sugars to form the more complex polysaccharides such as starch and cellulose (Williams et al. 1973). The most common oligosaccharides are the disaccharides with sucrose and maltose being the most abundant in plants. One sucrose molecule

contains one molecule each of glucose and fructose while maltose contains two glucose molecules.

Starch is a pure glucose polymer which is present in two forms: amylose and amylopectin. Amylose is a linear molecule consisting of between 50 and 1,500 glucose units, is soluble in hot water and forms 10 to 30% of most starches. Amylopectin is highly branched, insoluble in water and comprises the remaining 70 to 90% of the starch in most plants. Fructosans also occur in two forms: inulins and levans. Inulins are found mainly in dicotyledonous species while levans are the major fructosan of grasses (Walton 1983). The structural carbohydrates, hemicellulose (pentosans and hexosans) and cellulose, are not considered to provide a significant energy source to the plant (McCarty 1938, Sullivan and Sprague 1943, Weinmann 1948). Therefore, the terms total nonstructural carbohydrates (TNC) or total available carbohydrates (TAC) are generally used in reference to a plant's energy reserves.

The form of stored carbohydrate varies among plant species (Trlica 1977). Smith (1968) studied 28 native perennial grass species that occur in Canada and the northern United States and 16 grass species introduced from northern Europe and Asia to determine their predominant reserve polysaccharide. He found that most of the native species accumulated starch as the principle polysaccharide while all of the temperate-origin introduced species accumulated fructosans. Species in the Hordeae, Aveneae and Festuceae tribes, whether native or introduced, accumulated fructosans. His data, along with that of others (de Cugnac 1931, Weinmann and Reinhold 1946), has been used to classify grass species as to either tropical-origin (those storing principally starch)

or temperate-origin (those storing principally fructosans).

Carbohydrates are translocated from the photosynthesizing tissues (sources) to the rapidly growing or storage organs (sinks). These carbohydrate reserves may be stored at least temporarily in all plant parts. However, the major storage organs in grasses are the stolons, corms, rhizomes and stem bases (Walton 1983); in woody species, twigs may also be important storage sites (Cook 1966). Transformation of the sugars from one form to another often occurs within the storage organs. Weinmann (1952) found that sugars translocated to underground storage organs may be converted to either fructosans or starch.

The quantity of carbohydrates stored in plants varies with species and plant part. In a study on mountain snowberry (Symphoricarpos oreophilus) George and McKell (1978) observed the following TNC concentrations in different plant parts on the same date: small roots - 11.52%, large roots - 4.89%, root crowns - 5.72% and old stems - 8.47%. Perry and Moser (1974) suggested that the concentration of TNC in various storage organs should be determined for individual species in order to locate the storage organ with the greatest reserve concentrations.

Perennial plants use their stored reserves as substrate for growth and respiration (White 1973). Specifically, there are three major stages of phenological development when their use is required: (1) during the over-wintering period, (2) during growth initiation in the spring, and (3) during regrowth following herbage removal. For some plant species a fall regrowth period and/or reproduction may cause an additional drawdown of reserves (Trlica 1977).

McCarty and Price (1942) observed that winter respiration and the first 10% of the annual growth consumed about 75% of the root reserves before any replenishment occurred in mountain forage plants. Daer and Willard (1981) reported the low point in reserves of bluebunch wheatgrass (Agropyron spicatum) occurred during rapid spring growth when 29% of the vegetative growth was completed. In studying the carbohydrate reserves of six mountain range plants, Donart (1969) found that minimum root reserves were reached during the early spring after producing approximately 15% of their annual growth. These studies show that most perennial plants have a significant decrease in reserve levels in the spring; however, the extent and duration of drawdown varies considerably among plant species.

The level of TNC reserves for any one plant species is affected by internal and external factors including growth rate, plant development stage and environment (Trlica 1977). Numerous studies have shown an inverse relationship between carbohydrate reserve storage and rate of growth (McCarty 1938, Mooney and Billings 1960, Brown and Blaser 1965, Donart 1969, Menke and Trlica 1981). The results were the same whether the plants studied were grasses, shrubs or forbs. These same authors observed similar patterns when TNC reserves were related to phenological stage of plant development or annual growth cycles. Trlica (1977) stated that generally, carbohydrate reserve levels of perennial plants follow either a V- or U-shaped cycle. Plants with a V-shaped cycle have rapid depletion of reserves during the initiation of growth in the spring followed by a rapid accumulation of reserves. Plants with a U-shaped cycle generally maintain low levels of reserves during active

growth, with storage being replenished only after the growth rate declines as the plant approaches maturity or seed shatter.

Carbohydrate reserve levels also exhibit diurnal variations (Waite and Boyd 1953, Holt and Hilst 1969, Lechtenburg et al. 1972). Generally, levels are highest in the late afternoon, decline during the evening and night and reach the lowest levels in early morning. Time-of-day and percent change varies with species, plant part and type of carbohydrate studied. Holt and Hilst (1969) reported that variation in water-soluble carbohydrate content (monosaccharides, sucrose and fructosans) accounted for almost all of the daily variation in TNC content of Kentucky bluegrass (Poa pratensis). In studying the aerial parts of perennial rye-grass (Lolium perenne), Waite and Boyd (1953) found that while sucrose increased from a low of 5.3% to a high of 7.0% the hexoses only varied from 2.4% to 2.9%. They also found that the fructosan content varied irregularly throughout the day.

Environmental factors which have been found to affect carbohydrate reserves include soil temperature, water and nutrient content, air temperature and light. According to Walton (1983) the way in which temperature influences carbohydrate reserves is dependent upon the origin of the species and the relationship between the environmental temperature and the optimum temperature for photosynthesis. Optimum temperatures for growth and net photosynthesis of temperate-origin grasses are 20 to 25°C, whereas those for tropical-origin species are 30 to 35°C (Walton 1983). This difference is caused by the photosynthetic pathways of the two groups. The temperate-origin grasses have only the C-3 (Calvin) pathway while tropical species have both C-3

and C-4 (Hatch and Slack) pathways.

Blaser et al. (1966) studied the relationship between carbohydrate accumulation and growth of orchardgrass (Dactylis glomerata) under different air temperatures. They found that the fructosan content in above-ground growth was 15.5% at 15.6°C and 7.6% at 32.2°C when light was held constant. When temperatures were increased from 15.6°C to 32.2°C percent fructosan decreased and vice versa. Leaf expansion and cell division increased with rises in temperature to an optimum between 20 and 25°C but carbohydrate content was highest at low temperatures. Their results indicate that photosynthesis has a lower optimum temperature than growth. According to Colby et al. (1966) temperature is the most important weather factor affecting carbohydrate reserves in orchardgrass during active spring growth. Reserves increased during periods of cool weather and decreased at high temperatures. Even short periods of hot, dry weather caused sharp reductions in carbohydrate levels.

Winter survival has been found to be positively related to carbohydrate reserve levels. McCarty and Price (1942) found that high levels of stored reserves were associated with cold resistance and survival in mountain brome (Bromus carinatus) and slender wheatgrass (Agropyron trachycaulum). Smith (1964) found that plants with low reserves in the fall could not develop a high level of frost hardiness.

Effects of soil temperature on carbohydrate reserves are, like air temperature, dependent upon the plant's optimum photosynthesis and respiration temperatures. If the temperature is optimal for photosynthesis then either an increase or a decrease in temperature

should reduce carbohydrate reserves (Walton 1983).

When discussing the relationship between soil water and carbohydrate reserves one must again examine the effects of water on growth rate or photosynthesis and respiration. Studies by Eaton and Ergle (1948), Brown and Blaser (1965), Blaser et al. (1966) and Dina and Klikoff (1973) showed that total carbohydrates tended to increase in plants during periods of water stress. This was attributed to a reduction in growth indicating that photosynthesis and stomatal action are less inhibited by moisture stress than are cell expansion and differentiation. When growth was again stimulated by either a natural rainfall or irrigation, total available carbohydrates were reduced in crested wheatgrass (Agropyron cristatum) and Russian wildrye (Elymus junceus) (Trlica and Cook 1972).

Studies involving the nutrient enrichment of soils and its effects on reserves have produced conflicting results. It appears that not only the amount of fertilizer applied but also the plant's phenological stage at which it is applied and other abiotic factors, such as temperature and moisture, are involved. Nitrogen deficiency in grasses generally results in an accumulation of nonstructural carbohydrates because of reduced plant growth (Brown and Blaser 1965) while applications of nitrogen stimulates growth and tends to decrease carbohydrate reserves (Blaser et al. 1966, Colby et al. 1966, Lechtenburg et al. 1972).

Production of carbohydrate reserves in plants is directly related to photosynthetic rate which depends in turn on light intensity and duration (Wardlaw 1968). When intermediate wheatgrass (Agropyron intermedium) plants were covered on June 28 and August 11 to simulate an

early and a late etiolation treatment, total water-soluble carbohydrates in stem bases and roots were drastically depleted. At 1% of the dry weight the vigor was too poor for the plants to recover after clipping, resulting in mortality (Ogden and Loomis 1972). Young and Smith (1980) studied the influence of sunlight on photosynthesis of the forest understory species heartleaf arnica (Arnica cordifolia). When comparing plants from relatively open understory microhabitats to those from densely shaded microhabitats they found that stomatal behavior was similar with rapid stomatal opening during sunlit periods and closure during shaded periods. This resulted in rapid increases in photosynthesis during sunlit periods. However, sun plants had maximum photosynthesis values (photosynthetic rate per unit leaf area) that were approximately three times greater than the shade plants.

One of the essential features of any forage plant is that it should be capable of regrowth following successive defoliations (Walton 1983). Numerous researchers have studied the influence of clipping or grazing on the carbohydrate reserves and regrowth potential of forage plants (McCarty and Price 1942, Baker and Garwood 1961, Kinsinger and Hopkins 1961, Davidson and Milthorpe 1965, Donart and Cook 1970, Trlica and Cook 1972, Buwai and Trlica 1977, El Hassan and Krueger 1980). Earlier studies dealt with the question of whether or not reserve carbohydrates were indeed used by plants to replace the photosynthetic tissue removed by grazing. McCarty and Price (1942) compared the carbohydrate content in roots of grazed and ungrazed mountain brome plants. They found significantly less reserves in the grazed plants shortly after grazing began, eventually diminishing to 55% of the carbohydrates in ungrazed

plants. Since that time studies have concentrated on determining the effects of various defoliation techniques such as the frequency and intensity to which plants are grazed and the season of defoliation or phenological growth stage of the plants.

When orchardgrass was subjected to infrequent and frequent cuttings it was found that reserve levels in the stubble were higher in the infrequently cut plants than in the more frequently cut plants (Baker and Garwood 1961). Kinsinger and Hopkins (1961) clipped four grass species to two different levels simulating a moderate and a heavy grazing pressure. Their data indicated that moderate grazing of these species did not appreciably decrease root reserves while the heavily-clipped grasses suffered losses in carbohydrates and consequently, in vigor and productivity.

Donart and Cook (1970) studied the effects of heavy clipping at low and high reserve levels on six native range plants. Carbohydrate reserves were found to be significantly affected by defoliation for all species except senecio (Senecio integerrimus). Defoliation of the grasses and forbs was more detrimental early in the season (when reserves were low) than late in the season (when reserves were high). Defoliation of browse late in the season lowered reserves more than early defoliation.

CHAPTER III
STUDY AREA DESCRIPTION

Lubrecht Experimental Forest

Location

The Lubrecht Experimental Forest, approximately 117 square km in size, is located 56 km northeast of Missoula, Montana in the Blackfoot River Valley. Elevations on the forest vary from 1,110 to 1,920 meters and include flat or gently-rolling terrain to steep, mountainous topography (Steele 1964).

Climate

The annual average temperature on the forest is 4.0°C. January is generally the coldest month averging -8.4°C while July's 16.8°C average is the hottest. Annual precipitation averages 44.3 cm with January receiving the highest precipitation (6.0 cm) and July receiving the least (2.4 cm) (Steele 1981).

Geology and Soils

Six distinct parent material groups are found on the Lubrecht Forest (Brenner 1968). The Belt and Granite groups are associated with relatively steep (15-40%) slopes that have a mantle of colluvial material. These two groups comprise approximately 83% of the forest. The benches that occur on slopes of 8% or less are associated with Tertiary parent materials while the flats (slopes of 2% or less) are

mainly of Alluvium material. These two groups cover an additional 11% of the forest. The remaining 6% is comprised of either Limestone or Lamprophyre parent material.

Lubrecht Forest contains four soil orders: Alfisol, Entisol, Inceptisol and Mollisol (Nimlos, personal communication). Almost 90% of the soils are pedologically young (Inceptisols and Entisols) with little evidence of soil development.

Vegetation

The majority of Lubrecht Forest is second-growth timber, most of the area having been logged from 1904 to 1934 (Steele 1964). According to work by Teuber (1983) Pseudotsuga menziesii/shrub habitat types are the most common on the forest with the Pseudotsuga menziesii/Symphoricarpos albus and Pseudotsuga menziesii/Vaccinium caespitosum habitat types representing approximately 44% of the forest's timbered area. Picea and Abies lasiocarpa habitat types also exist.

Sampling Sites

Site 1 is a Pseudotsuga menziesii/Symphoricarpos albus habitat type (Pfister et al. 1977) at an elevation of 1,230 meters. The area slopes south at about 10%. Overstory vegetation is almost exclusively ponderosa pine (Pinus ponderosa) with a canopy cover of 50%. Understory vegetation is mainly pinegrass (Calamagrostis rubescens), elk sedge (Carex geyeri), common snowberry (Symphoricarpos albus) and serviceberry (Amelanchier alnifolia). This site is referred to as the PSME/SYAL forest.

Site 2 is a clearcut (canopy cover 0%) adjacent to Site 1. Elevation, slope and aspect are the same as those for Site 1. Vegetation on Site 2 is very similar to Site 1 except the overstory has been removed. This site is called the PSME/SYAL clearcut.

Site 3 is a Pseudotsuga menziesii/Vaccinium caespitosum habitat type at an elevation of 1,260 meters. Slopes are less than 5% on a northwest exposure. Overstory vegetation is a mix of western larch (Larix occidentalis) and Douglas-fir (Pseudotsuga menziesii) with a canopy cover of approximately 60%. Understory plants are pinegrass, elk sedge, snowberry, dwarf huckleberry (Vaccinium caespitosum) and kinnikinnik (Arctostaphylos uva-ursi). This site is called the PSME/VACA forest.

Site 4 is a clearcut adjacent to Site 3 with the same elevation, slope and aspect. Vegetation in Site 4 consists of the same understory species that are listed above for Site 3. Canopy cover is 0%. This site is referred to as the PSME/VACA clearcut.

Brenner (1968) mapped the parent material under all four sites as Tertiary basin deposits -- sandstones, siltstones, mudstones and conglomerates.

CHAPTER IV

MATERIALS AND METHODS

Plant Species Descriptions

All four species used in this study are perennial, native, cool-season plants commonly associated with several forest habitat types (especially Douglas-fir) of the Northwest.

Elk sedge is a caespitose, grass-like plant of the family Cyperaceae. It reproduces by seeds and by thick, scaly rhizomes. It is considered good forage for cattle and elk and is especially important in the winter because of its evergreen nature.

Snowberry, a member of the Caprifoliaceae family, is a wide-ranging shrub of the northern United States and Canada. It is a thicket-forming rhizomatous species which also reproduces by seed. Although no livestock losses have been reported, the leaves are reported to contain saponin, a poisonous substance. It is browsed in the fall, usually by deer.

Serviceberry is a shrub or small tree of the Rosaceae family. Its growth form is variable and includes small, single-stemmed plants and large bushy clumps. Reproduction is both sexual and asexual (sprouting from the root crown or lateral roots). The young growth is considered fair to good browse for livestock and excellent browse for deer and moose.

Pinegrass is a rhizomatous grass belonging to the tribe Aveneae. It is a slender, tufted grass with mostly basal leaves. Reproduction is by rhizomes or by seed in the more open areas. It is considered fair

forage for cattle and elk.

Field Work

The four sampling sites described in Chapter III were selected in March of 1983. The selection criteria included (1) the representation of two distinct habitat types, (2) a forested area and a clearcut (with the same elevation, slope and aspect) within each habitat type, and (3) representation of the study plant species.

Plant samples were collected at approximate two-week intervals from April 13 through October 22 in 1983. Pinegrass was also collected on ten dates from March 19 until August 22 in 1984. Serviceberry was not well represented on the PSME/VACA sites; therefore, it was not collected from these sites. Five plants per species were sampled on each collection date. Beginning May 27 only 3 serviceberry plants were collected at the PSME/SYAL sites because of the small number of plants present. Sampling began at dawn to minimize variation in TNC due to time-of-day.

The plant part or storage organ sampled varied with species as follows: elk sedge -- all roots to a depth of 20 cm for a belowground part and a 2 to 3 cm section of root crown for an aboveground part; snowberry and serviceberry -- a 3 to 4 cm portion of the root crown or stem base; pinegrass -- all roots and rhizomes to a depth of 20 cm. Samples were placed on dry ice to slow respiration.

The phenological stage of development was noted for each plant sampled. Soil temperature and gravitational soil water were measured at 15 cm depth on each site and collection date and at 30 cm depth on the

PSME/SYAL sites.

Laboratory Analysis

The samples were brought into the lab and washed free of all soil. Samples were dried at 105°C for ten minutes, then at 65°C for 7 days. The dried material was ground in a Wiley mill to pass a 60 mesh screen, then stored in air-tight containers.

Total nonstructural carbohydrates were determined in elk sedge, snowberry and serviceberry using an enzyme digestion technique developed by daSilveira et al. (1978). Because fructosans are a part of the TNC stored in pinegrass the enzyme process was revised by adding acid hydrolysis with 0.4 N sulfuric acid for 20 minutes (Appendix A). TNC concentration in the plant tissue was read spectrophotometrically and expressed on a mg/g dry weight basis.

Data Analysis

Data were analyzed using a two-factor analysis of variance (Sokal and Rohlf 1981) to compare TNC for each species by date and site. A Duncan's new multiple range test (Steel and Torrie 1960) was then used to test all possible comparisons between means. A 0.05 alpha level was used.

CHAPTER V

RESULTS AND DISCUSSION

Site and date were found to be significant factors affecting TNC levels in all four study species. Site by date interactions were significant for all species except serviceberry.

Elk sedge

TNC in elk sedge root crowns was greater in plants growing on the forested sites than the adjacent clearcuts. When the two habitat types were compared, TNC was greater in plants on the PSME/SYAL habitat type than the PSME/VACA habitat type (Table 1).

The PSME/SYAL sites had significantly greater soil water content at 0-15 cm depths than did the PSME/VACA sites; although, there was no significant difference between clearcuts and forested areas within each habitat type (Fig. 1). However, from August through October soil water content was significantly less in the forested areas as compared to the clearcuts. According to Blaser et al. (1966) when soil water becomes limiting for growth, TNC levels tend to increase in plants, indicating that growth is reduced more by water stress than is photosynthesis. The lower soil water content on the forested sites may be a cause for higher TNC levels in the plants growing on these sites. Greater TNC in plants on the PSME/SYAL sites as compared to the PSME/VACA sites could be a result of higher photosynthetic rates because of an increase in incoming solar radiation on the southern exposure.

Table 1. Total nonstructural carbohydrates (mg/g)
 averaged over all dates by site and species.

Species and Plant Part	Site			
	PSME/SYAL Forest	PSME/SYAL Clearcut	PSME/VACA Forest	PSME/VACA Clearcut
Elk sedge Root Crowns	75.4d ¹	71.5c	68.8b	61.8a
Elk sedge Roots	111.4b	105.0a	113.4b	105.5a
Snowberry Root Crowns	173.3c	133.2a	156.4b	149.9b
Serviceberry Root Crowns	119.8b	83.1a	----- ²	-----
Pinegrass ³ Rhizomes	71.1ab	79.4b	69.2a	90.4c

¹Means followed by a similar letter within each row are not significantly different at the 0.05 level of probability.

²No data were available for the PSME/VACA sites.

³Pinegrass data are from 1984. All other species data are from 1983.

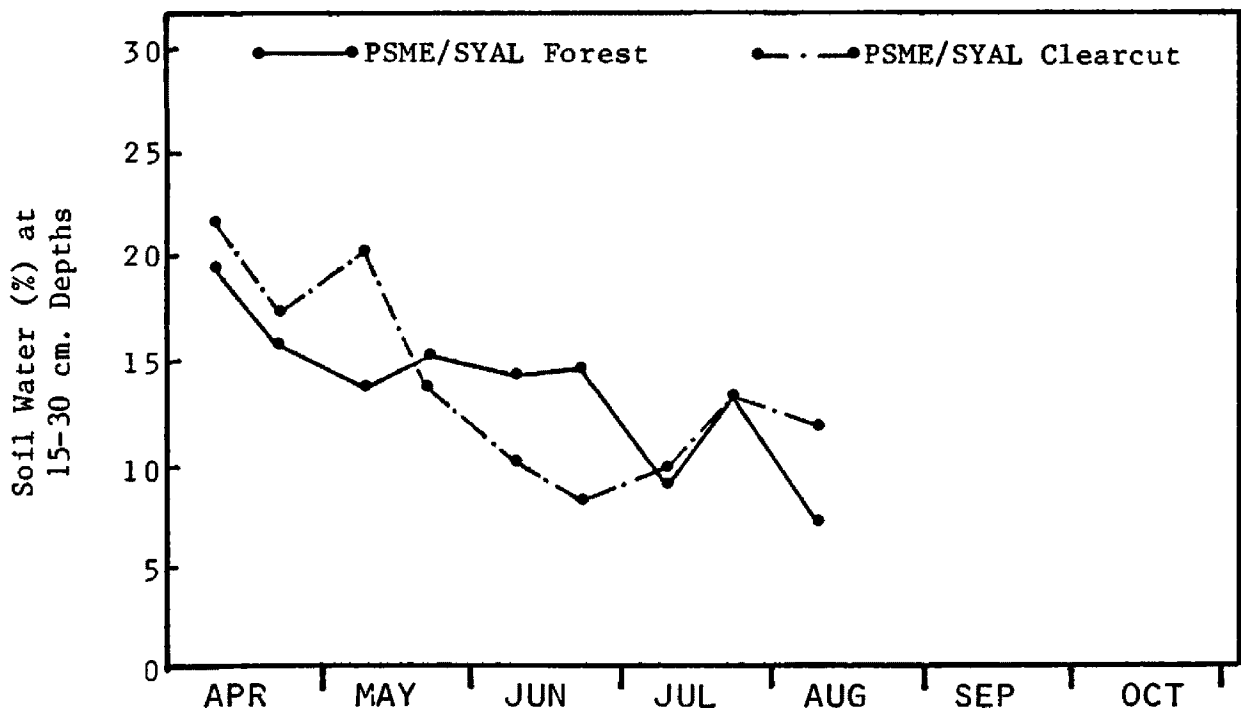
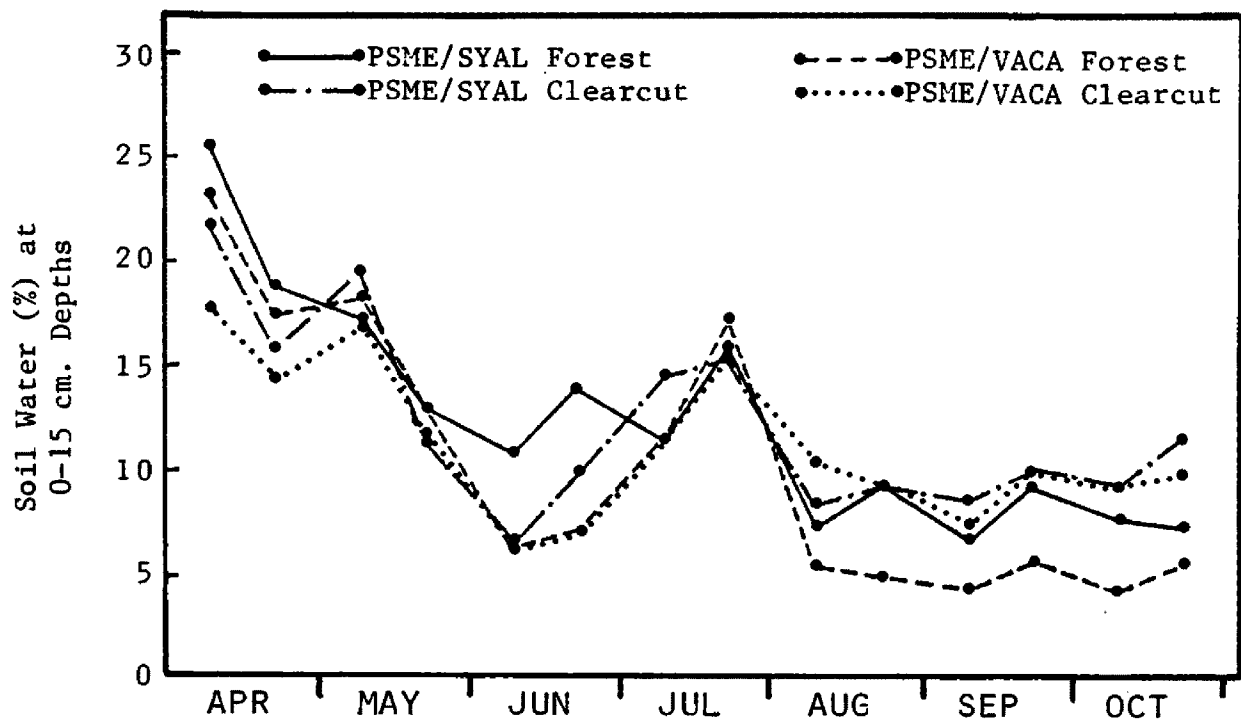


Figure 1. Soil water (%) at 0-15 and 15-30 cm. depths by site and date in 1983.

The effects of date and site by date interactions on TNC levels in elk sedge root crowns can be, at least partially, explained by differences in the phenological development of the plants (Figs. 2 and 3). Respiration during the winter months appears to use a small portion of the stored carbohydrates in root crowns. New leaf elongation and flowering in the spring also caused little or no decline in TNC levels (Table 2). Kramer and Kozlowski (1960) reported that seasonal carbohydrate trends may vary with different leaf habits. There is less fluctuation in the reserves of evergreen species than in deciduous species because of a greater dependence on current photosynthesis than stored food for spring growth. This applies to elk sedge plants which remain green over the winter months and retain the previous year's leaves until after new leaves are formed the following spring (Fig. 3). Although plants growing on both clearcut and forested areas flowered, a large portion of the forest plants' flowers did not fully develop and seeds rarely reached maturity. Flowering of the clearcut plants could then be an additional cause of lower TNC levels in these plants.

The time of leaf senescence and new rhizome and shoot development began 2 to 4 weeks later on the forested areas than the clearcuts. These differences in phenological development caused TNC to be increasing on one site while decreasing on another resulting in significant site by date interaction. In September and October TNC levels began to increase. According to Trlica (1977) translocation and storage of reserves is generally more active in autumn when plants are completing their annual cycle. These additional reserves are used for respiration during the quiescent or dormant period.

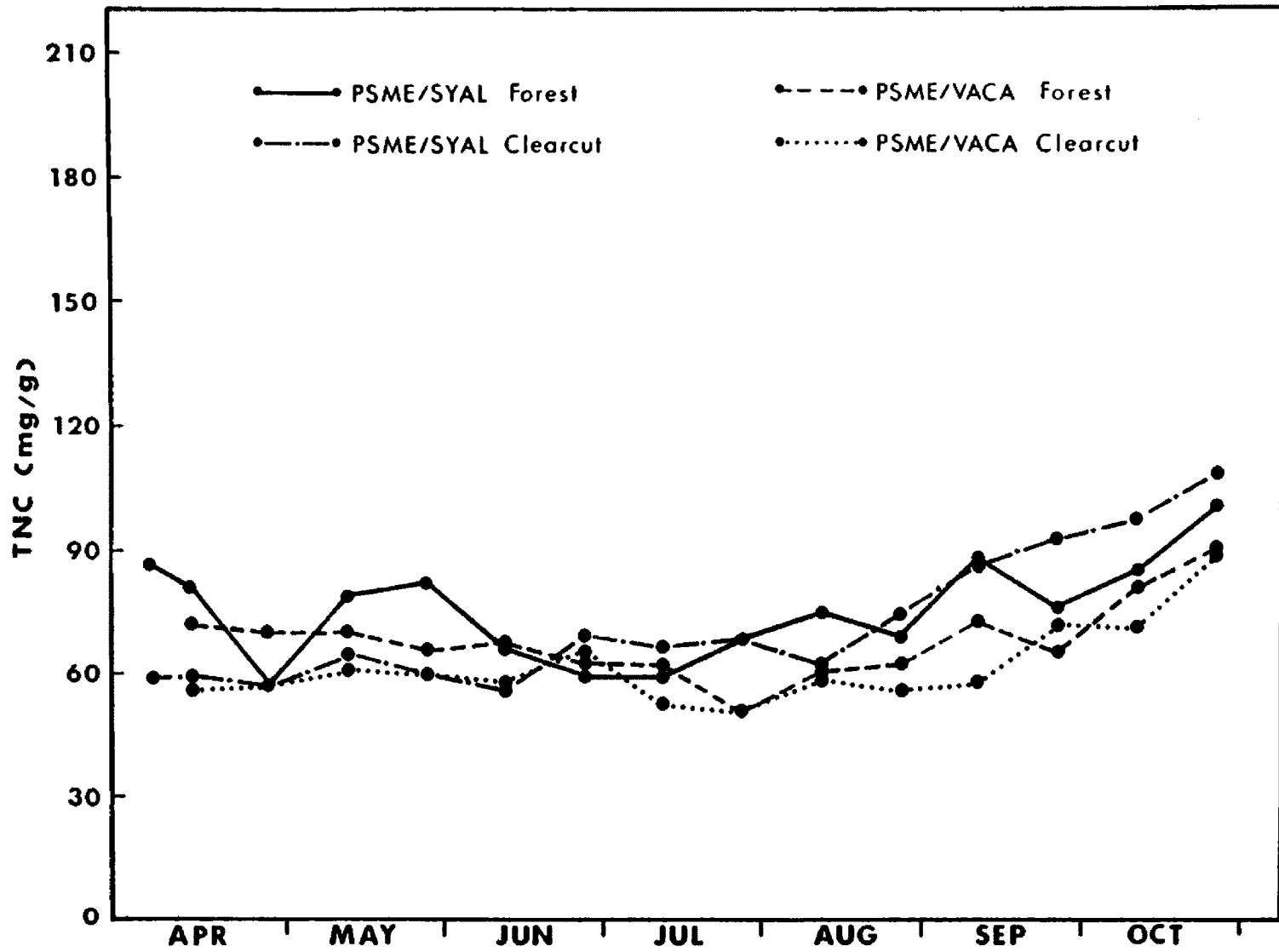


Figure 2. The influence of site and date on total nonstructural carbohydrates (mg/g) in elk sedge root crowns in 1983.

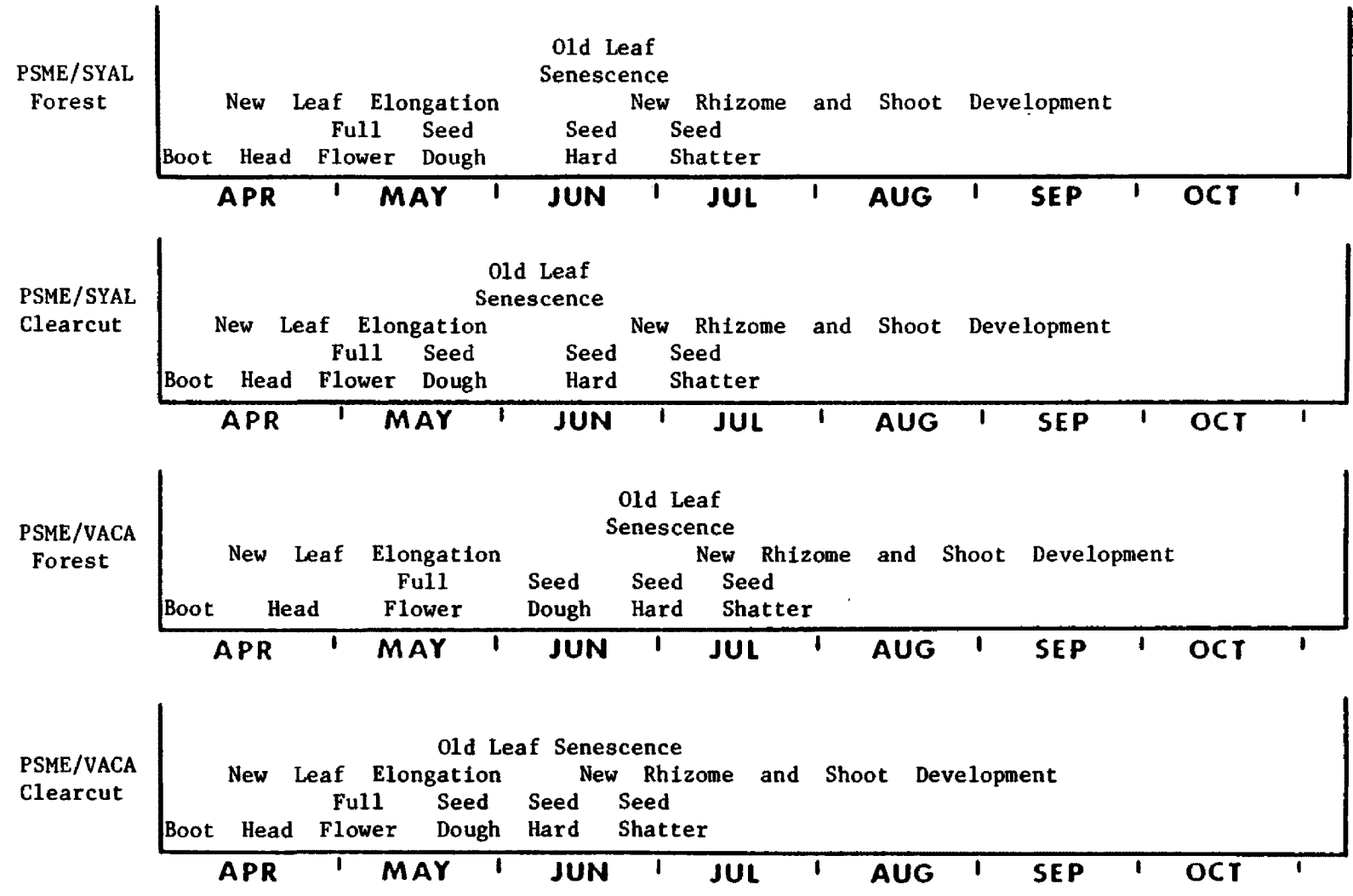


Figure 3. Phenology of elk sedge by site and date in 1983.

Table 2. Total nonstructural carbohydrates (mg/g) in elk sedge root crowns by site and date in 1983.

Date	Site			
	PSME/SYAL Forest	PSME/SYAL Clearcut	PSME/VACA Forest	PSME/VACA Clearcut
4/13	87.0b (yz) ¹	59.2a (w)	---- ²	----
4/18	81.3b (xyz)	59.2a (w)	73.7b (xyz)	55.7a (xy)
4/29	57.1a (v)	57.4a (w)	71.0b (xyz)	56.6a (xy)
5/13	78.2b (wxy)	64.1ab (wx)	70.4ab (xyz)	60.5a (xy)
5/27	82.0b (xyz)	59.2a (w)	66.6a (wxy)	59.7a (xy)
6/9	65.4a (vwx)	55.4a (w)	67.9a (wxy)	57.1a (xy)
6/22	59.8a (v)	68.5a (wx)	63.6a (wx)	64.9a (xy)
7/6	59.0a (vw)	66.5a (wx)	62.7a (wx)	53.2a (x)
7/21	67.8a (vwx)	67.1a (wx)	52.3a (w)	52.4a (x)
8/4	75.2b (wxy)	60.8a (w)	61.7a (wx)	58.5a (xy)
8/23	69.2a (vwxy)	73.1a (wx)	63.5a (wx)	56.9a (xy)
9/8	87.8b (yz)	85.5b (xy)	73.0b (xyz)	57.4a (xy)
9/23	76.1a (wxy)	92.2b (yz)	65.1a (wxy)	72.8a (y)
10/8	85.0ab (xyz)	95.9b (yz)	82.1ab (yz)	71.6a (y)
10/22	100.1a (z)	107.7a (z)	90.3a (z)	88.0a (z)

¹Means followed by a similar letter within each row or in parenthesis within each column are not significantly different at the 0.05 level of probability.

²No data were available for the PSME/VACA sites on 4/13.

Elk sedge roots were also analyzed for TNC content in 1983. Roots of elk sedge growing in the forested areas had greater TNC than those in the clearcut areas. There was no difference in TNC in roots between the two habitat types (Table 1).

Less soil water on the forested areas from August to October (Fig. 1) could have resulted in reduced growth and an increase in TNC levels in plants growing on the forested areas. Also, soil temperatures were significantly higher on the clearcuts than the forested areas (Fig. 4). The higher temperatures may have caused an increase in root respiration and a decrease in TNC on the clearcut sites.

Although TNC levels were greater in roots than in root crowns (for all dates that roots were collected) significance between dates and the relationships of TNC to phenology showed little difference between the two plant parts (Figs. 3 and 5). The major difference between levels of TNC in roots and root crowns occurred late in the season. The greatest TNC levels in root crowns were not reached until October 22 on all four sites (Table 2); whereas, the greatest levels in roots were reached in September on three of the sites and as early as August 4 on the PSME/SYAL forested site (Table 3). The cause of the reduction in TNC in late September and October cannot be matched with any phenological stage of development. Possibly the carbohydrates stored in the roots were translocated to another portion of the plant for the formation of new rhizomes and shoots.

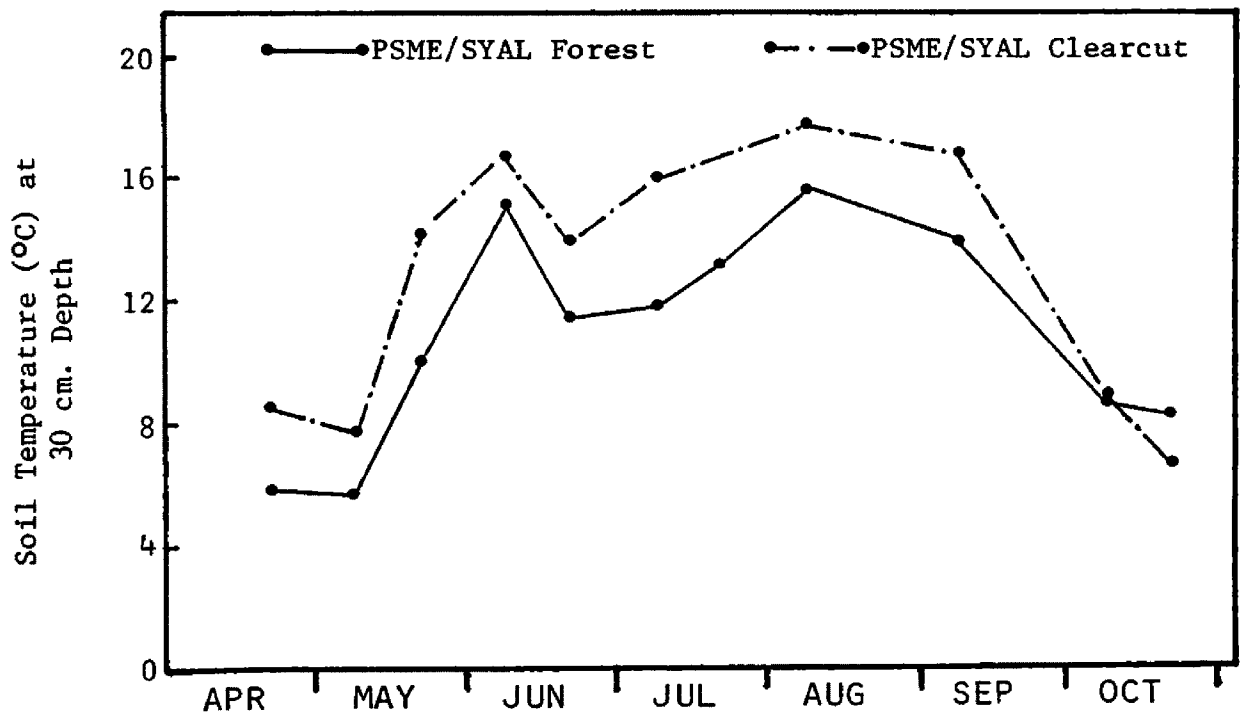
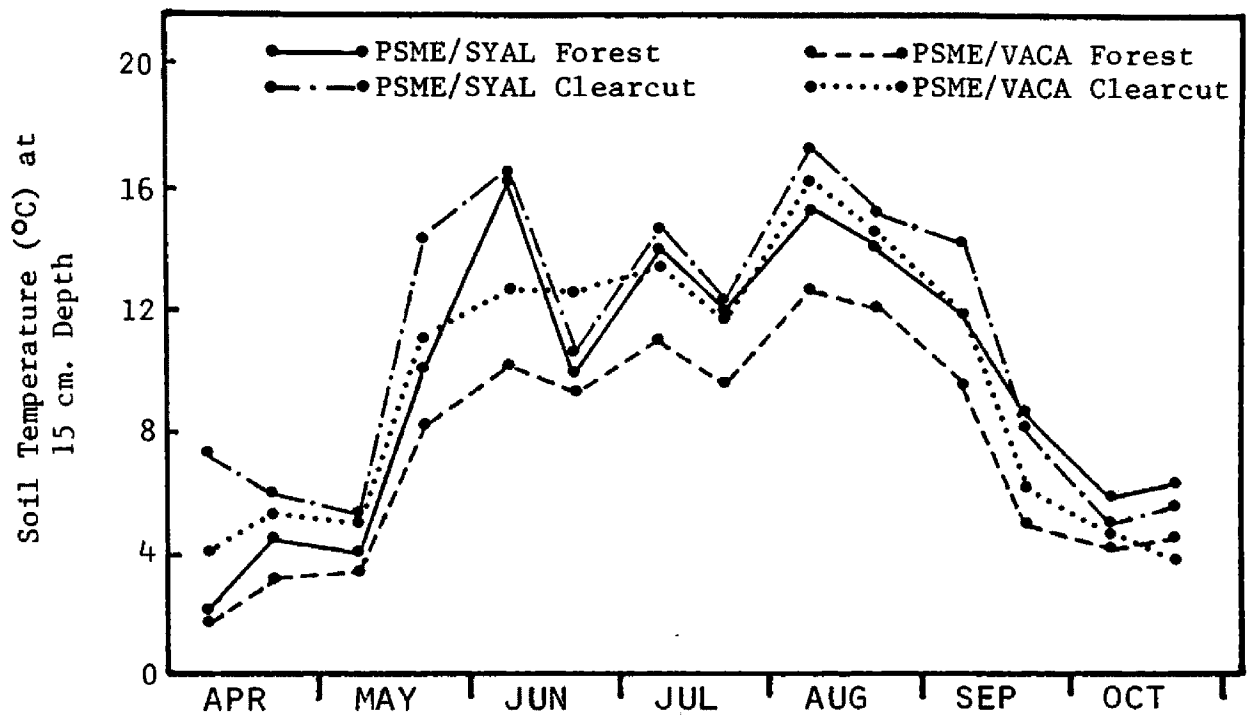


Figure 4. Soil temperature ($^{\circ}\text{C}$) at 15 and 30 cm. depths by site and date in 1983.

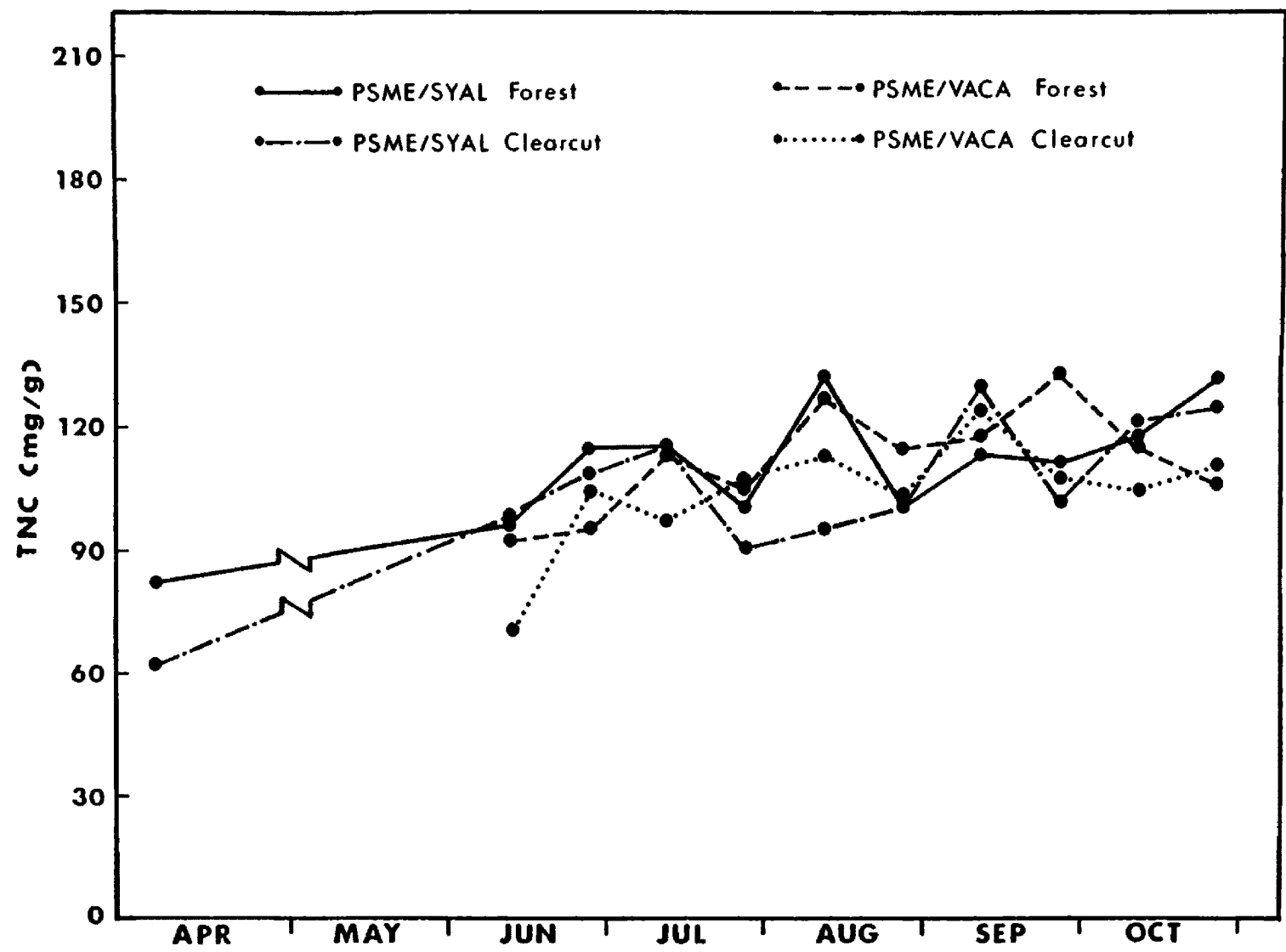


Figure 5. The influence of site and date on total nonstructural carbohydrates (mg/g) in elk sedge roots in 1983.

Table 3. Total nonstructural carbohydrates (mg/g) in elk sedge roots by site and date in 1983.

Date	Site			
	PSME/SYAL Forest	PSME/SYAL Clearcut	PSME/VACA Forest	PSME/VACA Clearcut
4/13	82.5a (x) ¹	63.4a (u)	---- ²	----
6/9	96.8b (x)	97.8b (vwx)	93.9b (x)	70.8a (x)
6/22	115.0b (yz)	109.1ab(wxyz)	95.6a (x)	104.9ab(yz)
7/6	116.2a (yz)	116.1a (xyz)	114.9a (xyz)	98.1a (y)
7/21	101.4a (x)	91.0a (v)	106.6a (xy)	108.0a (yz)
8/4	133.4b (z)	95.6a (vw)	127.9b (yz)	114.4ab(yz)
8/23	100.4a (x)	101.8a (vwxy)	115.5a (yz)	104.0a (yz)
9/8	114.5a (yz)	130.8a (z)	117.7a (yz)	125.0a (z)
9/23	113.6ab(yz)	102.2a (vwxy)	134.3b (z)	108.1a (yz)
10/8	118.2a (yz)	121.4a (yz)	115.7a (yz)	105.2a (yz)
10/22	133.1b (z)	125.5ab(yz)	107.8a (xy)	111.5ab(yz)

¹Means followed by a similar letter within each row or in parenthesis within each column are not significantly different at the 0.05 level of probability.

²No data were available for the PSME/VACA sites on 4/13.

Snowberry

The TNC content of snowberry root crowns was greater in the PSME/SYAL forest than the clearcut; however, there was no difference in TNC levels between the two PSME/VACA sites. A comparison of the two forested areas showed that TNC levels for snowberry were greater in the PSME/SYAL habitat type. For the two clearcuts snowberry TNC levels were greater in the PSME/VACA habitat type (Table 1).

The greater TNC level in plants on the PSME/SYAL forest compared to the clearcut area may be related to soil moisture and temperature (Figs. 1 and 4). An increase in TNC content could have resulted from increased water stress and reduced growth on this site. In plant species which naturally occur in both sun and shade environments it is generally found that those plants growing in full sun have higher root:shoot ratios than those under a forest canopy. Roots and rhizomes appeared to be larger in plants growing on the clearcut areas. The higher soil temperatures measured on the clearcuts could then have caused a greater loss of stored carbohydrates in these plants through increased root respiration.

The higher TNC in plants on the PSME/SYAL forest as compared to the PSME/VACA forest could be due to greater photosynthetic rates on this more open site. The PSME/SYAL forest canopy cover measurement was approximately 50% compared to 60% on the PSME/VACA forest. Also, less soil water on the PSME/VACA clearcut than the PSME/SYAL clearcut may have caused an increase in TNC on this site because of reduced plant growth due to an increase in plant water stress.

No difference was found in TNC levels of snowberry between the PSME/VACA forest and clearcut when averaged over all dates, although an examination of the individual dates and their relationship to phenological growth stages (Figs. 6 and 7) show differences between the sites. The period of leaf and twig elongation in the spring caused a significant decrease in TNC levels. This drawdown, however, was much more pronounced in plants growing on the clearcut. Forest plants used approximately 43% of their stored reserves while clearcut plants used 77% (Table 4). The seasonal TNC cycle of snowberry resembles the typical V-shaped curve described by Trlica (1977) with rapid depletion of reserves during growth initiation in the spring followed by a rapid accumulation of reserves after the low point has been reached. There was also a noted difference in the number of plants that flowered and produced mature fruits on these sites. Approximately 75% of the clearcut plants flowered while less than 20% of the forest plants flowered.

In general, most of the phenological stages of development in snowberry occurred approximately two weeks later in forest plants than clearcut plants causing site by date interactions to be significant.

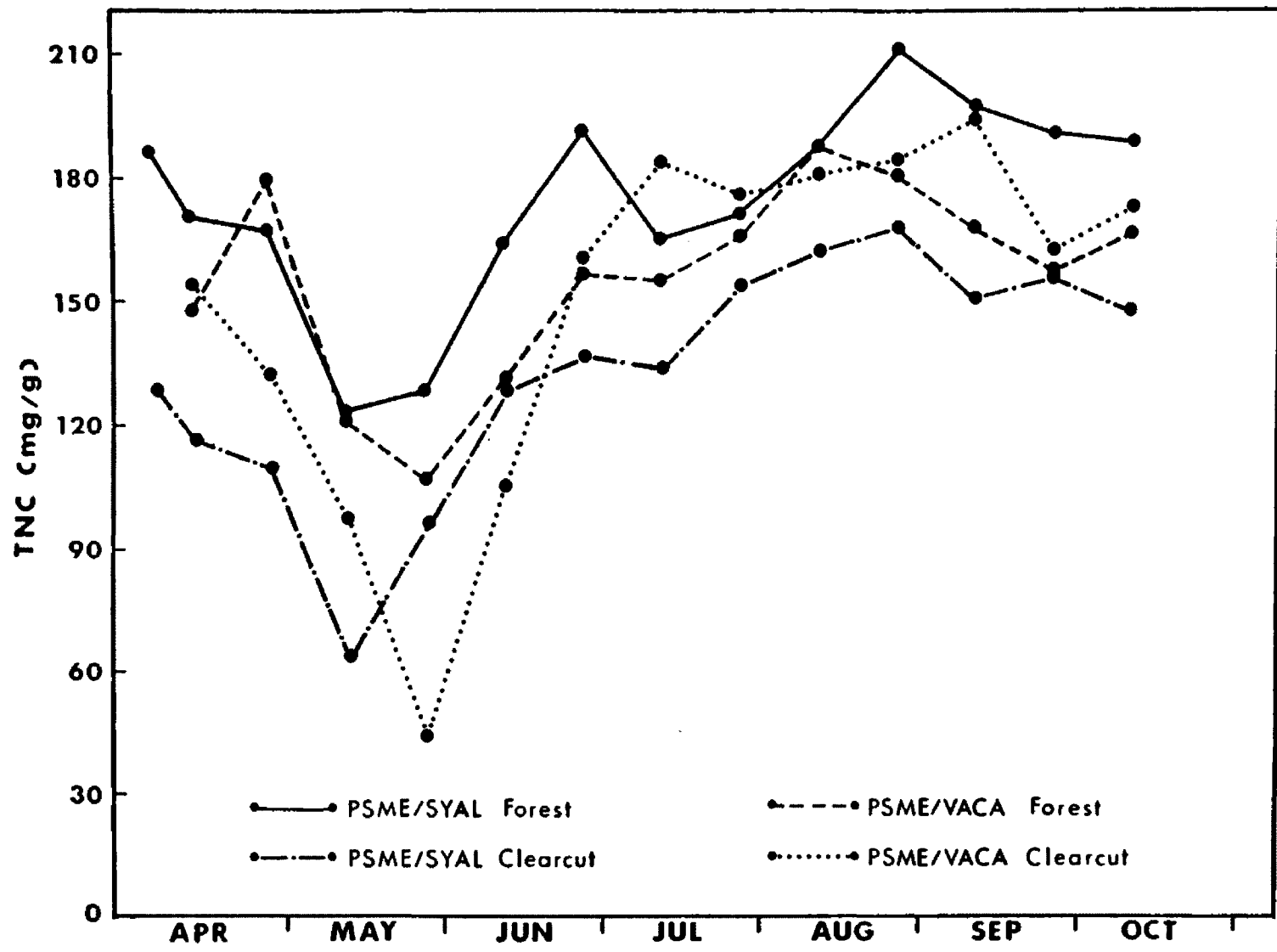


Figure 6. The influence of site and date on total nonstructural carbohydrates (mg/g) in snowberry root crowns in 1983.

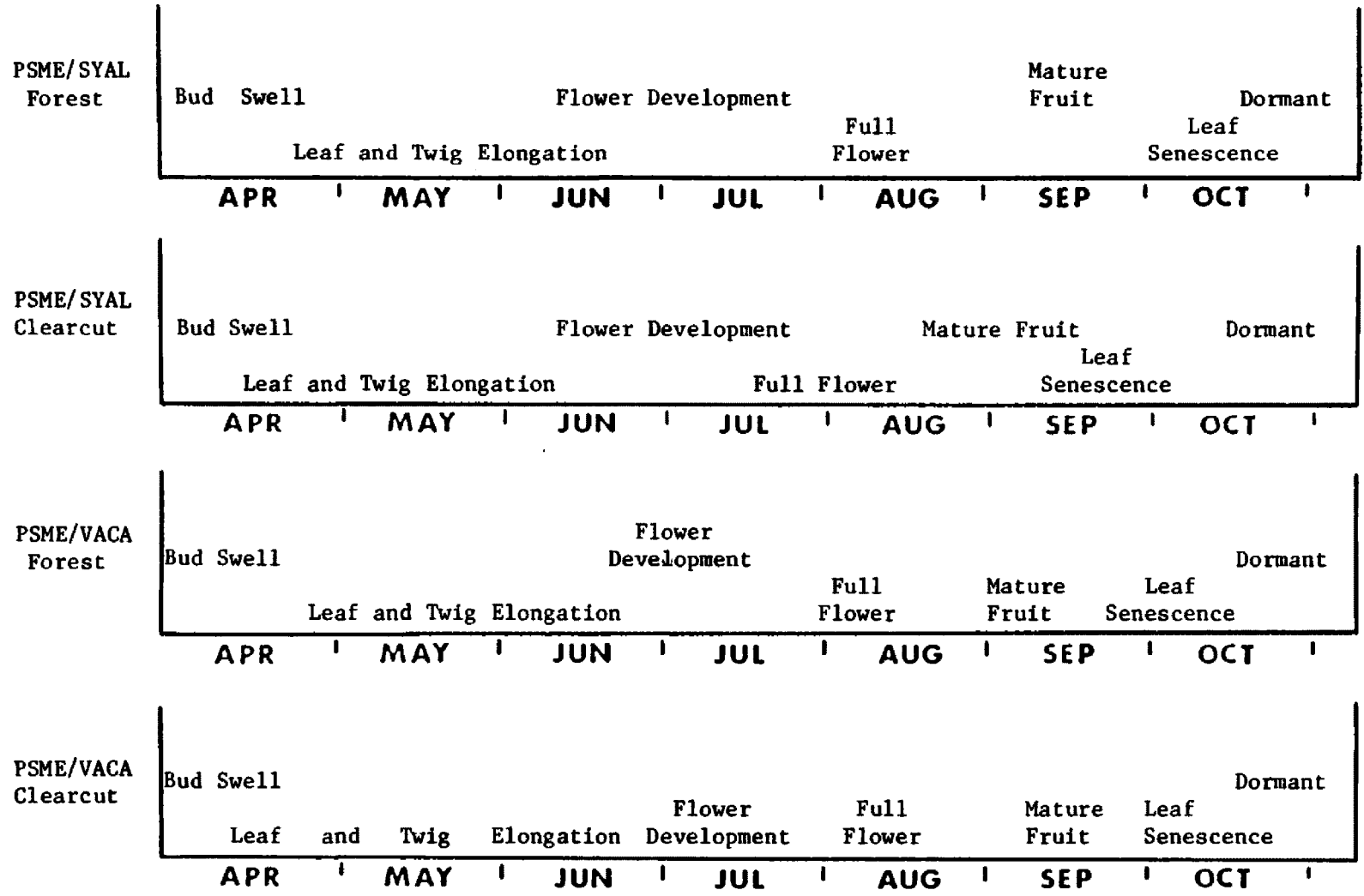


Figure 7. Phenology of snowberry by site and date in 1983.

Table 4. Total nonstructural carbohydrates (mg/g) in snowberry root crowns by site and date in 1983.

Date	Site			
	PSME/SYAL Forest	PSME/SYAL Clearcut	PSME/VACA Forest	PSME/VACA Clearcut
4/13	185.5b (yz) ¹	127.9a (vwx)	---- ²	----
4/18	170.0b (y)	116.2a (uvw)	148.6b (wxy)	154.5b (xy)
4/29	167.1c (y)	109.4a (uv)	180.7c (z)	132.9b (x)
5/13	122.7bc(x)	63.4a (t)	121.2c (vw)	97.6b (w)
5/27	127.3c (x)	95.9b (u)	107.6bc(v)	44.3a (v)
6/9	164.5c (y)	128.4b (vwxy)	131.2b (wx)	105.1a (w)
6/22	190.8b (yz)	136.0a (wxyz)	157.2a (xyz)	165.1a (y)
7/6	164.8b (y)	134.8a (vwxy)	155.7b (xyz)	184.3b (yz)
7/21	170.7a (y)	154.9a (xyz)	166.8a (yz)	175.6a (yz)
8/4	186.9b (yz)	162.9a (yz)	187.7b (z)	181.9ab(yz)
8/23	210.2b (z)	169.6a (z)	181.8a (z)	184.3a (yz)
9/8	197.6b (yz)	150.6a (xyz)	169.0a (yz)	195.2b (z)
9/23	190.6b (yz)	156.7a (yz)	158.2a (xyz)	162.7a (y)
10/8	189.8b (yz)	148.4a (xyz)	167.4ab(yz)	173.8ab(yz)

¹Means followed by a similar letter within each row or in parenthesis within each column are not significantly different at the 0.05 level of probability.

²No data were available for the PSME/VACA sites on 4/13.

Serviceberry

Serviceberry plants on the PSME/VACA forest and clearcut were not analyzed for TNC due to a shortage of plants on these sites. TNC in serviceberry root crowns was higher in plants growing on the PSME/SYAL forest than the clearcut (Table 1).

Differences in the soil water content and temperatures on the two sites suggest that the difference in TNC levels may be, at least in part, a result of these two factors (Figs. 1 and 4). Reduced growth (both above and below ground) in serviceberry plants on the forested site may have caused an increase in TNC levels in these plants due to greater water stress. Smaller root:shoot ratios on the forested plants may have resulted in decreased root respiration and an increase in TNC levels.

Differences in dates can be related to the phenological stages of the plants on the two sites (Figs. 8 and 9). Leaf and twig elongation in April and May required a large amount of stored reserves. For the forest plants approximately 70% of the TNC was used while nearly 80% was used in the clearcut plants (Table 5). The seasonal TNC curve of serviceberry can be described as a V-shaped cycle; however, depletion and accumulation of reserves in the spring is not as rapid as in snowberry plants. Flower development began in the clearcut near the end of May reaching full flower near the first week of July. In the forested area no serviceberry plants flowered. Most plants began a fall regrowth period in mid August, developing new shoots from the root crown, new leaves and buds. Regrowth was greater on the clearcut plants

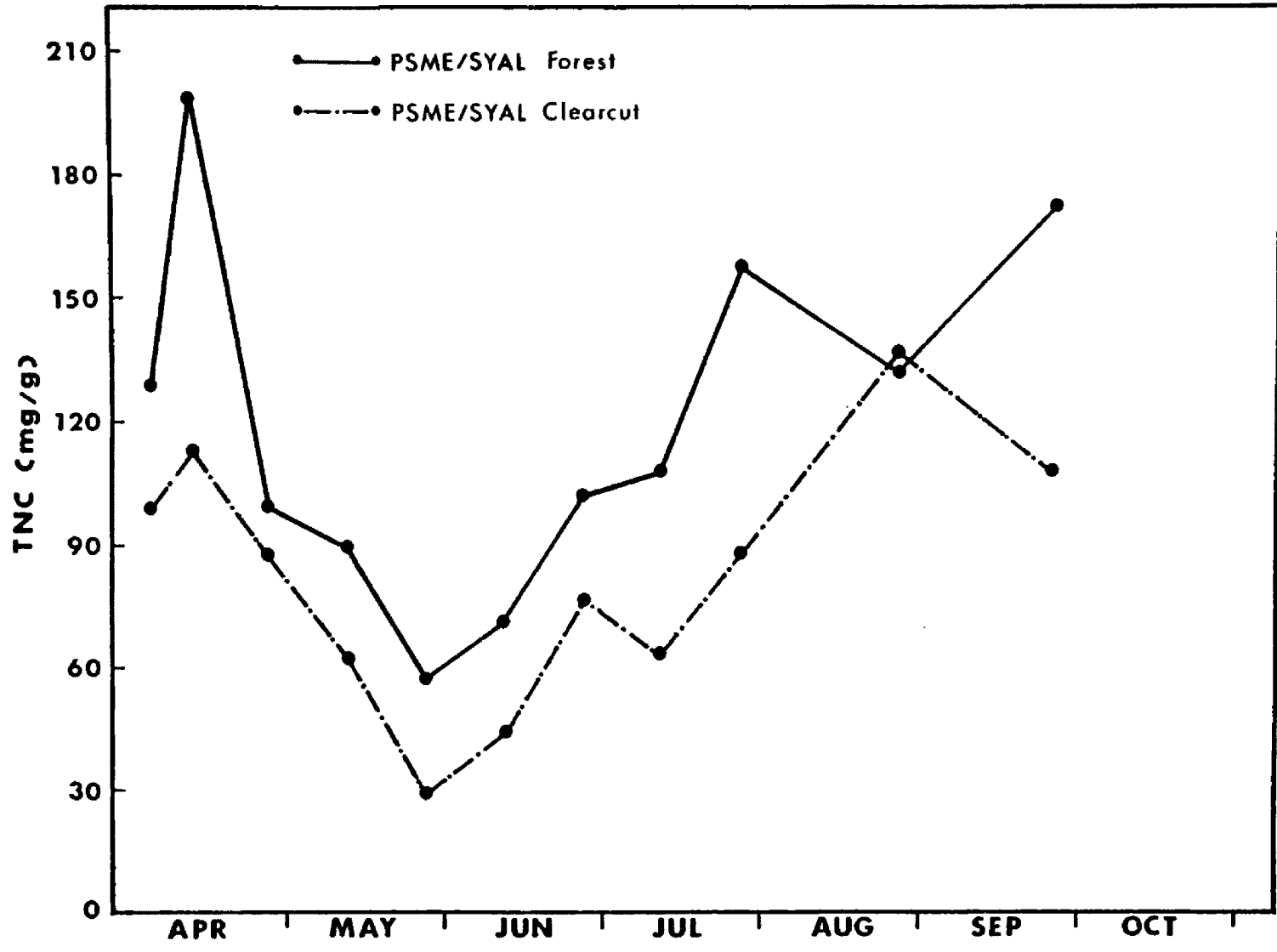


Figure 8. The influence of site and date on total nonstructural carbohydrates in serviceberry root crowns in 1983.

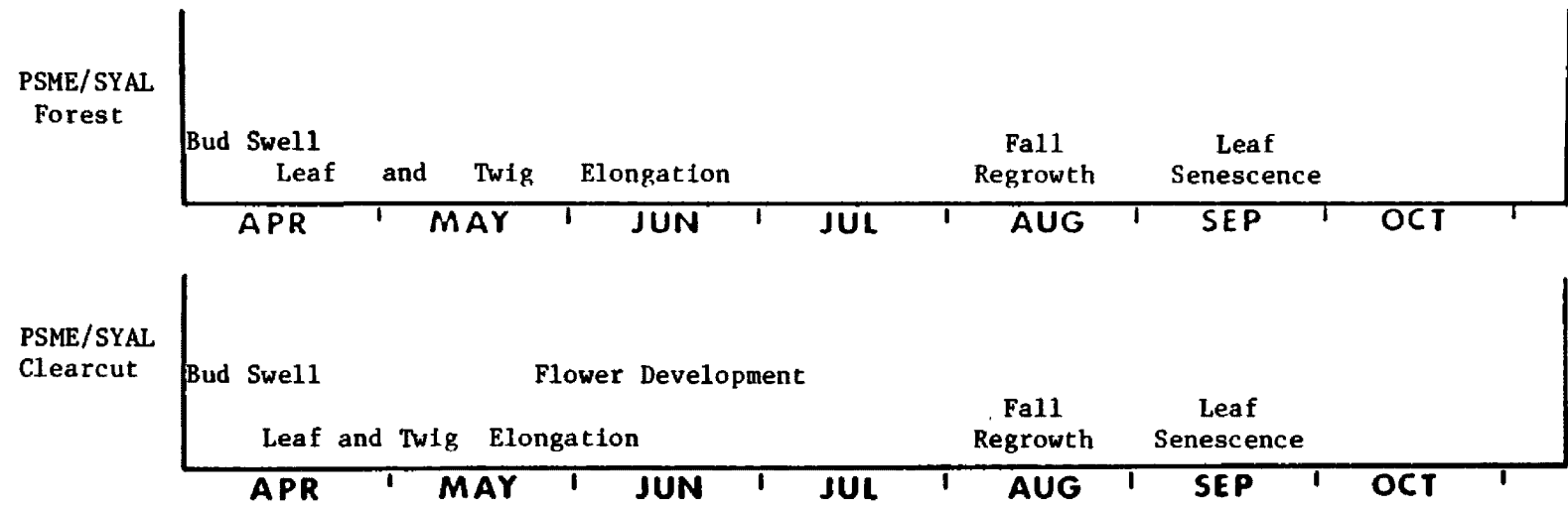


Figure 9. Phenology of serviceberry on the PSME/SYAL sites in 1983.

Table 5. Total nonstructural carbohydrates (mg/g) in serviceberry root crowns by site and date in 1983.

Date	Site	
	PSME/SYAL Forest	PSME/SYAL Clearcut
4/13	129.7a (vwxy) ¹	99.0a (yz)
4/18	198.6b (z)	113.1a (yz)
4/29	99.9a (uvwx)	83.7a (xyz)
5/13	90.0a (uvw)	63.2a (wxy)
5/27	57.3a (u)	29.8a (w)
6/9	71.3a (uv)	44.3a (wx)
6/22	102.2a (uvwx)	76.7a (xy)
7/6	108.5a (uvwx)	63.3a (wxy)
7/21	158.3b (xyz)	88.5a (xyz)
8/23	133.0a (wxy)	136.7a (z)
9/23	172.5b (yz)	108.5a (yz)

¹Means followed by a similar letter within each row or in parenthesis within each column are not significantly different at the 0.05 level of probability.

causing a trend toward decreased TNC levels (Table 5). By the 3rd week of September most leaves were brown and many had dropped.

Site by date interaction was not found to be a significant factor affecting TNC levels in serviceberry plants on these two sites. The phenological development of serviceberry plants on the forest and clearcut were quite similar throughout the season.

Pinegrass

Pinegrass was collected in 1983 but was not statistically analyzed because of difficulties in the laboratory (Appendix B). However, seasonal trends in TNC (Appendix C) can be examined with the phenological development of the plants (Appendix D). The following discussion relates to the pinegrass collected in 1984.

TNC levels were greater in pinegrass rhizomes on the PSME/VACA clearcut than the forest. There was no difference between the PSME/SYAL clearcut and forest (Table 1). Pinegrass plants on the PSME/VACA clearcut had greater TNC than those on the PSME/SYAL clearcut. Although there was no difference between TNC levels on the two forested sites, there appears to be a trend toward greater TNC in pinegrass plants growing on the PSME/SYAL forest.

No significant difference was found in soil water content between any of the four sites in 1984 (Fig. 10). Soil temperatures, however, were found to be consistently higher on the clearcut areas than the forested areas (Fig. 11). These data suggest that, all other factors being equal, soil temperatures and light conditions on the PSME/VACA clearcut were the most conducive to carbohydrate accumulation in

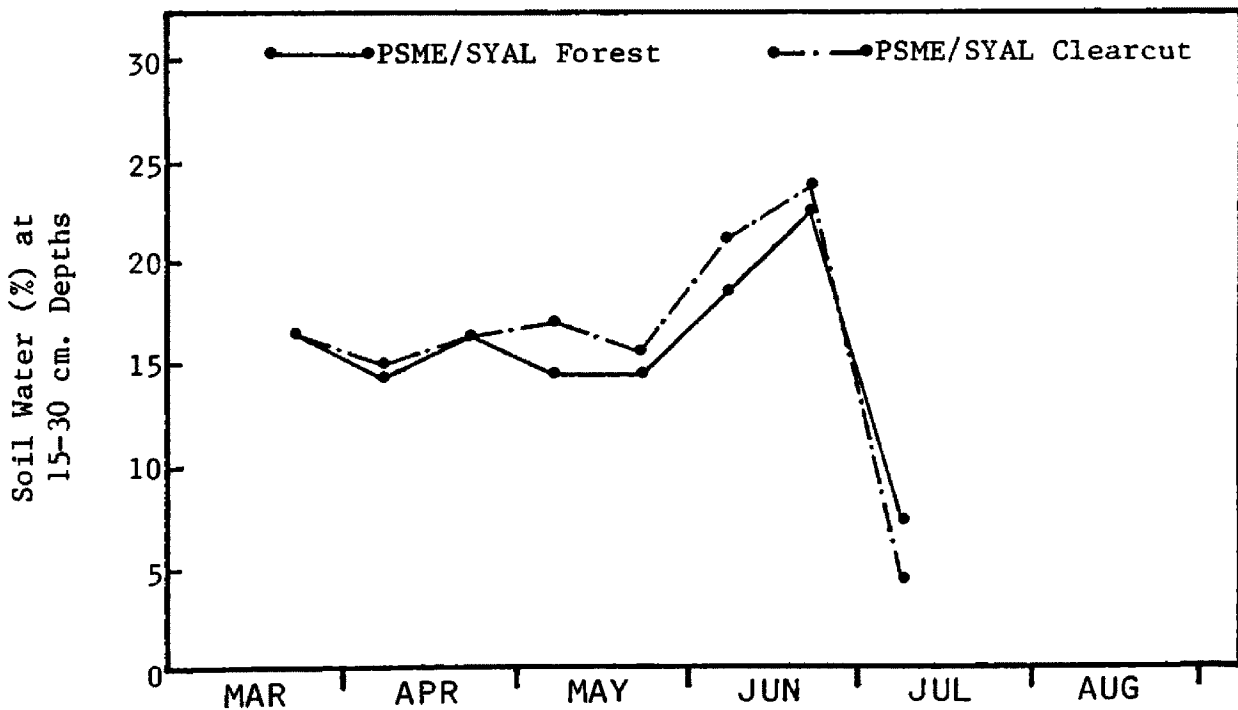
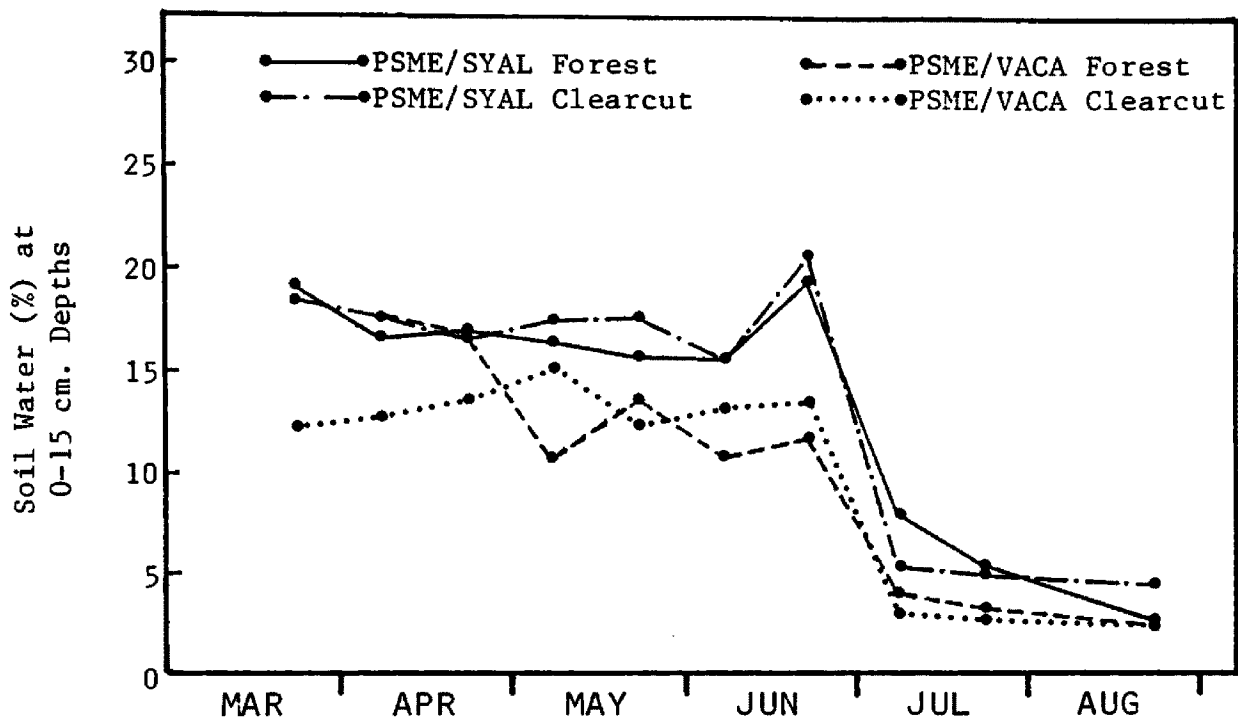


Figure 10. Soil water (%) at 0-15 and 15-30 cm. depths by site and date in 1984.

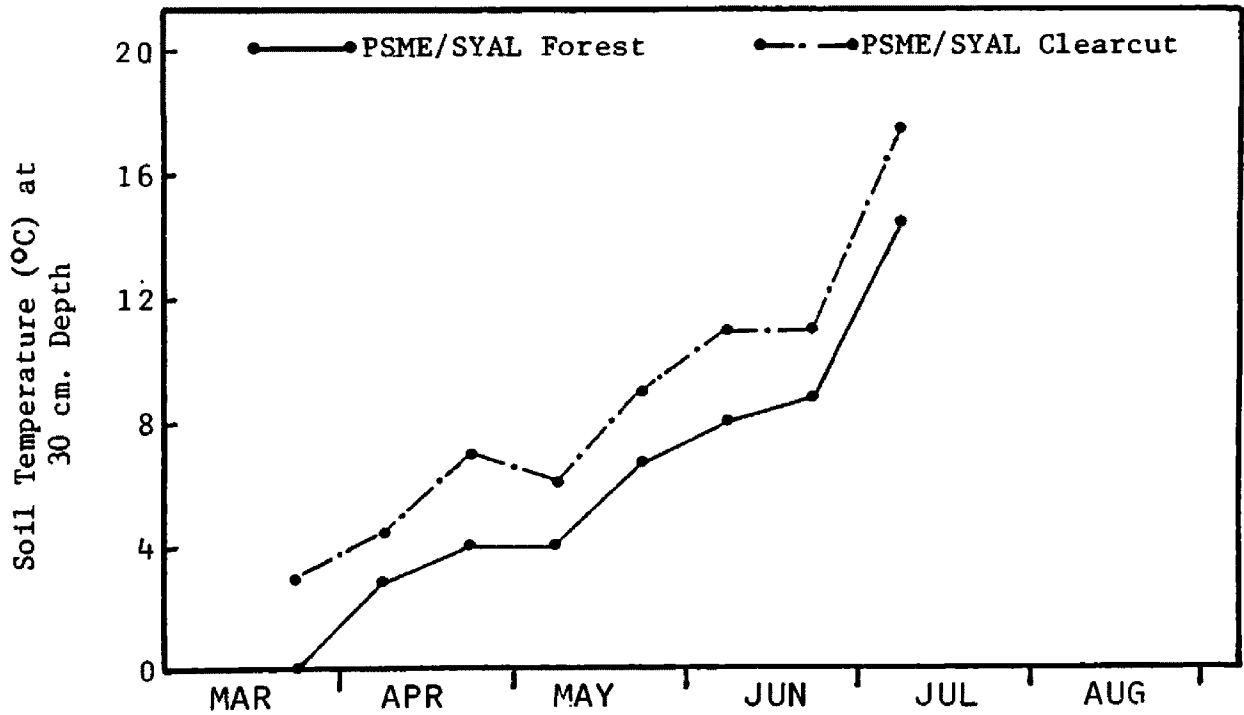
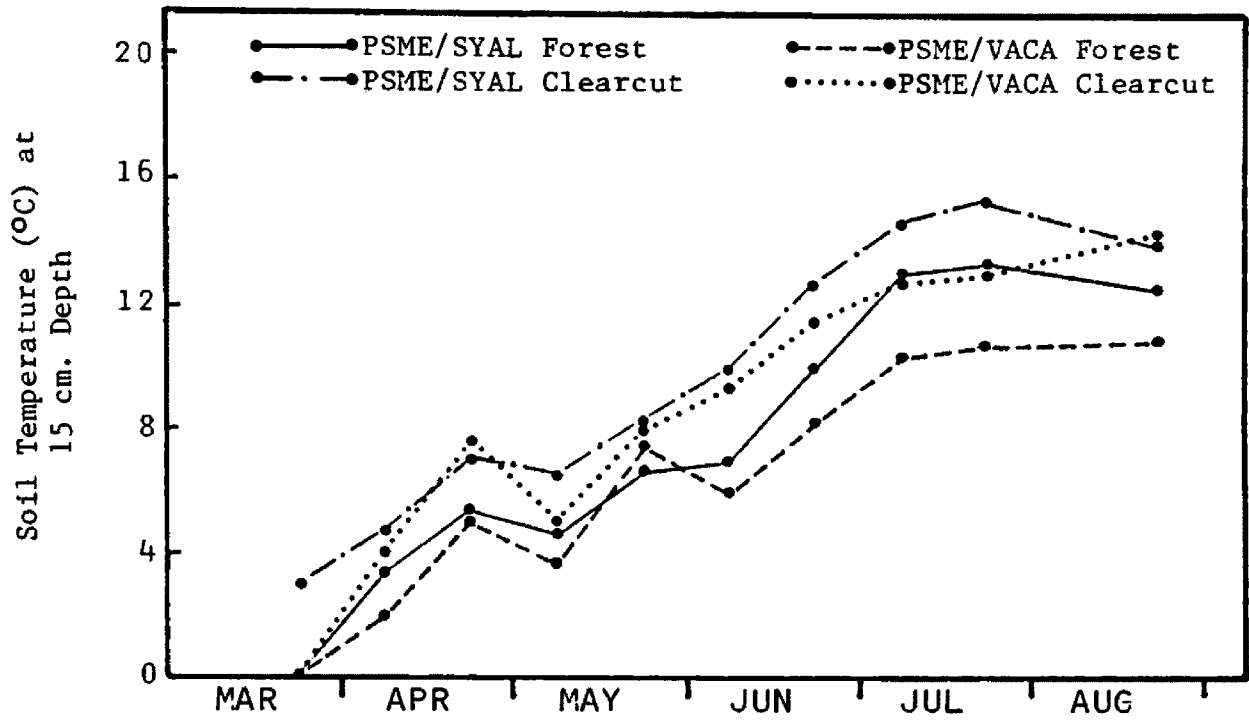


Figure 11. Soil temperature (°C) at 15 and 30 cm. depths by site and date in 1984.

pinegrass plants. Since carbohydrate levels in plants are dependent upon the balance between photosynthesis and respiration it must necessarily follow that net photosynthesis was highest in plants growing on the PSME/VACA clearcut. Measurements taken on photosynthetic rates of pinegrass plants growing in shade versus full sun sites at Lubrecht Experimental Forest showed significantly higher rates in the sun plants (Sheryl Vogel, personal communication).

TNC in pinegrass followed closely the phenological development of the plants (Figs. 12 and 13). Growth initiation in the spring caused significant decreases in TNC content with the lowest levels being reached between the 3rd and 4th leaf stages (Table 6). In general the various stages of phenological development in pinegrass plants were delayed 2 to 4 weeks on a forested site as compared to a clearcut site. The difference in phenology caused TNC levels to be increasing on one site while decreasing on another resulting in significant site by date interactions.

Descriptions of pinegrass (USDA 1937, Stubbendieck et al. 1982) generally state that reproduction is primarily by rhizomes except on open sites where flowering sometimes occurs. Only four plants were found to produce flowers in the two years of collections and these were all on the PSME/VACA clearcut; thus, it could not be determined whether flowering had any effect on TNC levels. New tiller development in June caused no significant reductions in TNC content (Table 6) the plants relying on the concurrent production of photosynthates. By August 22 soil moisture had dropped to between 2.7 and 4.7% and most plants appeared quiescent.

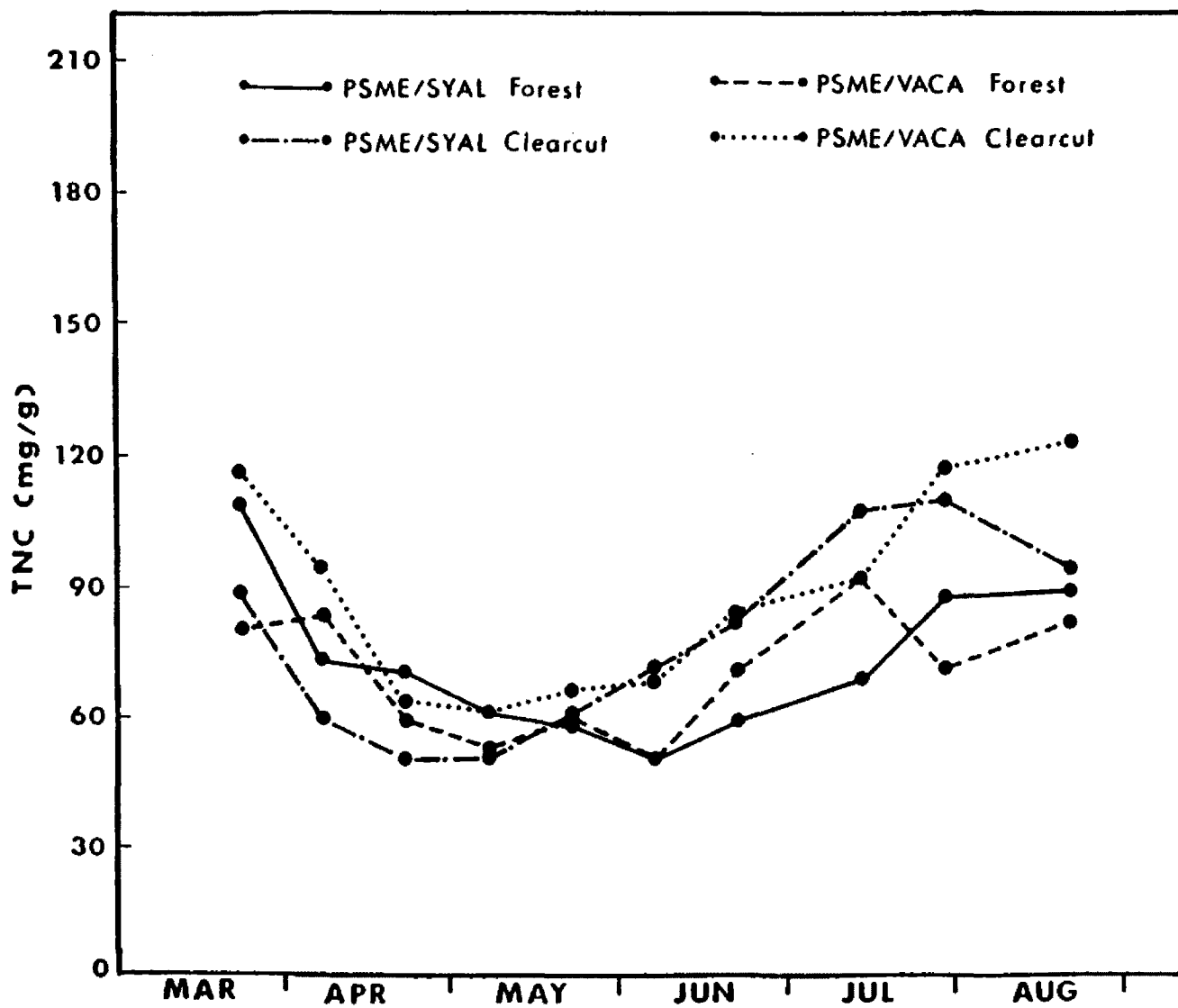


Figure 12. The influence of site and date on total nonstructural carbohydrates (mg/g) in pinegrass rhizomes in 1984.

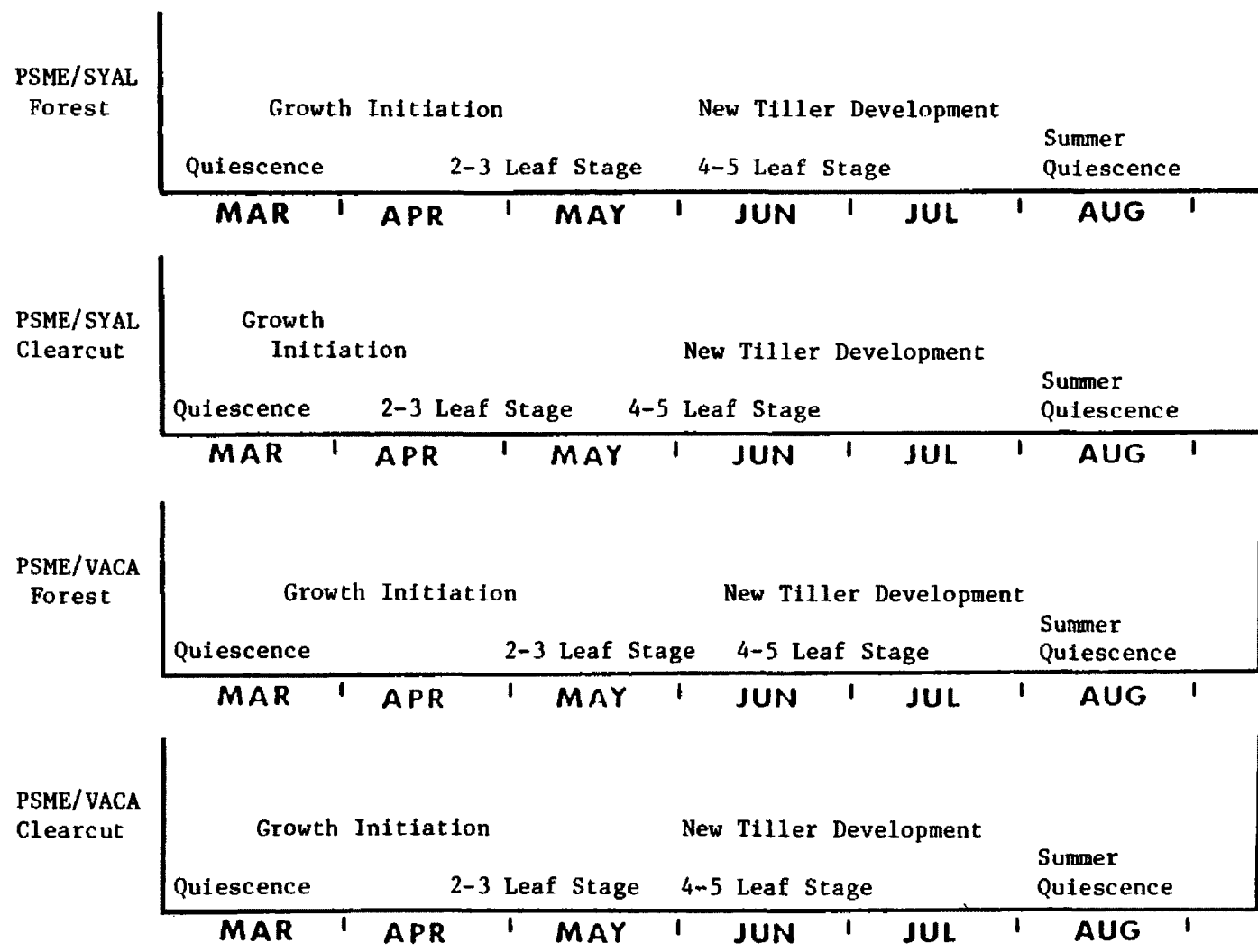


Figure 13. Phenology of pinegrass by site and date in 1984.

Table 6. Total nonstructural carbohydrates (mg/g) in pinegrass rhizomes by site and date in 1984.

Date	Site			
	PSME/SYAL Forest	PSME/SYAL Clearcut	PSME/VACA Forest	PSME/VACA Clearcut
3/19	108.2ab(z) ¹	89.3ab(xyz)	81.8a (xyz)	116.6b (yz)
4/7	73.0ab(xy)	60.1a (vw)	84.8ab(yz)	94.5b (xyz)
4/22	69.8a (xy)	50.5a (v)	59.2a (wxy)	62.9a (vw)
5/5	60.9a (x)	51.7a (v)	53.1a (w)	60.2a (v)
5/24	57.4a (x)	60.7a (vw)	59.0a (wx)	66.0a (vwx)
6/8	50.4a (x)	72.4a (vwx)	50.5a (w)	67.9a (vwx)
6/22	59.5a (x)	82.7a (wxy)	70.5a (wxyz)	84.5a (wxy)
7/13	68.6a (xy)	108.2b (yz)	93.1b (z)	93.8b (xyz)
7/30	88.7b (yz)	111.7bc(z)	70.5a (wxy)	117.6c (yz)
8/22	89.7a (yz)	95.8a (xyz)	83.3a (xyz)	124.1b (z)

¹Means followed by a similar letter within each row or in parenthesis within each column are not significantly different at the 0.05 level of probability.

The seasonal TNC cycle of pinegrass plants can be described as a V-shaped curve although depletion of TNC during growth initiation in the spring is not as rapid nor as great as in snowberry and serviceberry plants. This trend in TNC levels of pinegrass rhizomes is similar to that found in British Columbia, Canada by Stout et al. (1983).

CHAPTER VI

SUMMARY AND CONCLUSIONS

Total nonstructural carbohydrate levels were studied in elk sedge, snowberry and serviceberry plants in 1983 and pinegrass plants in 1984 growing on different forest habitat types and forest canopy classes. Site and date were found to be significant factors affecting TNC levels in all four species. Site by date interactions were significant for all species except serviceberry.

In general, TNC levels in elk sedge, snowberry and serviceberry were greater in plants growing on a forested area compared to a clearcut area. This difference appeared to be related to lower soil water content and soil temperatures on the forested sites. Lower soil water may have caused an increase in water stress in the forest plants. Water stress has been related to a decrease in plant growth and an increase in TNC levels. Noticeable differences were observed in plant size with the forested areas having much smaller plants. Lower TNC levels in clearcut plants may also be the result of an increase in root respiration from higher soil temperatures.

A comparison of the two habitat types produced inconsistent results. In elk sedge root crowns TNC levels were greater on the PSME/SYAL sites than the PSME/VACA sites. No difference was found in the TNC of elk sedge roots between the two habitat types. For snowberry plants the TNC levels were greater on the PSME/SYAL forest than the PSME/VACA forest while plants on the PSME/VACA clearcut had greater TNC than those on the PSME/SYAL clearcut. This comparison was not made for

serviceberry plants.

TNC levels in pinegrass plants were greater on the clearcut than the forested site within the PSME/VACA habitat type. There was no difference between TNC in plants on the PSME/SYAL clearcut and forest. No difference was found in soil water content on any of the four sites in 1984. However, soil temperatures were higher on the clearcuts than the forested areas. It was assumed that soil conditions on the PSME/VACA clearcut were more conducive for photosynthesis in pinegrass plants resulting in higher TNC than the forested site.

A comparison of pinegrass TNC levels on the two habitat types gave inconsistent results. The PSME/VACA clearcut had greater TNC than the PSME/SYAL clearcut while the two forested areas showed no difference.

Significant site by date interactions in all species except serviceberry were related to differences in the phenological development of the plants on the different sites. In general, there were 2 to 4 week delays in the phenological stages of development of plants growing on forested sites compared to clearcut sites. These differences were not detected in serviceberry plants.

These data can be useful to rangeland managers in the establishment of grazing guidelines for the four study species. Generally forage plants should not be grazed when TNC levels are decreasing. Additional drawdown on a plant's reserves at this time may cause levels to drop below the level needed for maintenance and regrowth resulting in reduced vigor or possibly even death of the plants.

For snowberry, serviceberry and pinegrass plants TNC levels did not begin to increase until after the newly formed leaves were nearly full

grown. The dates at which this period of development occurred differed by species and by site. Therefore, it is important that range managers establish grazing seasons based on a plants phenological development and not dates. Because of the wintergreen nature of elk sedge plants no one period of development results in a large decrease in TNC levels. Proper frequency and intensity of use are probably more important to the maintenance of elk sedge plants than is season of use.

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Appendix A. Determination of total nonstructural carbohydrates (TNC) in plants containing fructosans.

DIGESTION AND EXTRACTION:

1. Place a 100 mg sample in a test tube.
2. Add 2.0 ml of 0.02 M acetate buffer.
3. Cap loosely and autoclave for 15-20 minutes at 15 lbs./sq. in.
4. Cool to room temperature by immersing in tap water.
5. Add 4.0 ml of 0.3% enzyme solution.
6. Cap tightly and incubate for 20-24 hours at 38-40°C. (Swirl approx. every 2 hrs. Let sit overnight.)
7. Remove from incubation and add 4.0 ml of distilled water. Shake vigorously 25-30 times and centrifuge for 5 min. at 2500-3000 rpms.
8. Let tubes stand for a minimum of 5 min. to a maximum of 60 min.
9. Transfer a 1.0 ml aliquot of the supernatant liquid to a Folin blood sugar tube.
10. Add 1.0 ml 0.4 N H₂SO₄.
11. Boil at 99°C for 20 minutes.
12. Cool in tap water.
13. Add 0.25 ml of 1 N NaOH solution.

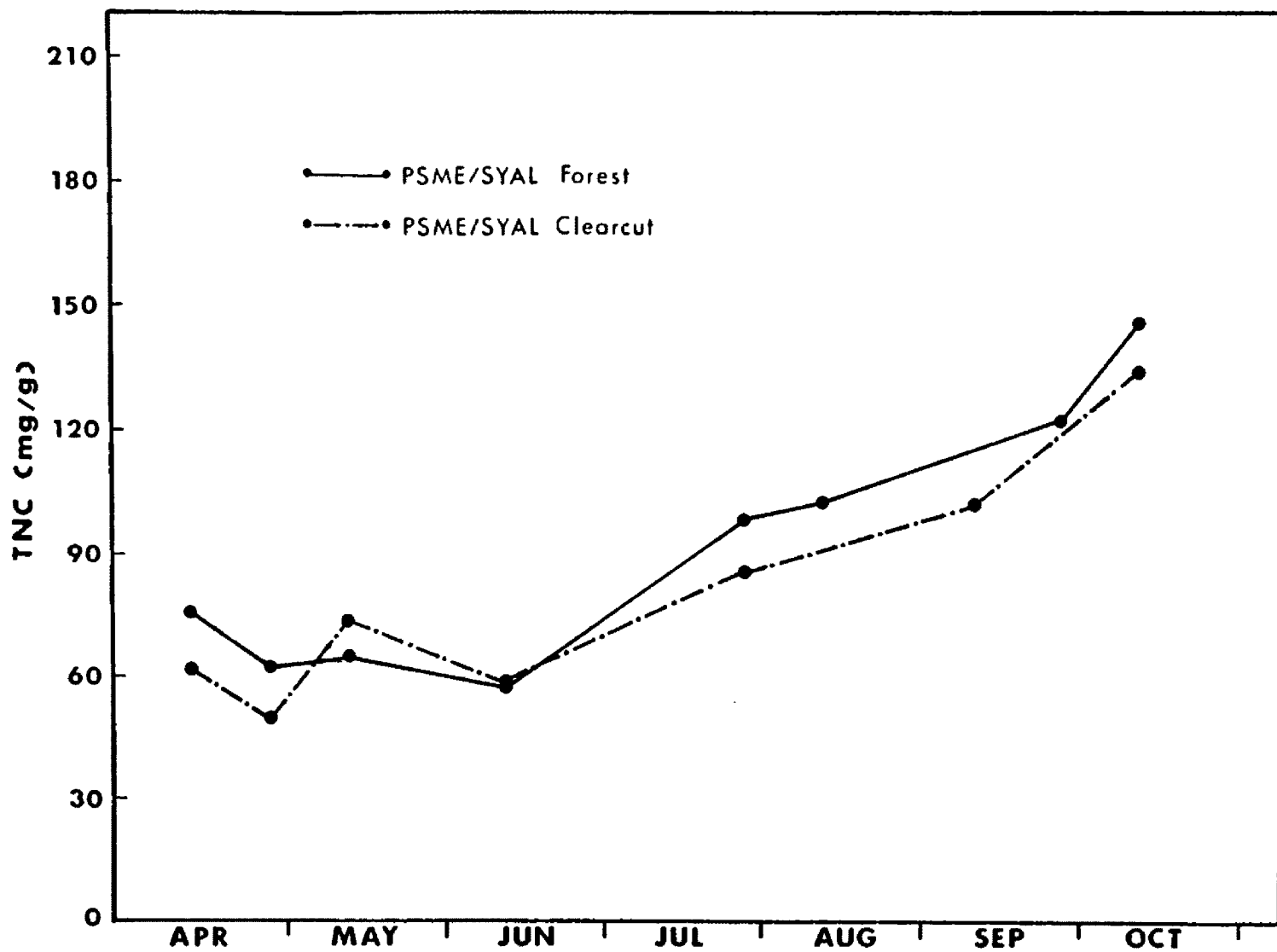
COLORIMETRY:

1. Add 2.5 ml of Teles reagent and stopper with a dry, rubber stopper.
2. Immerse the bottom of the tubes (4-6 cm) in a violently boiling water bath for exactly 6 min.
3. Cool in cold tap water for a minimum of 5 min.
4. Complete the volume to the 12.5 or 25 ml mark depending on the TNC concentration in the tissue.
5. Read %transmittance at 520 nm.

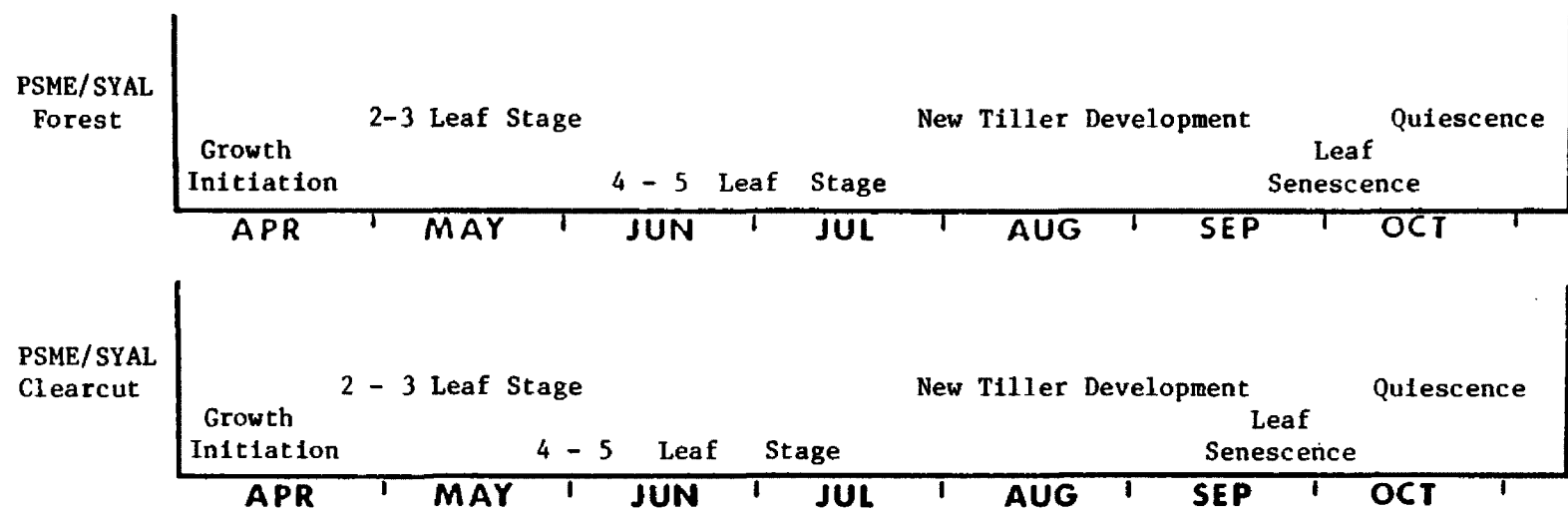
Appendix B. Total nonstructural carbohydrates (mg/g) in pinegrass rhizomes by site and date in 1983.

Date	Site	
	PSME/SYAL Forest	PSME/SYAL Clearcut
4/18	76.8	62.8
4/29	63.3	50.0
5/13	65.5	74.5
6/9	58.2	59.0
7/21	99.3	86.7
9/8	102.8	103.3
9/23	123.5	---- ¹
10/8	146.7	134.5

¹No data were available for the PSME/SYAL clearcut on 9/23.



Appendix C. The influence of site and date on total nonstructural carbohydrates (mg/g) in pinegrass rhizomes in 1983.



Appendix D. Phenology of pinegrass on the PSME/SYAL sites in 1983.

Appendix E. Soil water (%) at 0-15 and 15-30 cm. depths by site and date in 1983.

Date	Site							
	PSME/SYAL Forest		PSME/SYAL Clearcut		PSME/VACA Forest		PSME/VACA Clearcut	
	15	30	15	30	15	30	15	30
4/13	25.4	19.9	21.6	22.0	23.0	----- ¹	17.5	-----
4/18	26.7	22.5	23.9	19.8	20.3	-----	17.4	-----
4/29	18.7	16.0	15.7	17.6	17.3	-----	14.2	-----
5/13	17.1	14.0	19.4	20.5	18.2	-----	16.7	-----
5/27	12.9	15.4	11.1	13.9	12.9	-----	11.4	-----
6/9	10.8	14.6	6.3	10.2	6.0	-----	6.3	-----
6/22	13.9	14.9	9.9	8.4	6.9	-----	7.0	-----
7/6	11.3	9.1	14.3	9.8	11.1	-----	11.5	-----
7/21	15.9	13.6	15.3	13.5	17.2	-----	15.0	-----
8/4	7.1	7.4	8.1	12.0	5.3	-----	10.1	-----
8/23	9.0	-----	9.1	-----	4.7	-----	9.4	-----
9/8	6.8	-----	8.3	-----	4.2	-----	7.1	-----
9/23	9.1	-----	9.9	-----	5.4	-----	9.7	-----
10/8	7.5	-----	9.1	-----	4.2	-----	9.3	-----
10/22	7.1	-----	11.6	-----	5.4	-----	9.8	-----

¹No data available.

Appendix F. Soil temperature (°C) at 15 and 30 cm. depths by site and date in 1983.

Date	Site							
	PSME/SYAL Forest		PSME/SYAL Clearcut		PSME/VACA Forest		PSME/VACA Clearcut	
	15	30	15	30	15	30	15	30
4/13	2.2	----- ¹	7.3	-----	1.7	-----	4.0	-----
4/18	-----	-----	-----	-----	2.8	-----	5.7	-----
4/29	4.7	6.0	6.0	8.8	3.2	4.5	5.2	7.0
5/13	4.0	5.8	5.3	7.7	3.5	4.8	5.0	6.7
5/27	10.0	10.2	14.2	14.3	8.2	8.7	11.0	11.3
6/9	16.0	15.3	16.3	16.7	10.2	10.7	12.5	15.0
6/22	9.8	11.5	10.7	14.0	9.2	8.0	12.2	-----
7/6	14.0	11.8	14.5	16.3	11.0	-----	13.3	-----
7/21	12.0	13.2	12.2	13.2	9.5	10.0	11.5	10.5
8/4	15.2	15.5	17.2	17.8	12.7	-----	16.0	-----
8/23	14.0	-----	15.0	-----	12.0	-----	14.5	13.3
9/8	11.8	14.0	14.2	16.8	9.7	-----	11.8	-----
9/23	8.7	-----	8.2	-----	5.0	-----	6.2	-----
10/8	5.8	8.8	5.0	9.0	4.3	6.0	4.5	6.2
10/22	6.3	8.3	5.5	6.8	4.5	6.0	3.8	6.0

¹No data available.

Appendix G. Soil water (%) at 0-15 and 15-30 cm. depths by site and date in 1984.

Date	Site							
	PSME/SYAL Forest		PSME/SYAL Clearcut		PSME/VACA Forest		PSME/VACA Clearcut	
	15	30	15	30	15	30	15	30
3/19	19.1	16.7	18.5	16.5	----- ¹	-----	12.3	-----
4/7	16.8	14.7	17.3	15.0	17.3	-----	12.7	-----
4/22	17.0	16.6	16.8	16.6	16.9	-----	13.6	-----
5/5	16.7	14.7	17.3	17.2	10.8	-----	15.0	-----
5/24	15.9	14.6	17.6	15.8	13.5	-----	12.3	-----
6/8	15.8	18.7	15.5	21.1	10.8	-----	13.0	-----
6/22	19.5	22.6	20.7	23.9	11.8	-----	13.4	-----
7/13	8.0	7.3	5.3	4.6	4.0	-----	3.0	-----
7/30	5.6	-----	5.2	-----	3.2	-----	2.9	-----
8/22	3.0	-----	4.7	-----	2.7	-----	2.8	-----

¹No data available.

Appendix H. Soil temperature (°C) at 15 and 30 cm. depths by site and date in 1984.

Date	Site							
	PSME/SYAL Forest		PSME/SYAL Clearcut		PSME/VACA Forest		PSME/VACA Clearcut	
	15	30	15	30	15	30	15	30
3/19	0.0	0.0	3.0	3.0	0.0	----- ¹	0.0	-----
4/7	3.5	3.0	4.8	4.5	2.0	-----	4.0	-----
4/22	5.5	4.0	7.0	7.0	5.0	-----	7.5	-----
5/5	4.8	4.0	6.7	6.2	3.7	-----	5.0	-----
5/24	6.8	6.7	8.3	9.0	7.5	-----	8.0	-----
6/8	7.0	8.0	10.0	11.0	6.0	-----	9.2	-----
6/22	10.0	8.8	12.8	11.0	8.2	-----	11.3	-----
7/13	13.0	14.5	14.7	17.5	10.3	-----	12.7	-----
7/30	13.3	-----	15.3	-----	10.7	-----	13.0	-----
8/22	12.6	-----	14.0	-----	10.9	-----	14.2	-----

¹No data available.