LONG TERM PREDICTION OF VEGETATION PERFORMANCE ON MINED SANDS

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ABSTRACT

This project on the "Long Term Prediction of Vegetation Performance On Mined Sands" (V.E.6.1) was undertaken to provide management with answers on the predictive ability to maintain different kinds of vegetation on raw sands. The research was designed as an integrated, multi-disciplinary program that would concentrate on the role of water stress in a dynamic soil-plant-atmosphere system of a planted grass cover and a natural Jack pine forest. To date only the latter project has been initiated because of the lack of funding and approval to work on the GCOS dike in 1975. This and the Syncrude dyke represent the worst (driest) environmental situation and therefore revegetation of other sand deposits should be more easily accomplished. The Richardson Fire Tower site was chosen because of the representativeness of its Jack pine - lichen woodland on deep sands, a forest type so characteristic of northeastern Alberta.

The results of the first full year show that climatically this southwest-facing sand slope warms more rapidly in spring than do level sites at Mildred Lake and Fort McMurray and that the 1976 summer was above normal for temperature. Precipitation was near normal based upon the 1941 - 1970 period. Of the >60 days of precipitation, over 60% were 4 mm or less and thus little if any water entered the soil due to tree, lichen, and litter interception. Both needle duff and lichens provide a significant barrier to surface evaporation compared with open sand. Resistance to evaporation is 2 to 3 times greater with a lichen cover than with litter.

The soils are very porous which is advantageous for water entrance, thus preventing erosion but porosity is a disadvantage in maintaining higher water levels near the soil surface for plant growth. These soils recharge during snowmelt in late March - early April; little runoff occurs

and over the summer soil water drawdown takes place. Soil moisture content (volume basis) is generally 8 - 15% near the surface in spring, but by late September is 1 - 3% at all depths.

Xylem water potentials, a measure of tree water content, were never very low (mean maximum at dawn -5 to -7 atm. and mean minimum at midday -11 to -14 atm.) which reflect a year of average precipitation with frequent light rains and periodic heavier storms. Transpiration and stomatal closure were controlled largely by vapour pressure deficits. Jack pine avoided spring drought by remaining dormant when air and needle temperatures were above freezing, yet when soils were still frozen.

Although Jack pine did not show indications of severe drought in a relatively moist summer, it did develop xylem water potentials of -16 to -18 atm., values which are probably detrimental to many of the species being used in revegetation trials on the dike (*Bromus inermis*, *Phleum pratense*, and species of *Agropyron*). This means that potential species must be drought hardy and tested under laboratory rather than only under field conditions to determine their survival under severe drought conditions that may occur but once in 30 to 50 years.

The studies of mycorrhizae show that a large number of species of fungi infect the roots of Jack pine and that the infecting flora from disturbed soils (old burns) is quite different from that of undisturbed forests. Since mycorrhizae are critical for the proper growth and survival of pines, care in innoculating tree seedlings with the proper species is essential.

The energy and water balance mathematical model predicts the heat and water status of the Jack pine forest. Examination of the model outputs suggests that late season resistance to water uptake occurs because of increased root resistance in autumn. If this is confirmed with further experimental data, and model runs, it means that fall droughts may be especially critical because of the reduced ability of the trees to absorb water through their roots.

A second field season coupled with the laboratory studies to determine lethal and sublethal levels of water stress in Jack pine will provide the added inputs to the models necessary for predicting tree response to severe climatic stress. These data, gathered in a highly integrated manner, will permit the calculation of tree survival on sands, be they dikes or other kinds of mined sand, in terms of soil water content and tree density (including crown extent) in relation to the exceptional dry year that may occur once in 30 to 50 years. Data from field trials of grasses or woody species, without supporting measurements of plant physiological responses to environmental conditions cannot provide this essential predictive tool for management unless the one in 30 to 50 year drought cycle is encountered. It is for this reason that modelling of the data in order to predict plant response to unusual environmental conditions becomes so useful.

In summary, this study should be able to provide sufficient data to determine whether or not an open stand of Jack pine or similar conifer is the desired end point in maintaining vegetation at a low maintenance cost on sands, the result of open pit mining of the oil sands.

LONG TERM PREDICTION OF VEGETATION PERFORMANCE ON MINED SANDS

1 INTRODUCTION

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To date, oil extraction from the oil sands utilizes the Clark Method of an alkaline hot water solution. This produces large amounts of alkaline sand which is stored in tailings ponds retained by a hydrolically built dike. One of the greatest environmental problems of this operation is how to retain the huge piles of sand, keep them from eroding, and at the same time, convert these seemingly barren mounds of sand and their impoundments into useful production. Revegetation and its long term management are central to solving this problem.

The early research by GCOS and most of the research sponsored by AOSERP within the Vegetation Subcommittee has centered on use of agronomic grasses and mostly non-native shrubs and trees. Most of these species are adapted to mesic sites (see Selner and Thompson 1977 and Vaartnou (1976)). As a result of using grasses not native to dry sands, it has been found that annual irrigation and application of fertilizer are essential in order to maintain a dense plant cover. There has also been a rather high mortality of the woody species.

This project was conceived as a multidisciplinary integrated study to determine the physiological limits of native and non-native species to dry, nutrient-poor environmental conditions on a steep-sided sand dike and on sand piles. We believe that only when the limits of survival are known for native and non-native species, can there be a successful selection of species made that will survive the unusually severe climate of a drought year that may occur on the average of only every 25-50 years. The chance of field trails falling within one of these severe years is small. Thus this project, via field and laboratory tests, was designed to determine the limits to growth of native and non-native graminoid and woody species under moisture stress conditions.

In the most severe environments, native species are those that can best survive heat and drought. It is for these reasons that we are studying natural succession on sands to select the species most capable of survival and to determine the best combination of species.

The objectives of this integrated study are: 1) to determine responses of pioneer and climax species to drought stress conditions from field and growth chamber-greenhouse studies; and 2) via modelling the data on soil water dynamics, micro and mesometeorology, tree water dynamics, lichen water relations, and the role of mycorrhizae of woody plants, be able to better predict the kinds of species and the density at which they can survive and maintain a plant community under severe water stress. (We originally intended to study soil nutrient stress but this portion of our project was never funded).

Since it was not possible to initiate research on the GCOS dike the first year, an extensive aerial survey resulted in the selection of a 30-35 year old Jack pine - lichen woodland at the Richardson Fire Tower. This vegetation was chosen because it is the dominant forest type on sands (level and steep slopes) in northeastern Alberta, and thus the natural end point of plant succession on porous sands. The analysis of how this forest system solves its drought problems in terms of understory development and tree density will greatly aid in determining the desirability and feasibility of developing an open forest on the sand dikes and sand piles (Fig. 1). The research underway on burned forests and open sand dunes north of the Fire Tower (Fig. 2) will aid in the selection of native species and in the determination of their potential success in developing a stable plant community with low maintenance costs (irrigation and fertilization) on dikes and similar severe habitats on disturbed sands.

This project was organized so as to continuously monitor certain air and soil environmental parameters within a forest stand and to monitor intensively for 24-48 hr periods the reponse of the trees and lichens to environmental conditions at key seasonal plant development stages (spring snow melt, spring growth, mid and late summer, fall initial dormancy and winter dormancy).

The papers which follow are authored by the researcher of that component of the study.

1.2 ACKNOWLEDGMENTS

This research project V.E.6.1 was funded by the Alberta Oil Sands Environmental Research Program. Many people have contributed to the study including support staff and graduate students not funded from the project. We greatfully acknowledge their help.

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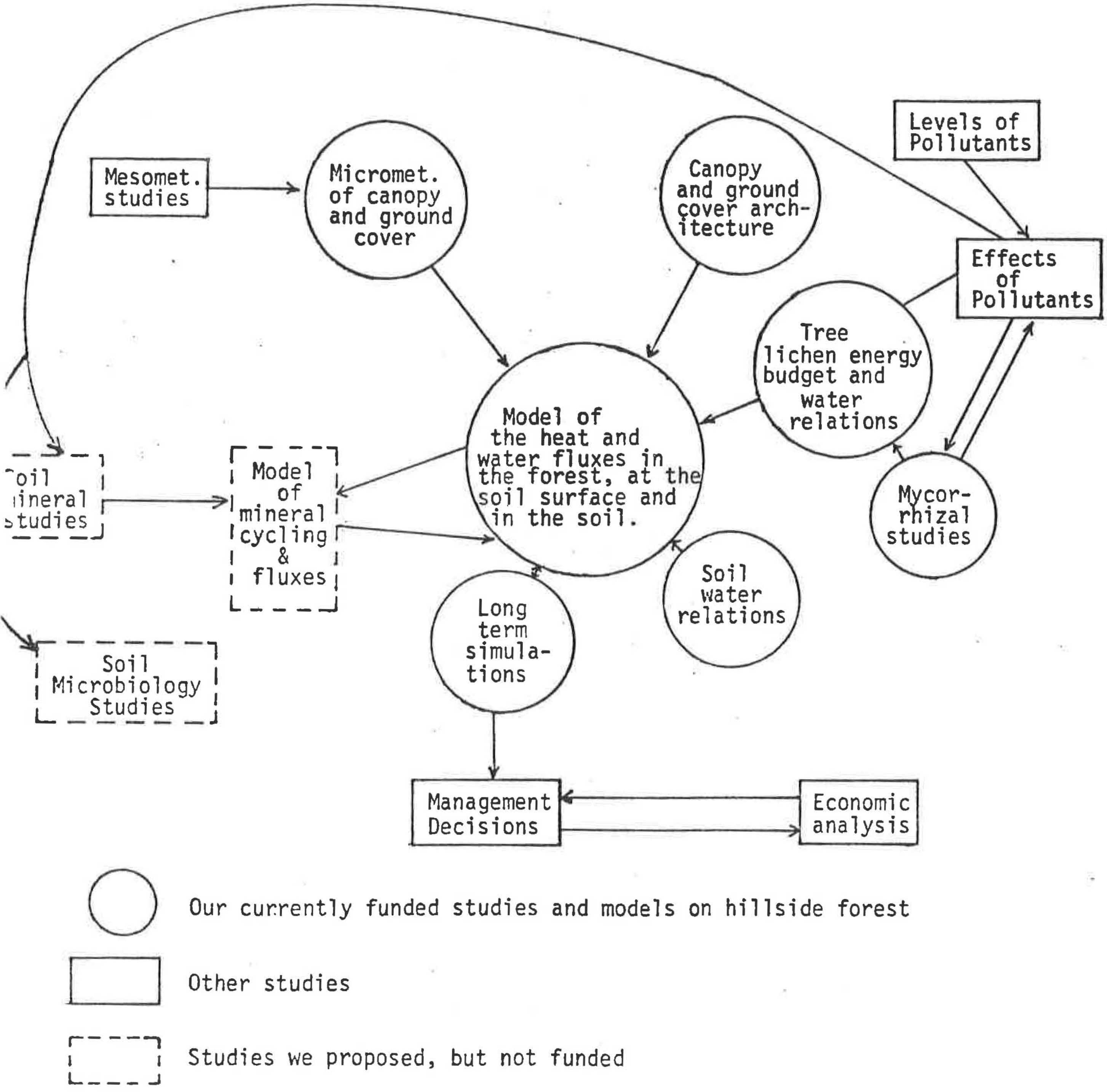

Figure 1. Studies of a stable Jack pine-lichen woodland on steep, deep sand, Richardson Fire Tower and how it relates to other research.

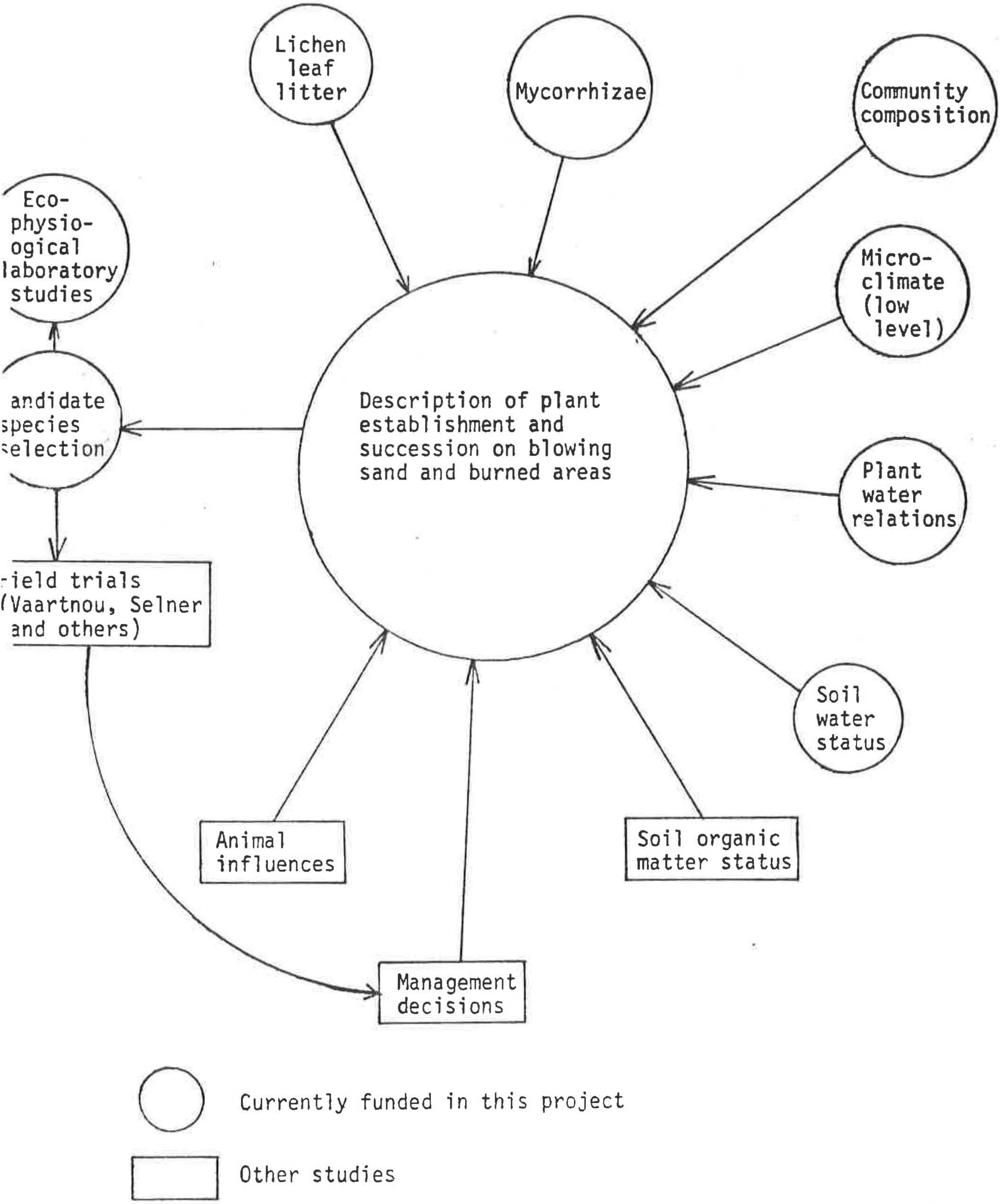

Figure 2. Plant responses to the severe environments of burned forest and open sand dunes near the Richardson Fire Tower.

2. SITE DESCRIPTION

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The Richardson Fire Tower site (subdivisions 15 and 16, Sect. 30, Twp. 102, R6 W4 and subdivisions 1 and 2, Sect. 31, Twp. 102, R6 W4) was chosen because it is: 1) representative of pine-lichen woodland; 2) similar to a WSW sand dike slope, environmentally the most severe for plant growth; and 3) accessible via an airstrip. The hill slope (2.3:1 rise, 19° slope and 20° S of W aspect) has a porous sand surface which shows no evidence of surface erosion even with heavy summer rains.

This pine-lichen woodland, dominated by *Pinus banksiana* shows evidence of past fires, so characteristic of these forests on dry sites. A few scattered wolf trees are 60-65 years old, but the average age of trees from cores is 30-35 years, and examination of a fire scarred older tree reveals that the slope was burned in 1930 or 1931.

Open stands of *Pinus banksiana* with a ground cover of lichens, mostly *Cladina mitis*, scattered dwarf shrubs of *Arctostaphylos uva-ursi* and a few forbs are characteristic of dry sandy soils in northeastern Alberta, northern Saskatchewan, and rocky sites of the Canadian Shield to the east and north (Rowe 1959). This region is termed the Athabasca South Section of the Boreal Forest Region. The only published account of these pine-lichen woodlands, but without quantitative data, are contained in the early paper by Raup (1935) on plant communities of Wood Buffalo National Park and Stringer (1976) on the vegetation of the oil sands region. The importance of fire in these northern forests is discussed by Rowe and Scotter (1973).

Two sets of plots were set up on the slope (Fig. 1). All plots were 10 m on a side; the lower set includes 56 plots and the one above the trail contains 30 plots. Intensive meteorological sampling is confined to plot #47; the transect for canopy attenuation of solar energy runs through plots #23 and 24.

A summary of the tree data is contained in Table 1 for the lower set of plots and for the intensive plot. Trees are defined as stems 2 m high and/or stems 2 cm dbh at 1 m height. Five quadrats ($1m^{-1}$) were sampled in each of four plots to determine ground cover. Ground cover in early October consisted of 1.4% herbs (mostly *Muhlenbergia cuspidata*); dwarf shrubs (8.7%), mostly *Arctostaphylos uva-ursi*; mosses 6.4% (mostly *Polytrichum poliferum*), lichens 47.0% (mostly *Cladina mitis*) and litter 36.7%. A list of vascular plant species is included as an Appendix.

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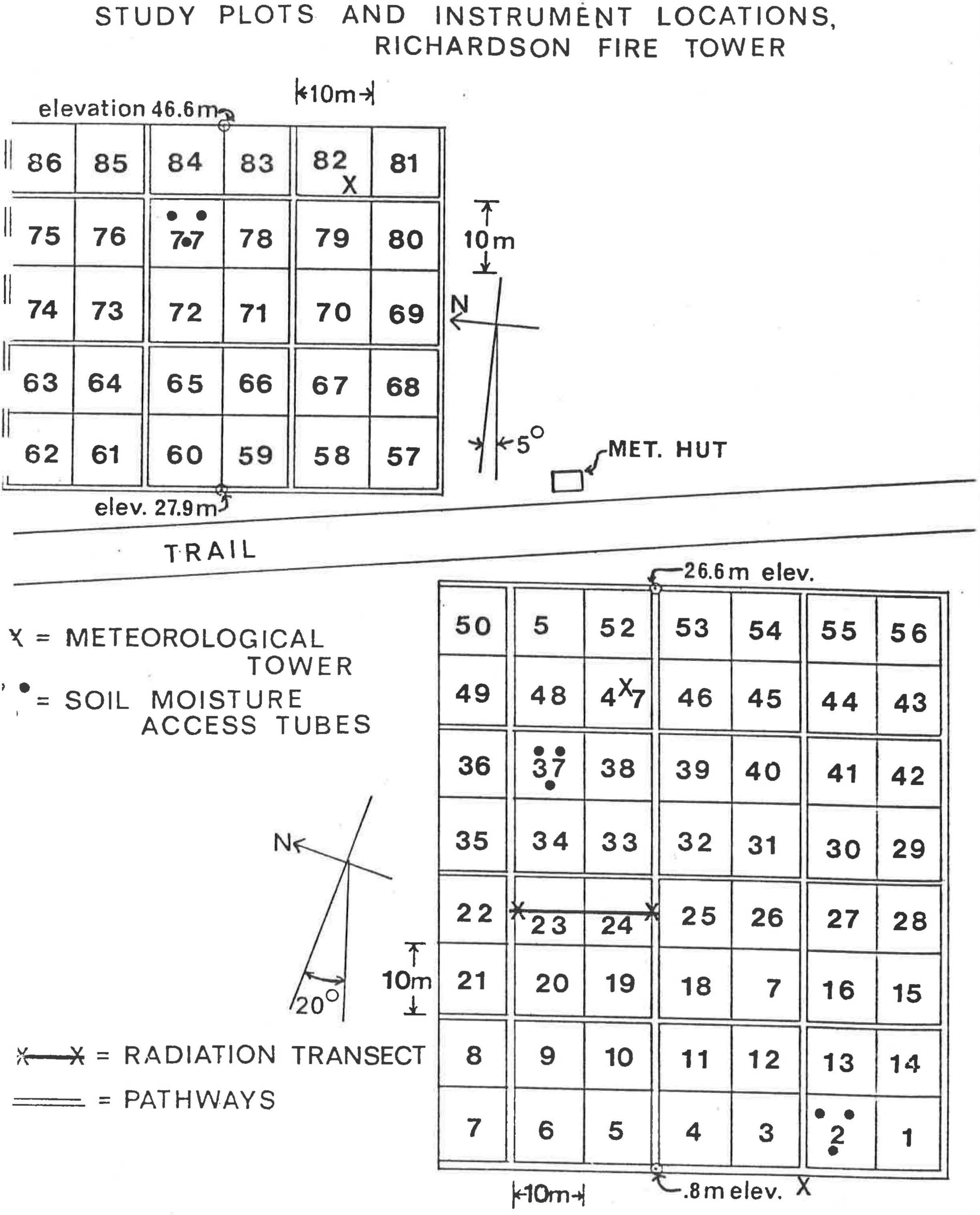

Fig. 1. Location of study plots and instrumentation, Richardson Fire Tower.

Table 1. Stand data for Jack pine forest at Richardson Fire Tower means ± SD.

Characteristic	Lower Block of Plots (n=56)	Intensive Study Plot #47
Tree Density (100 m^2)	62.9 ± 24.3	72 (live) + 9 (dead
Tree Height (m)	(7.4 ± 1.2)*	5.4 ± 1.8 (live only)
DBH (cm)	6.75 ± 2.54*	4.8 ± 2.6 (live only)
Canopy Cover (%)	28.8 ± 9.0	35

*These were not determined by random sampling and are probably overestimates.

Appendix A. List of vascular plant species collected within the study plots at the Richardson Fire Tower, autumn 1975.

2.2

Trees

Betula papyrifera Marsh.
Pinus banksiana Lamb.
Populus tremuloides Michx.

Shrubs

Alnus crispa (Ait.) Prush
Amelanchier alnifolia (Nutt.) Nutt.
Arctostaphylos uva-ursi (L.) Spreng.
Hudsonia tomentosa Nutt.
Lonicera involucrata (Richards.) Banks
Prunus virginiana
Rosa acicularis L ndl.
Symphoricarpos albus (L.) Blake
Vaccinium myrtillus L.
Vaccinium vitis-idaea L.

Herbs

Anemone canadensis L.
Arceuthobium americanum Nutt.
Artemisia campestris L.
Aster ciliatus (Ledeb.) Fedtsch.
Calamagrostis rubescens Buckl.
Campanula rotundifolia L.
Carex sp.
Galium boreale L.
Hieracium umbellatum L.
Maianthemum canadense L.
Muhlenbergia cuspidata Lindl.
Saxifraga tricuspidata Rottb.
Solidago gigantea Ait.

3. MICROMETEOROLOGY

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3.1 INTRODUCTION

A micrometeorological field measurement program was undertaken on the forested south slope of the Richardson Fire Tower site in order to supply the atmospheric driving variables for the model described in Section 11 and to provide more detailed data for model verification and refinement. The micrometeorological observations together with measurements of plant properties and soil properties constitute a unique and comprehensive portrayal of physical and biological processes for one eight-month period in a Jack pine forest on a lichen-covered sand slope in northern Alberta. It was clear at the outset from recent literature on the micrometeorology of coniferous forests (American Meteorological Society, 1975; Jarvis *et al.*, 1976) that results of work elsewhere could not be extrapolated because of the combination of soil, slope, latitude, and native vegetation at the Richardson Fire Tower site.

The ecosystem model which forms the nucleus of this project is intended for operational use with a small set of so-called driving variables. The micrometeorological observations provide a basis for correlations with standard weather observations at first-order stations such as Embarras Airport (past data only), Fort Chipewyan, and Fort McMurray Airport or at the special weather station established by the Meteorology and Air Quality program of the Alberta Oil Sands Environmental Research Project at Mildred Lake. In other words, it is intended that, on completion of model verification and refinement, it will no longer be necessary to continue a micrometeorological observation program at the study site.

The complete data acquisition system was installed in May, 1976 and operated continuously until January, 1977 when the data logger was removed for servicing and recalibration. Work has progressed on two fronts. In the first place it was necessary to prepare and run computer programs for editing and preliminary analyses of the continuous variables. Secondly, it was necessary to carry out intensive but discontinuous programs of measurement of special variables such as precipitation interception, vertical profiles of wind speed, temperature, and humidity, and horizontal profiles of radiation components below canopy. Many of these special measurements are concerned with the problem of representativeness of the data - a problem of vital concern on a slope and below a tree canopy.

3.2 METHODS

Two main types of data acquisition systems were used in order to fulfill the two objectives of the meteorological phase of the project. One, labelled as the continuous system, was used to measure the driving variables and is summarized in Table 1. The second, labelled as the intensive run system, was used for several short periods throughout the growing season and is summarized in Table 2. The timing of intensive runs was specified by the modelling component of the project on the basis of plant-status information. Apart from the automatic acquisition of data during the intensive runs, profile measurements of wind and water vapour were measured and recorded manually. For the profiles of wind within the canopy, a series of sensitive RIMCO three cup

Table 1. Continuous data logging system and sensors used to measure and produce atmospheric driving variables.

Sensor	Parameter Measured
Eppley Precision pyranometer (280-2850 nm)	Global Incoming Radiation
Eppley Infra Red Radiometer (3500-50,000 nm)	Long Wave Incoming Radiation
Eppley Precision pyranometer with optical filter (695-2850 nm)	Global Filtered Incoming Radiation
Kipp and Zonen solarimeter with shadow band	Diffuse Sky Radiation
Kahlisco Radiation Balance Probe (Sauberer-Dirmhirn Model) (300-6000 nm)	All Wave Incoming Radiation All Wave Outgoing Radiation
Copper-Constantan Thermocouples	Wet Bulb-Dry Bulb Temperature 8 m Wet Bulb-Dry Bulb Temperature 0.05 m
Climet Model 011-2B anemometer	Wind speed at 8 m
Stewart Electric Wind Vane	Wind direction at 8 m
C.S.I.R.O. Soil Heat Flux Plates	Soil Heat Flux (not a driving variable)

Data Logger: D.C. Operated Campbell CR-5 Digital Recorder

Data Recorder: D.C. Operated Facit 4070 Paper Tape Punch

Sampling Time: Integrated values over 30 min period, printed every 30 min.

Table 2. Data logging system and sensors used during intensive runs.

Sensors	Parameter Measured
Eppley Precision pyranometer (280-2850 nm)	Global Incoming Radiation
Eppley Infra Red Radiometer (3500-50,000 nm)	Long Wave Incoming Radiation
Eppley Precision pyranometer with optical filter (695-2850 nm)	Global Filtered Incoming Radiation
Kipp and Zonen solarimeter with shadow band	Diffuse Sky Radiation
Kahlisco Radiation Balance Probe (Sauberer-Dirmhirn model) (300-6,000 nm)	All Wave Incoming Radiation All Wave Outgoing Radiation
Copper-Constantan Thermocouples	Air Temperature 0.25, 0.5, 1.0, 2.0, 3.0, 4.0, 5.0, 6.0 m Soil Temperatures 0.01, 0.02, 0.04, 0.08, 0.125, 0.25, 2.0, 6.0 m Leaf Temperatures Lichen Thallus Temperature
Gill UVW Anemometer	Three Components of Wind

Data Logger: A.C. Operated Fluke 2240A

Data Recorder: A.C. Operated Facit 4070 Paper Tape Punch

Sampling time: Every three minutes during intensive runs.

anemometers were installed at several heights. For most of the field season these heights were 0.8, 2.0, 4.0, 5.0 and 6.0 m until more anemometers were made available. The distribution then became 0.25, 0.5, 1.0, 1.5, 2.0, 3.0, 4.0, 5.0, and 6.0 m. For water-vapour profiles a model 880 Dew Point Hygrometer (Environmental Equipment Division) with four sensors was used. The sensors were installed at 0.5, 2.0, 4.0, and 6.0 m. As stated previously both wind profiles and water-vapour profiles were recorded manually during the intensive runs; every 14 min for the wind and every 15 min for the dew point. Both the anemometers and the dew point hygrometers were on loan from the Meteorology Division, University of Alberta.

Precipitation measurements were measured both automatically using a Weather Measure tipping bucket attached to an event recorder, and manually using a Taylor Clear View rain gauge read in the morning at 0900 hr. Special investigations of precipitation interception including measurements of stemflow were undertaken. Juice cans (48 oz) were used to measure interception at 14 sites on the hill. Whistance-Smith (1973) found that these work well as rain gauges. The cans were located 0.5 m from the trunk of the tree and, in most cases, a companion rain can was established in a nearby clear area. No attempt was made to measure variation of interception under the canopy and the cans were not moved throughout the field season. The standard rain gauges mentioned above were used as a check of the clearing rain cans. Stemflow was measured by stapling and sealing 2.5 cm polyethelene tubing which had been previously cut in half, to the trunk, at diameter breast height (DBH). Whatever stemflow occurred would collect in a covered can attached to the tree. All cans were read as soon as possible after a precipitation event.

In order to understand radiation interception and reflection within the canopy, a radiation transect system was installed. This consisted of two supporting towers 20 m apart with four wire transect tracks stretched out between them. Three Lambda sensors (one pyranometer, one quantum sensor and one infra red sensor) were mounted on a small cart while three others were installed above the canopy on one of the supporting towers. As the cart travelled through the canopy during a transect, all sensors were monitored continuously. Many problems were encountered in forcing the cart to travel at a steady rate but these now have been solved. Several transects were measured in the latter part of the 1976 field season. However, some further electronic testing of the sensor signals remains to be done before the system is fully operational for the 1977 season.

The decrease in field activity since October 1976 has allowed more time to be spent on data analysis. This has been mainly in the form of data processing: writing the programs to read the original data from the paper tapes, translating the data into required units, initial editing of data to remove and to correct obvious errors and gaps and a second but more tedious editing to check the validity of the data. The amount of information is great and this work will continue until spring, 1977. There are, however, some results which can be presented at this time.

3.3 RESULTS AND DISCUSSION

3.3.1 Climate

The climate of the 1976 field season at Richardson needs to be looked at in order to assess how the project study area fits into the larger AOSERP study area and how this field season compares with other years.

In Fig. 1, based on long term means, one can see that Richardson is warmer than Fort McMurray especially in June and July. Figure 2 for the 1976 field season shows Mildred Lake also to be warmer than Fort McMurray. Richardson, (our site) was 2 to 3°C warmer than either Ft. McMurray or Mildred Lake. This was true particularly in May and June and the differences diminished as the season progressed. The tendency for high temperatures during the early part of the season was most probably a result of the southwest exposure of the hill side. In May and June with high insolation, the hill site warmed up much more than either Fort McMurray or Mildred Lake.

Turning our attention to precipitation we find that Richardson in 1976 was a drier site than Fort McMurray (Fig. 3) in agreement with the general trend as one goes north from Fort McMurray. When compared with long-term records (Table 3) we find that Richardson (our site) was either near normal or slightly above normal in May, June and July but drier than normal in August. At present, comparative studies of this nature are continuing for other climatic variables and for the rest of our data collection period. This is necessary in order to understand how Richardson fits into the overall climatic pattern of the region. One of our future activities will be to model the microclimatic conditions at Richardson from the standard climatic station network data now available. Knowledge of the most important relationships between the climate of the study site and the regional climate will permit full use of the long-term records of neighbouring stations for estimation of expected frequency, duration and intensity of periods of climatic stress. In the area of interest, long-term records of hourly weather data are available from the Atmospheric Environment Service for Embarras Airport, Fort Chipewyan, and Fort McMurray Airport.

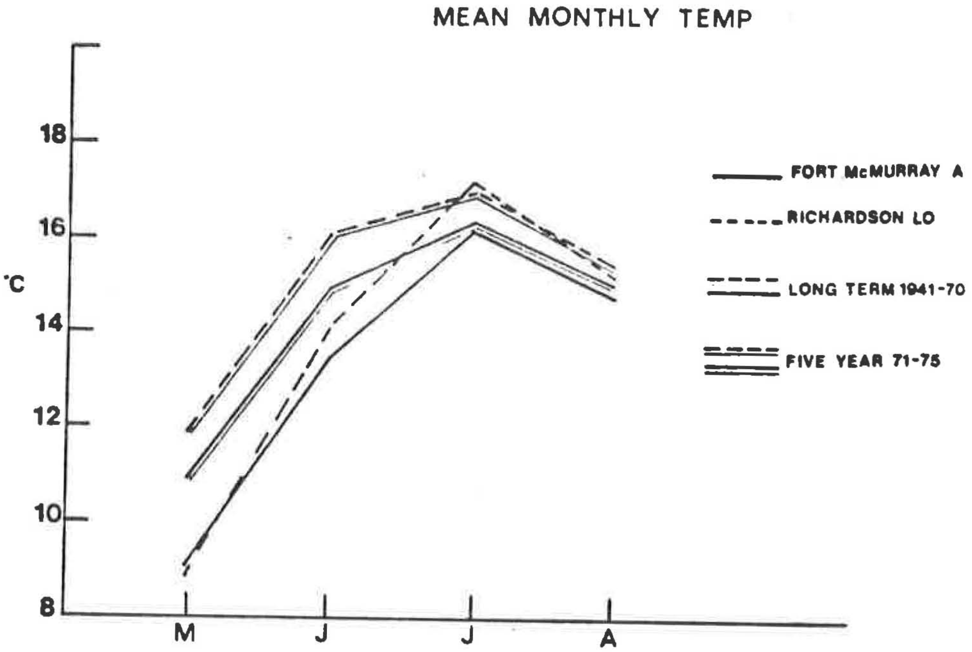

Fig. 1. Mean monthly temperatures for Ft. McMurray Airport and Richardson Lookout. Long term and recent five year means are shown.

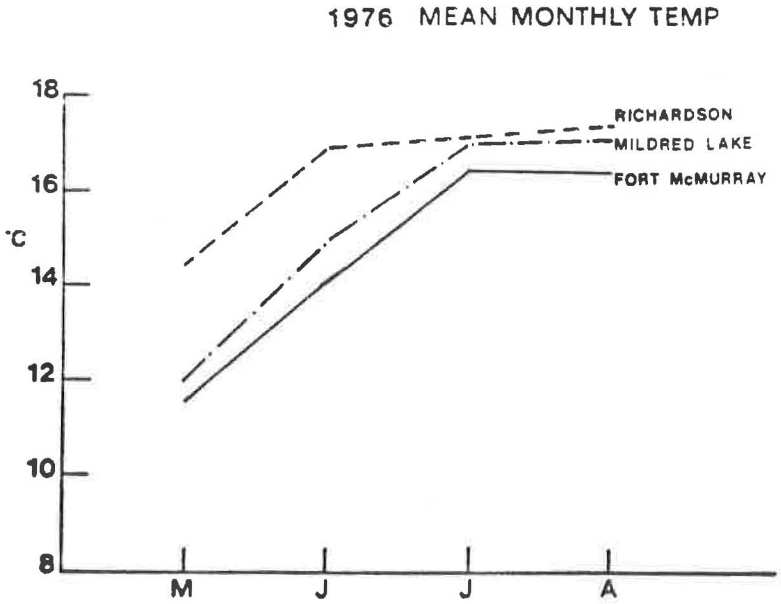

Fig. 2. Mean monthly temperatures for 1976 (May to August) for Richardson (our site), Mildred Lake and Ft. McMurray Airport.

3.3.2 Radiation

Radiation is one of the main controlling factors of any ecosystem. The amount of incoming, absorbed and outgoing radiation will define the amount of radiant energy available. One of the main components of the model is radiation and, therefore, a fairly comprehensive range of radiation parameters was measured at our study site. On a seasonal basis (Fig. 4) one finds that incoming solar radiation followed the trend expected at these latitudes. From mean daily values of 250-275 Wm^{-2} in May and June there was a slow and steady decline to 200 Wm^{-2} in August, 125 Wm^{-2} in September, down to 75 Wm^{-2} in October and very low values (25 Wm^{-2}) in early December. Also plotted on this graph is the solar diffuse radiation. There was much less variation with time of this parameter than there was with solar radiation. Values decreased steadily from 100 Wm^{-2} in the early part of the season down to 25 and 10 Wm^{-2} in October and December, respectively. It is also of interest to note that the daily mean values of both parameters were almost the same during times of cloudiness and simply scanning the graph one can see the frequency of clouds at Richardson. In Fig. 5 we find somewhat similar trends for all-wave incoming and all-wave outgoing radiation as measured by the Kahlisco radiation balance meter (300-6,000 nm). Since it does include most of the solar short-wave spectrum, there is a similar pattern of dips in the curve because of cloudiness. The seasonal variation is similar to that of solar radiation except that the values were lower in all cases. We find that the mean daily values dropped from an average of 225-250 Wm^{-2} in early May and June down to 50 Wm^{-2} in October and 10-25 Wm^{-2} in early December. Outgoing radiation did not show this dramatic decrease because this component results from reflected shortwave radiation from the tree canopy and ground surface

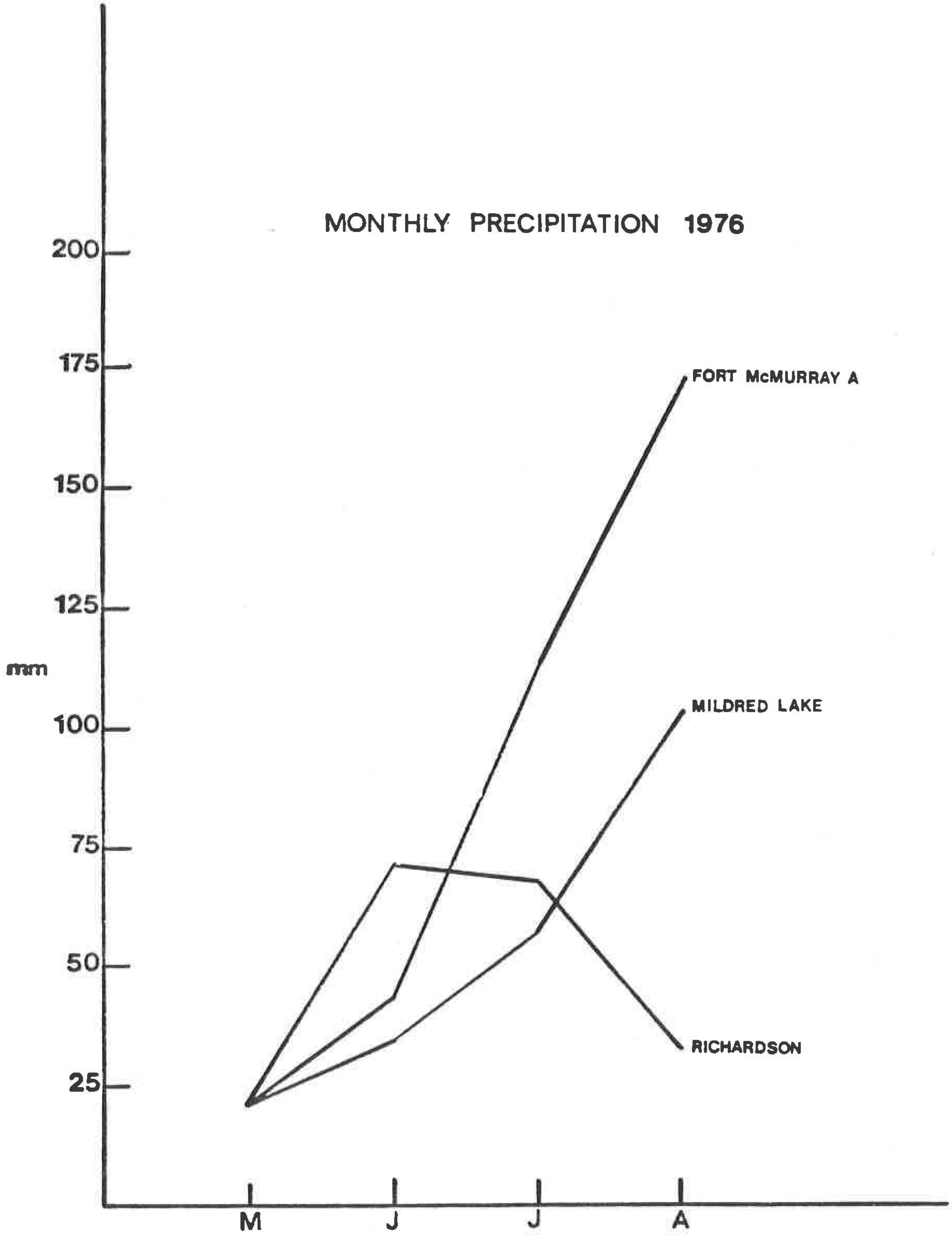

Fig. 3. Monthly total precipitation for Ft. McMurray Airport, Mildred Lake and Richarson.

Table 3. Total precipitation data for Richardson, Richardson L.O. and Ft. McMurray (mm).

Station	May	June	July	Aug.
Ft. McMurray (1941-1970)	33.0	61.5	73.7	64.0
Richardson (L.O.) (1941-1970)	24.9	56.6	57.4	73.4
Richardson (our site) (1976)	22.3	71.9	67.7	33.3

Table 4. Classification of storms based upon total precipitation per storm.

	Precipitation (mm)		
Characteristics	1 to 2.5	2.6 to 7.6	7.6 to 14.4
Av. ppt per storm	1.3	5.3	12.1
Av. intensity	2.5	2.9	3.4
No. of storms	6	3	5
Av. % intercepted	57.3	24.0	9.9

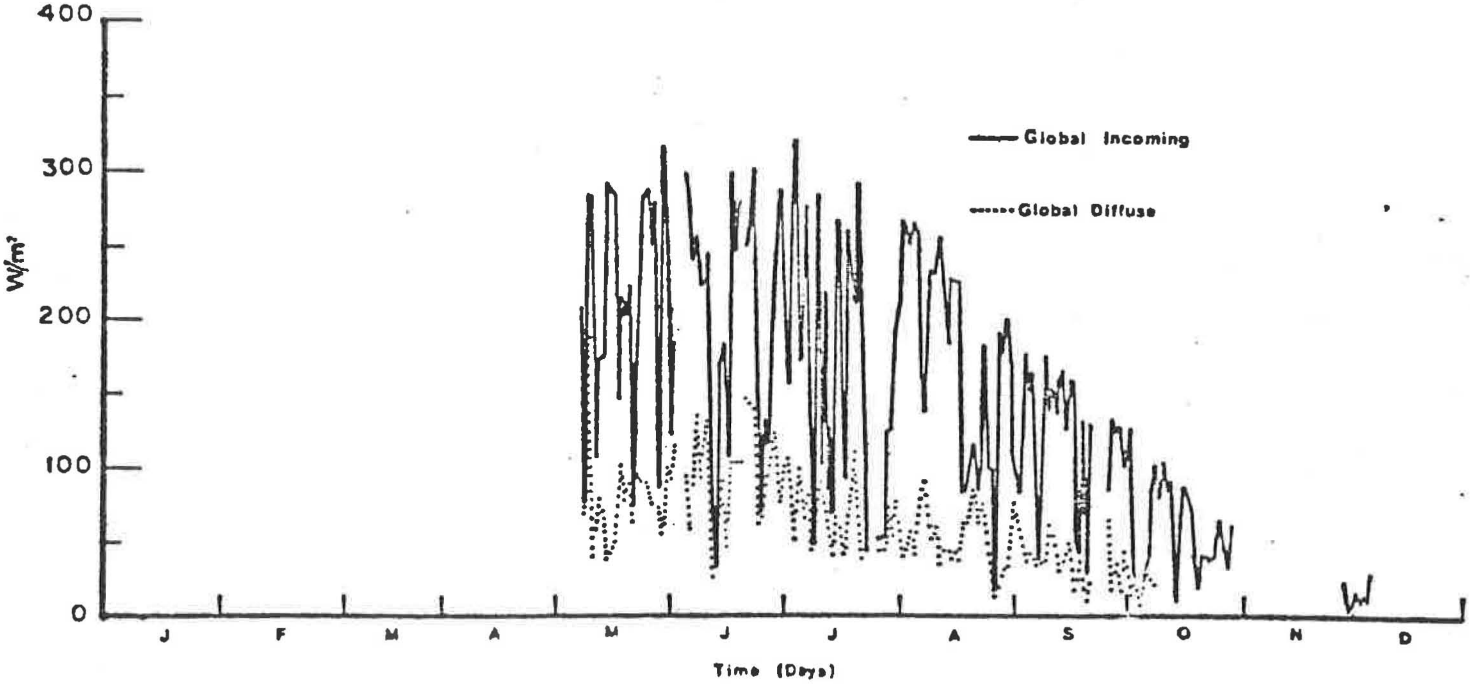

Fig. 4. Mean daily values of shortwave global incoming radiation and global diffuse radiation.

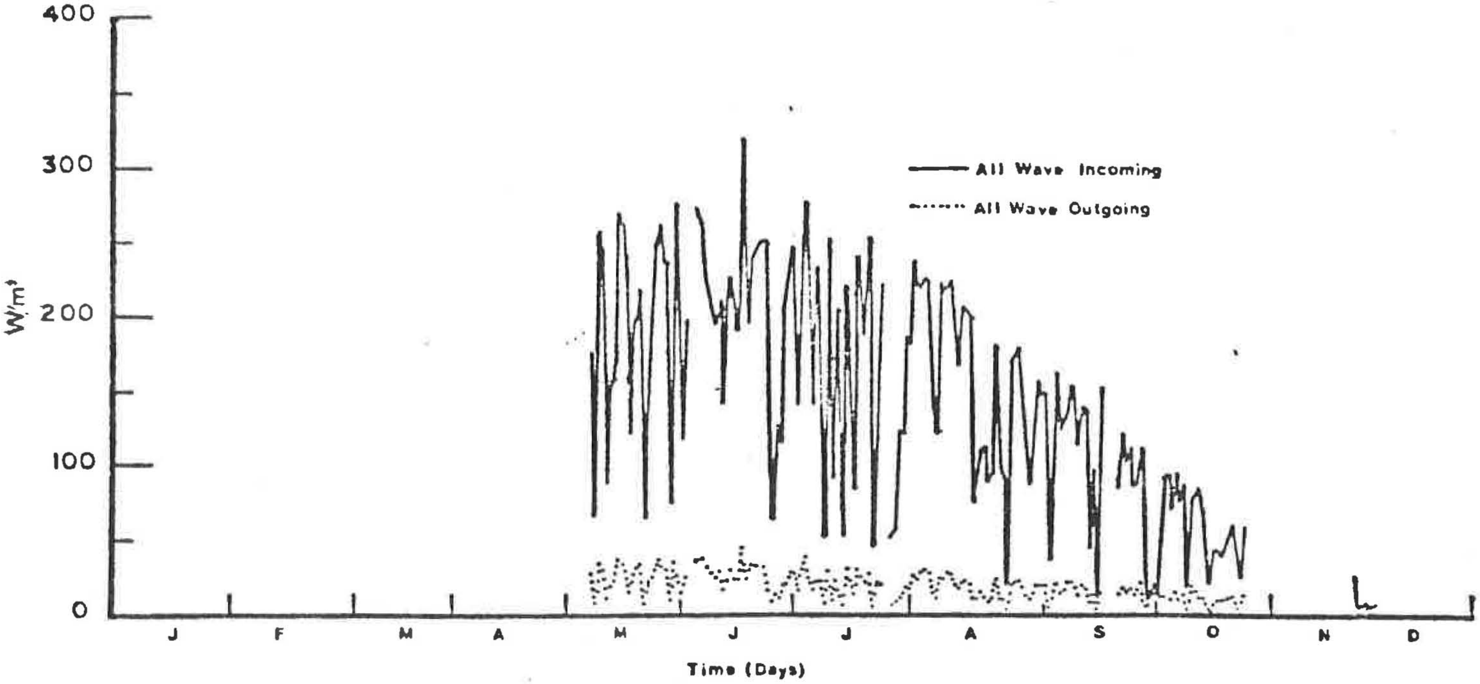

Fig. 5. Mean daily values of all wave incoming (300-6000 nm) and all wave outgoing radiation.

and from long-wave radiation emitted by these same objects. The change in the seasonal pattern was from 35 Wm^{-2} in May and June to 10 Wm^{-2} in late October and 5 Wm^{-2} in early December. It is interesting to note that the area between the two curves is the amount of energy or net radiation that was absorbed by the Jack pine forest. Maximum net radiation, of course, occurred in June and decreased with time until it was nearly zero in early December. As was mentioned previously the next important step will be to look at radiation levels within the canopy and to determine what happens to radiation as it travels down through the trees.

Two days have been chosen to show the diurnal trends of the radiation components. The first, 29 May (Fig. 6) was a sunny day with only small clouds temporarily blocking the sun at 1800 and 1930 hr. The curve of incoming solar radiation shows the typical bell shape of a sunny day with maximum incoming radiation of 820 Wm^{-2} at 1330 hr. The all-wave incoming radiation curve followed the solar radiation curve except for two differences; in the first place the values were 70-80 Wm^{-2} lower than solar radiation because of it's spectral range does not extend into the shorter wave lengths and secondly, there was a 1.5 hr lag time at sunrise before the all-wave incoming curve caught up to that of solar radiation because the all-wave sensor was situated on the side of the hill at our central tower and the other radiation sensors were on top of the hill. The outgoing all-wave radiation rose from 5 Wm^{-2} at 0400 hr to a maximum of 100 Wm^{-2}between 1400 and 1600 hr and then dropped to 3-5 Wm^{-2} at 2300 hr. Thus there was negative net radiation or radiative cooling occurring for several hours before sunrise and after sunset.

Since long-wave radiation (3500-50,000 nm) is essentially a function of the sky radiant temperature, there was not as much variation as with other components. It was lowest (265 Wm^{-2}) between 0400 and 0600 hr and rose to a maximum (370 Wm^{-2}) at 1500 hr. Finally the diffuse solar radiation remained fairly constant at 60 Wm^{-2} most of the day except near sunrise and sunset at which time it closely followed solar incoming radiation. With low sun angles it is difficult to maintain the radiometer within the shadow band.

The last day of May (Fig. 7) was chosen as an example of a cloudy day. It is as close as possible in time to the sunny day in order to minimize seasonal radiation differences. With cloud cover the most dramatic change was in incoming solar radiation. Values were between 100 and 400 Wm^{-2} for most of the day except for a short "burst" at 1630 hr. All-wave incoming radiation showed similar values for most of the day because the shorter wavelength difference between the two radiometers was essentially eliminated by cloud cover. Also, with increased cloud cover, we find an increase in diffuse solar radiation. Midday values were approximately 280 Wm^{-2} or almost four times the values for the sunny day. All-wave outgoing radiation again was 3-5 Wm^{-2} from 0000 to 0600 hr and from 2000 to 0000 hr. For these time periods we again find negative net radiation. Long-wave sky radiant energy showed less diurnal change and was generally higher on this cloudy day than during the sunny day. Values ranged from 320-360 Wm^{-2} early in the day to 420 Wm^{-2} near midday then dropped down to 375 Wm^{-2} at the end of the 24 hr period.

3.3.3. Wind

The exchanges of water vapour, carbon dioxide, heat and momentum between a canopy and the bulk air above it, depend upon the turbulent exchange properties of the wind profile generated in the boundary layer above the canopy (Jarvis, *et al.* 1976). Figure 8 shows the mean daily

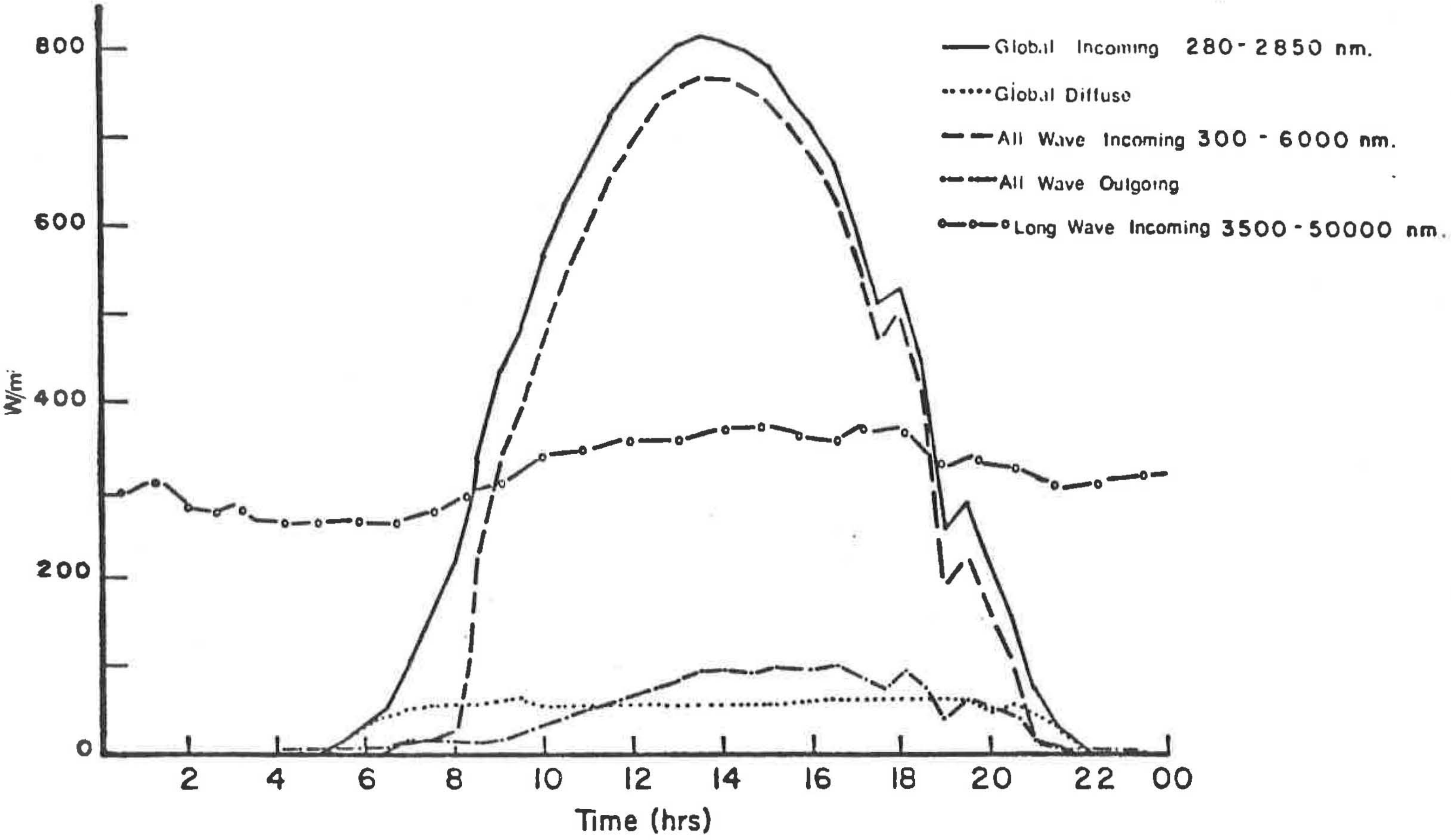

Fig. 6. Half hourly integrated values of the radiation components for 29 May 1976.

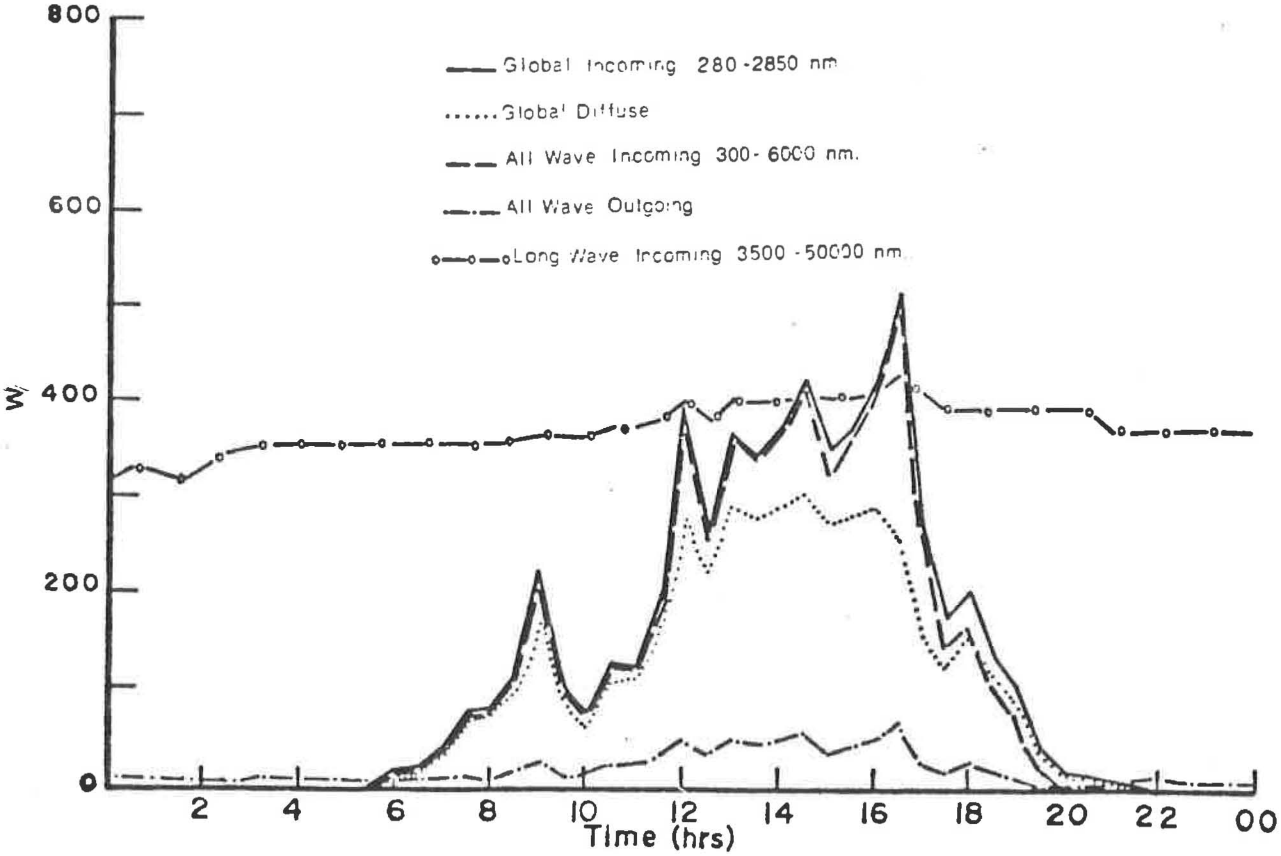

Fig. 7. Half hourly integrated values of the radiation components for 31 May 1976.

wind speed from May to October. The data are from the anemometer situated above the canopy at 8 m and provide an indication of the mean air flow of the area. The variation was from 0.6 to 0.7 m sec^{-1} at low wind speeds, to 3.2 to 3.9 m sec^{-1} in the high ranges. Mean values varied from 2.0 m sec^{-1} in May and June down to 1.0 m sec^{-1} in July and August, and back up to 2.0 m sec^{-1} in September and October.

Although it is the wind above the canopy which is a main controlling factor for the turbulence within the forest canopy, the structure of the wind profile itself needs to be looked at to try and understand the flow of air within the forest. The recent review by Jarvis, *et al.* (1976) discusses the problems of measuring wind profiles within the canopy. Geiger (1965) discusses how the air movement is less restricted in a trunk area free of branches particularly when the wind can blow in through the open borders of the stand. This phenomenon of "blow through" has also been found to occur in ideal conditions of fetch. The fact that our site is a slope with many openings in the canopy makes it more difficult to measure and understand wind profiles. Wind profiles of 26 and 27 September were chosen for illustration because this was a period with strong and steady winds. Profiles during lighter winds need to be analyzed also but their interpretation is more difficult. The profiles shown in Fig. 9 represent a day with a small range of wind speeds. The center profile is the mean of all the profiles while the other two profiles were observed during the periods of highest and lowest wind speeds. All three profiles show a sharp decrease from 8 m (just above the canopy) to 5 m well within the needle zone. The mean profile and the highest wind speed profile show a slight bulge at 0.5 m rather similar to the profile shown by Geiger (1965). Another interesting

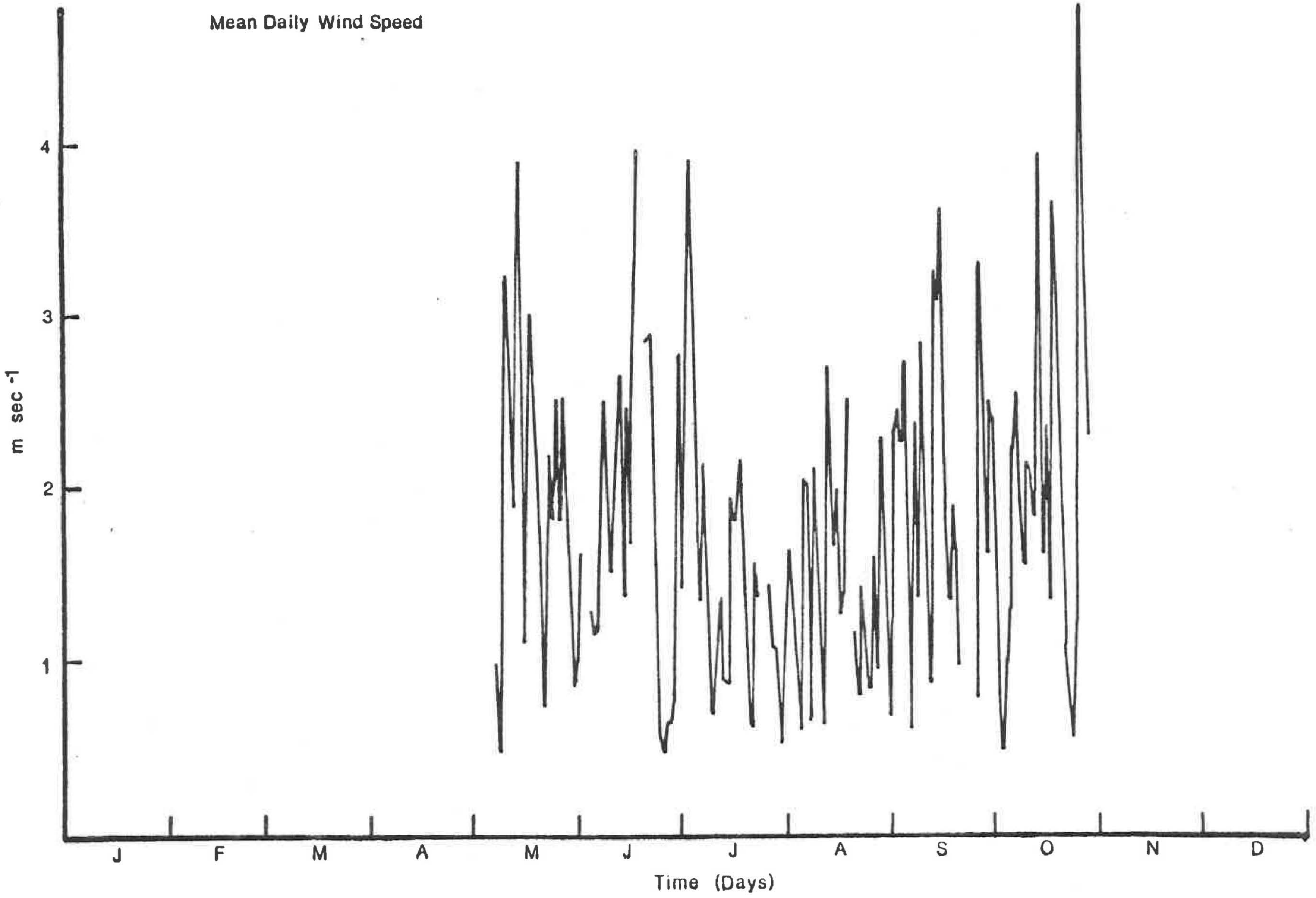

Fig. 8. Mean daily wind speed at 8 m.

feature of these profiles is the very obvious bulge at 2 m for the low wind speed profile. This is just below the branch-needle zone and could be a similar phenomenon to the "blow through" near the surface. It has been suggested by Jarvis, *et al.* (1976) that blow-throughs result from a horizontal pressure gradient which is sustained by persistent up-and down-draughts at varying points in the stand. In our situation, however, a third and probably dominant reason for blow-throughs is that, because we are dealing with a slope, horizontal wind eddies of dimension comparable to holes in canopy can enter below the canopy. This occurs probably even if the wind is not perpendicular to the slope.

3.3.4. Profiles of Temperature and Dew Point

Another important part of the atmospheric structure within the canopy is the distribution of temperature and water vapour with height. Figures 10, 11 and 12 show 0.5 hr means of temperature and dew point for three selected days. Figure 10 is for 20 July, a hot, dry day. The profiles of dew point show very little gradient with values ranging from 4 to 6°C and the greatest difference occurring at 1730 hr between 0.5 and 2.0 m. This could well be the result of surface evaporation increasing the water-vapour content in the surface layers. The temperature profiles for that same day showed greater variations. The lowest temperature occurred at 0800 hr which was the time of high wind speeds above the canopy. There is an indication of cooling near the surface from 1600 to 1730 hr yet at the same time the temperatures at 4 m are increasing. This could be as a result of several factors; the blow-through phenomenon with increased mixing below 2 m which is carrying heat to upper layers or because of the vertical distribution of radiative cooling and advective heating of the air. However, there was no indication of this phenomenon in the dew-point temperature data.

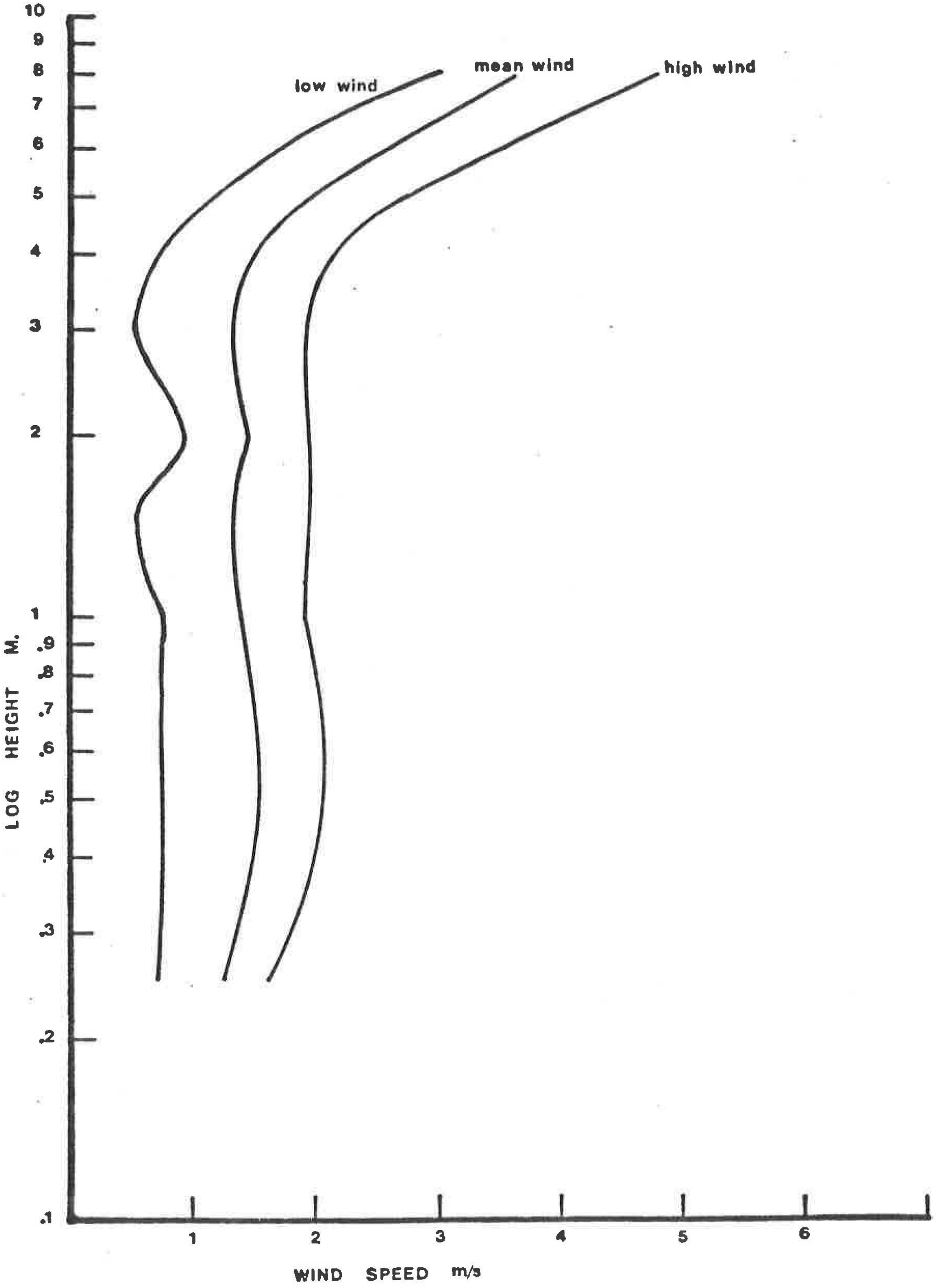

Fig. 9. Wind speed profiles showing the mean profile for the measuring period and the highest and lowest wind speed profile.

The next set of profiles (Fig. 11) are for 26 September. Again there is very little difference in the dew point profiles. The temperature profiles showed a more consistent cooling and the gradients became very small with time. Finally, the profiles of 27 September (Fig. 12) again showed fairly monotonic profiles. The dew points in the upper canopy increased slightly with time and the temperatures showed a steady drop with time at all levels. In all three sets of profiles shown, no evidence was found for maximum temperatures at the top of the canopy. However, perhaps this is not surprising for an open and ill-defined canopy top.

Thus we find that the canopy is often homogeneous in dew point and temperature possibly as a result of good mixing due to the blow-through phenomenon previously discussed. Because the gradients are very small it is difficult to determine the source or sink strengths for heat or water vapour by differentiation of flux profiles. Analyses of the profiles are continuing for a variety of conditions and wind speeds. The project modellers have assumed a constant water vapour profile based on these and other similar results. However, temperature is not assumed constant with height because large temperature gradients occur at times.

3.3.5. Precipitation and Infiltration

Figure 13 shows the distribution of total daily precipitation at the Richardson site. As stated earlier, the 1976 field season was near normal or slightly above normal when compared with long term records. The normal peak of precipitation is in July (Alberta Forest Service, 1971) but in 1976, June had the most rain (71.9 mm in June vs. 67.7 mm in July).

One important aspect of the study of precipitation at Richardson was the measurement of interception and stemflow. The amount of rain intercepted normally decreases radially outward from the stem (Lunt 1934).

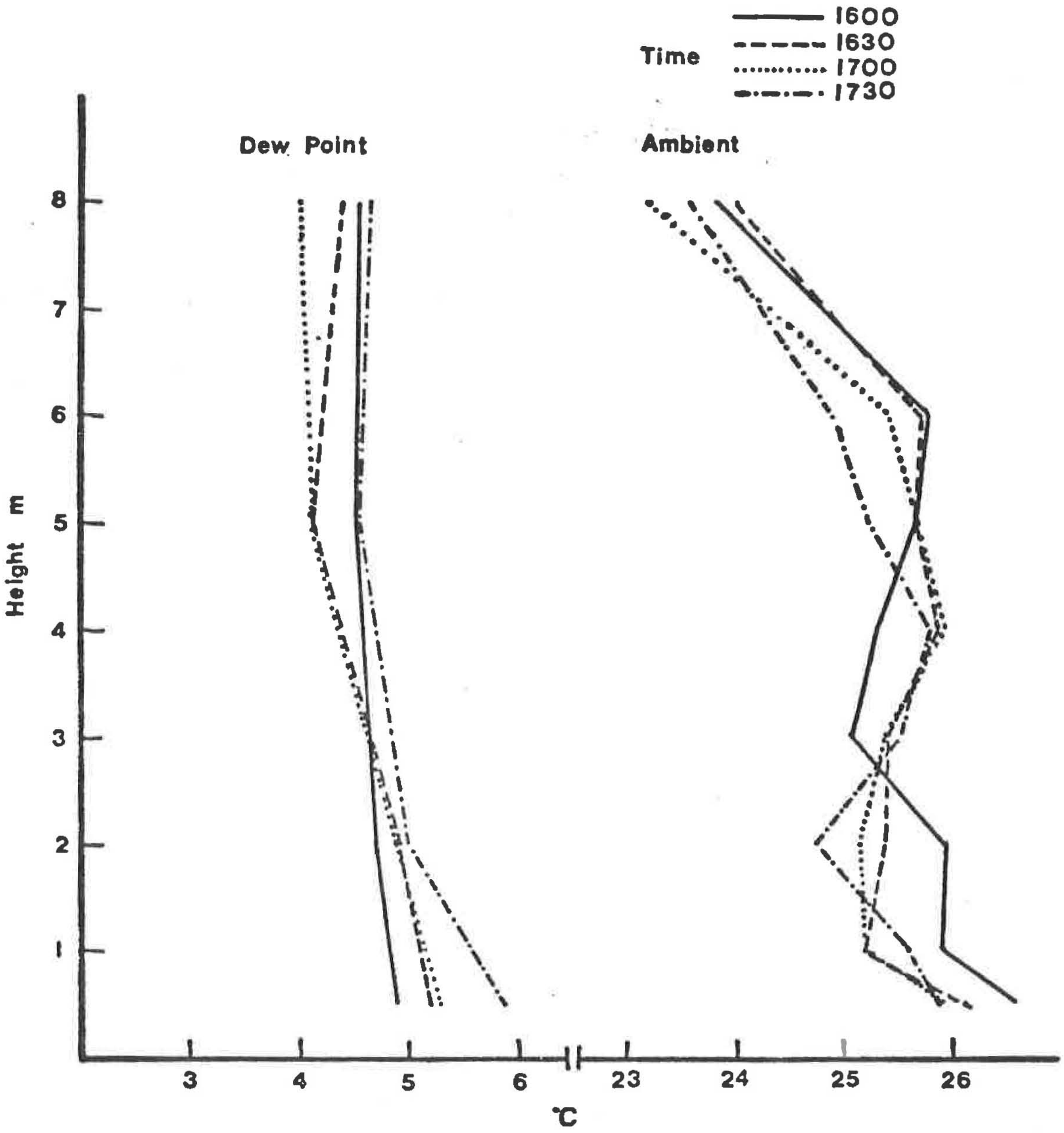

Fig. 10. Half hourly mean dew point and ambient air temperature profiles for 20 July.

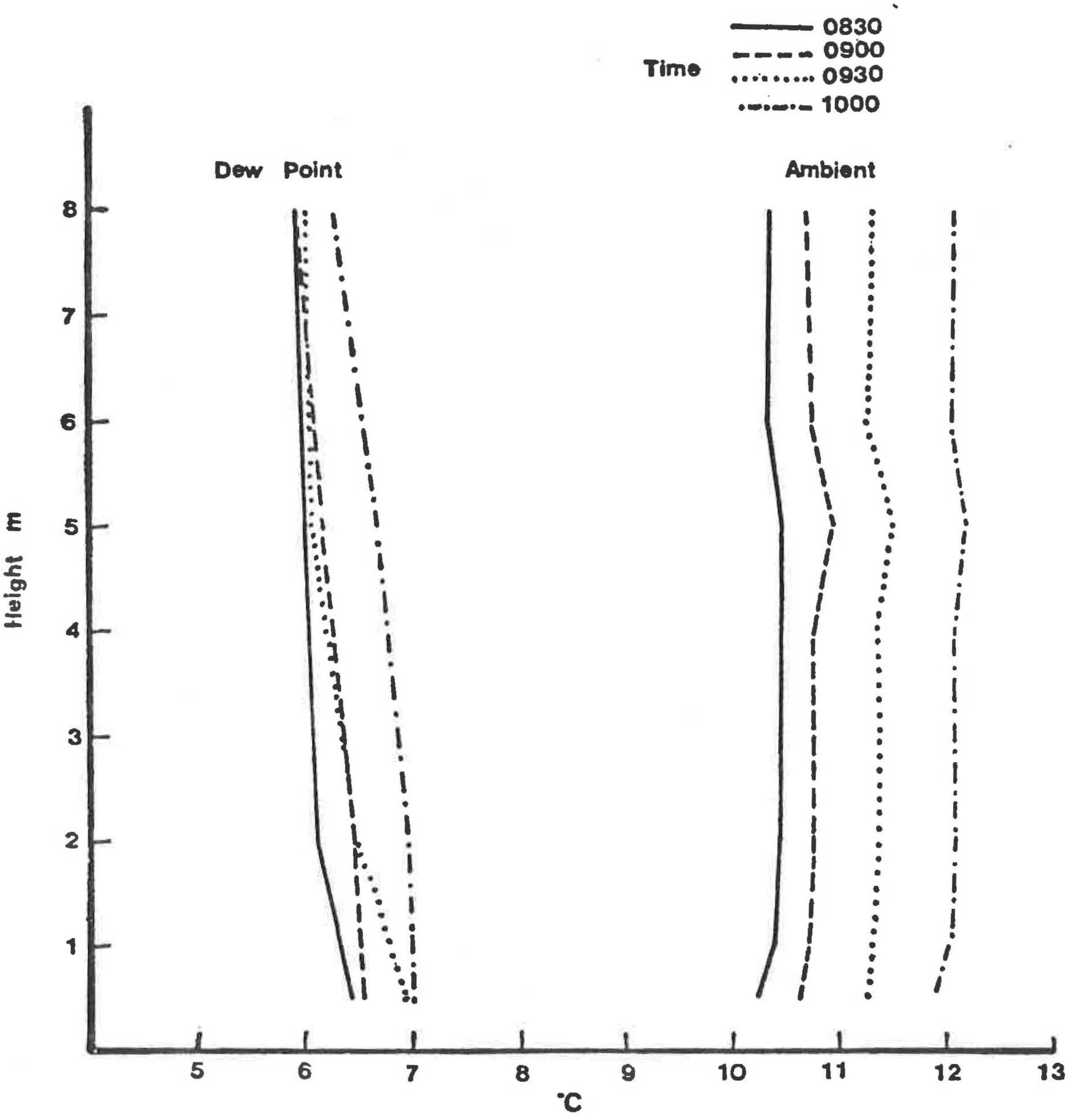

Fig. 11. Half hourly mean dew point and ambient air temperature profiles for 27 September.

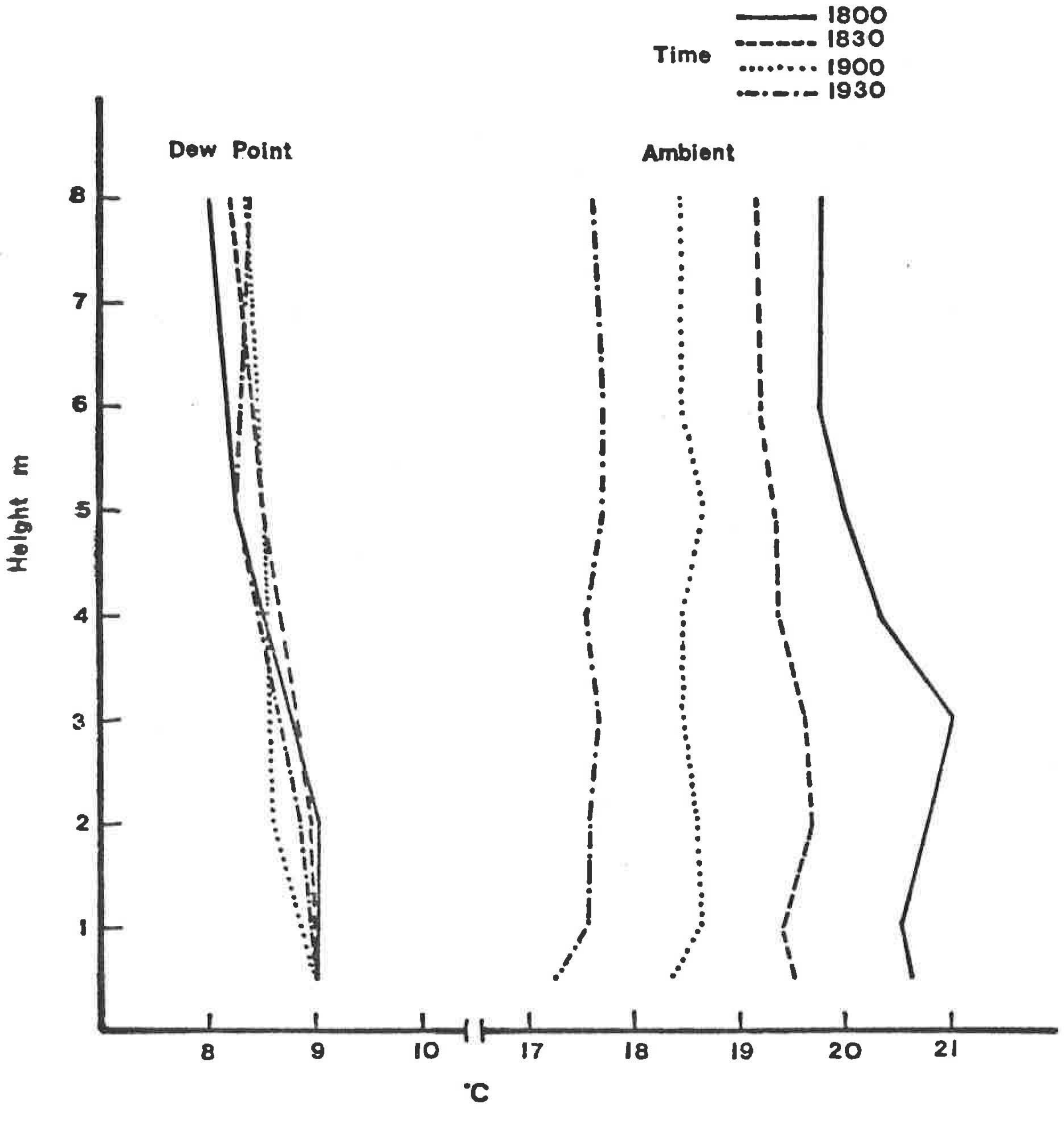

Fig. 12. Half hourly mean dew point and ambient air temperature profiles for 27 September.

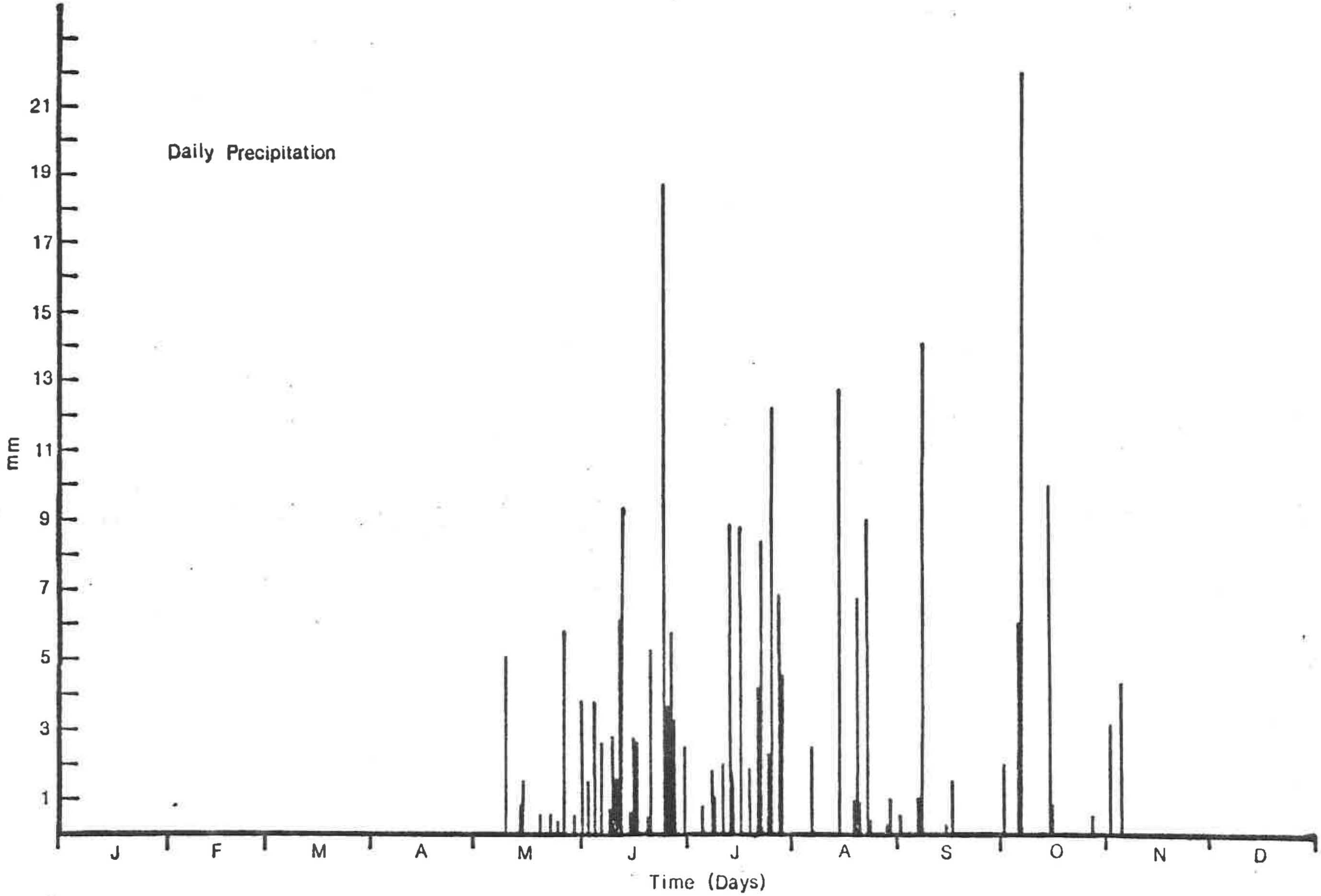

Fig. 13. Total daily precipitation at Richardson.

Kittredge et al.,(1941) found that interception varies under different parts of the crown and is highest on the leeward side of the tree increasing as wind velocity increases. Our objective in this study was not to find differences of the throughfall under the crown but to relate storm size to the amount intercepted. By placing throughfall collectors at 0.5 m from the stem and allowing them to remain stationary throughout the study, we were able to obtain a consistent measurement of rain through the canopy. Figure 14 illustrates the percent canopy interception in relation to total precipitation. Here the average interception percent is highest for light rains then decreases steadily to assume a near-constant value of 10% for the heavy storms.

Kittredge et al. (1941) devised two methods of storm classification, one being total precipitation per storm, and the other being the intensity of precipitation in mm hr^{-1}. The storm intensity classification was found inaccurate because storms with light precipitation were obscured by heavier storms within the same intensity class. Therefore storm classification using total precipitation per storm was used at Richardson. Table 4 shows these three classes and their characteristics. For these storms a mean was calculated and the mean interception was 30.4%. This compares reasonably well with a 50 year old Jack pine stand with a seasonal average of 21.0% intercepted (Mitchel 1930), when one considers differences in stand density, topography and age of stand.

Because of the small breast height diameter, a more open exposure and a somewhat low crown density, we found from observation that direct rainfall was collecting on the collars and measured as stemflow while very little water was actually flowing down the trunk. Stemflow results are not shown because of the unreliability of the data. Other studies have shown stemflow to average 1 to 16% of the total precipitation

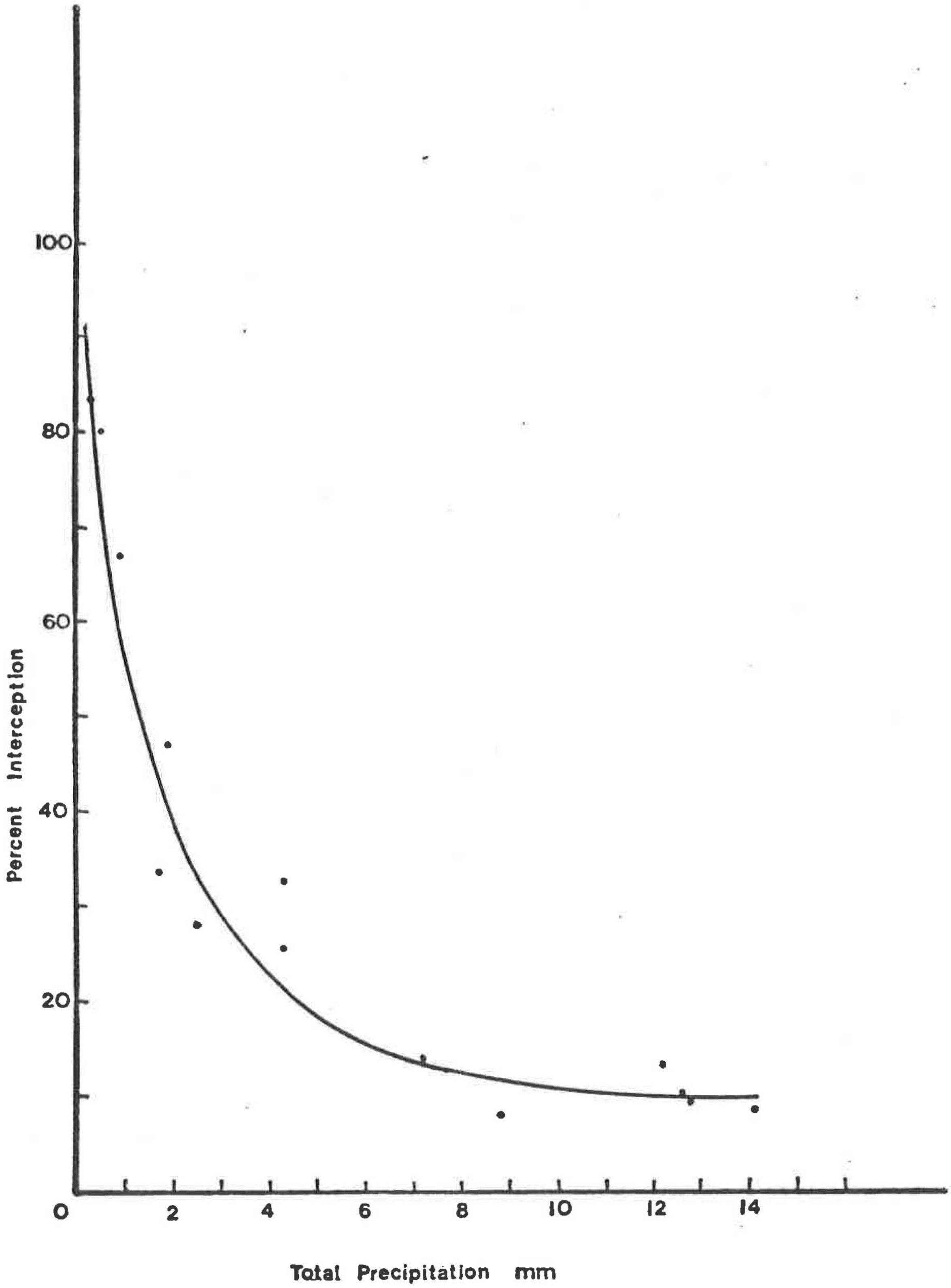

Fig. 14. Percent interception of total rainfall in relation to the total amount of precipitation for each storm.

depending on storm size (Kittredge, 1948) while Rowe and Hendrix (1951) showed stemflow to be 0.5 to 3.5% for small trees (DBH 10.2 to 25.4 cm). However, because Jack pine at Richardson have a mean value of 6.5 cm DBH, stemflow values would be within this latter range and probably near the lower values.

3.4 CONCLUSIONS AND FUTURE WORK

The work described in this section of the report is descriptive and does not deal with many of the active processes of the atmosphere both above and below the canopy. Our main role has been to measure and provide values of the atmospheric driving variables for the model. Now that this is underway more emphasis will be directed towards further analysis of the data. Such analyses will be designed to clarify some of the processes as needed to properly understand the micrometeorology within the canopy.

The analysis of data to date has shown us where there is a need to improve or increase our measurements for certain parameters. In this category we find inadequacies in our measurements of wind and radiation profiles and of interception and stemflow. This past field season has given us an initial understanding of the processes involved with a forested slope and has given us some indications of the relationships of our study site to the general macroclimate of the area. This will be needed when we start modelling microclimatic variables using the macro-climatic station network data.

3.5 3.5 REFERENCES

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SOIL PHYSICS

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4.1 INTRODUCTION

The purpose of the soil physics component is to obtain laboratory information on moisture characteristics of the sand at Richardson Fire Tower, and field information on soil temperature and moisture regimes which together can be used for mathematical modelling purposes.

4.2 LITERATURE REVIEW

Information on moisture conditions in sands is sparse because of their low economic importance relative to other soils. Because sands exhibit a high hydraulic conductivity at low moisture tensions and a very low hydraulic conductivity at high tensions, there is a fairly pronounced moisture level or "field capacity" to which they rapidly drain. Richards (1949) quotes 100 mbars as the tension at field capacity for sandy soils while Russel (1961), Salter et al. (1967) and Webster and Becket (1971) suggest values closer to 50 mbars. Some of the most recent work on moisture characteristics of sands has been carried out in Australia (Elrick 1963, Roberts 1966, Carbon 1975) where considerable variation is shown to occur, depending on sand size composition.

4.3 MATERIALS AND METHODS

4.3.1 Soils

The soils are Eutric Brunisols. The litter and H layers are both thin, their combined thickness ranging from 1 to 3 cm. Beneath the H layer is an Ae horizon, which although almost absent in places, is more than 15 cm thick on the lower slopes. This overlies a Bm horizon which is around 20 cm thick, ~~this~~ which in turn merges into the very pale brown loose sand of the C horizon.

The sand is mainly in the medium and fine categories but variations occur, lenses of finer and more coarse material in many places being interwoven. Occasionally a lens high in silt is encountered, but generally non-sand material is very low. There are a few boulders 5 cm to 50 cm across, but these seem too few to much affect water movement.

4.3.2 Laboratory Methods

4.3.2.1 Routine analyses

Particle size analysis was performed by the pipette method (Kilmer and Alexander 1949) with modifications made by Toogood and Peters (1953). Soil reaction was determined on a 1:2.5 soil: water mixture using a glass electrode. Total nitrogen was determined by the semi-micro Kjeldahl method (Bremner 1965). Calcium carbonate was obtained from inorganic carbon determinations using the method of Bundy and Bremner (1972), while organic carbon is the difference between total and inorganic carbon; total carbon having been obtained by combustion in a LECO induction furnace (Canadian Society of Soil Science 1975).

4.3.2.2 Bulk density and core samples

Cores taken in 2.6 cm diam. brass rings were used to obtain bulk density. With the possible exception of surface soil, bulk densities of sand are not easily varied, and it was found possible to obtain the same values as in the field by filling a ring closed at one end, with disturbed material while tapping the ring lightly on the table top. Because taking intact cores in the field without disturbance is very time-consuming, these laboratory-packed cores were used in certain determinations.

4.3.2.3 Hydraulic conductivity

Saturated hydraulic conductivity was determined by the constant head method (Klute 1965). Rings (2.6 cm diameter, 6 cm long) were packed to a bulk density similar to that in the field and saturated with distilled water under vacuum. Because of the high permeability of the sands, it was necessary to minimize flow impedance by using 0.05 mm opening wire mesh screens at both ends of the ring in place of ordinary filter paper, while loss of fine material was minimized by reducing the quantity of water flow, by using micro-burettes at both the inlet and outlet ends of the core.

Unsaturated hydraulic conductivity was determined using an apparatus similar to that described by Elrick and Bowman (1964). Cellulose acetate filters of suitable pore size for the required pressure range were used at either end of similarly packed rings to those used for saturated conductivity. Pressures were controlled by drilling numerous small holes in the ring wall and enclosing the whole apparatus in a pressurized container.

4.3.2.4 Moisture retention

Moisture retention curves in the range 0.01 bar to 1 bar have been obtained by the pressure plate method using small intact cores obtained with minimum disturbance in individual pressure cells. Liquid movement is slow in sands at low moisture content and therefore pressure plate results were found to be increasingly unreliable at higher tensions. Container thermocouple psychrometers (Korven and Taylor 1959) which depend on vapour movement, and function well only at higher tensions have however been used in the range 1 to 50 bars. Several small 'chunks' from the same cores used in the pressure plate cells were partially dried in air and sealed in the psychrometer containers. These were then placed in a water bath. Microvoltmeter readings were made periodically until they stabilized (2 to 24 hr). The sand from each psychrometer container was then placed in weighing bottles for moisture determination by oven drying at 105° C.

4.3.3 Field Methods

4.3.3.1 Field sites and field monitoring

Three field sites were selected, one just below the top of the hill, one near the middle and one near the bottom of the hill, all close to meteorological recording sites and as closely as possible on the same contours while avoiding disturbed or non-typical areas. Monitoring was begun in November 1976, continued monthly until spring, and then intensified considerably between 1 April and mid-September. Readings have only been taken occasionally over this winter.

4.3.3.1.1 Instrumentation at all sites

All three sites were equipped with:

a) Three neutron probe access tubes to a depth of 600 cm.

b) One set of copper constantan thermocouples at 1, 2, 5, 10, 20, 50, 100, 150, 200, 300, 450 and 600 cm below the surface.

c) Three sets of tensiometers at 20, 50, 100 and 200 cm, and one tensiometer at 300 cm.

4.3.3.1.2 Instrumentation at specific sites

Four more sets of thermocouples were added to the middle site at all depths between 1 and 100 cm, and one set of tensiometers was also added at 10, 20 and 30 cm below the surface. Two additional tensiometers were placed at 300 cm at this site, and three sets of psychrometers were installed at depths of 10, 20, 30 and 50 cm. Water table access tubes were installed at the lower site, between the lower and middle site, and at the bottom of the hill.

4.3.3.2 Field methods and interpretation

4.3.3.2.1 Soil temperature

Thermocouples were read with a simple microvoltmeter using an ice-water mixture in a vacuum flask for a reference junction. The microvoltmeter was insulated from cold in winter.

4.3.3.2.2 Moisture tension

Tensiometers with mercury manometers, similar to those described by Webster (1966) were used. Normally they are useful in the range 0 to 0.8 bar, however the low level of non-sand material at Richardson results in very slow liquid movement over most of the unsaturated range, with consequent large response times. Very fine manometer tubing was used to minimize water movement into and out of the tensiometers, but their range of usefulness appeared to be still limited to 0 to 200 mbars at most.

The large unfilled pore space in sand however favours good response from thermocouple psychrometers which depend on vapour movement. They are useful in the range 1 to 40 bars, but only a few were installed this year. Tensions in the range 200 mbars to 1 bar cannot be determined easily, and have to be inferred from moisture content using moisture retention curves.

4.3.3.2.3 Soil moisture

Aluminium access tubes for the neutron probe were inserted in augered holes which were then backfilled around the pipe with the excavated sand. Counts of 1 minute duration were taken with a Nuclear Chicago P19 Neutron probe at depth intervals between 10 and 600 cm. Calibration was carried out by inserting similar, but shorter access tubes into augered holes, taking counts, and measuring the moisture content of the augered material gravimetrically. Since snow cover influences near-surface readings, the effects of snow depth and density on winter readings needs to be taken into account, but its effects have yet to be measured. For near-surface moisture determinations, the neutron probe has severe limitations because of its large sphere of influence, and it is therefore necessary to resort to gravimetric sampling. It is hoped that a thermal method can be developed for near-surface measurements as this would reduce site damage and increase accuracy of near-surface measurements.

4.3.3.2.4 Water table

Water wells were read by inserting and blowing down a measured plastic tube inserted into the well until bubbling was heard.

4.4 RESULTS AND DISCUSSION

4.4.1 Particle Size Analyses

Particle size analyses (Table 1) show that the non-sand content of the sands is extremely low except in the occasional sample and most of it is distributed fairly evenly between the medium and fine fractions. Of note also (Table 2), is the absence of calcium carbonate, and the low pH except in deep samples.

4.4.2 Bulk Density

Bulk densities ranged from 1.35 to 1.45 in the surface Ae horizon to 1.50 to 1.60 in the C horizon.

4.4.3 Hydraulic Conductivity

Several results for saturated hydraulic conductivity are given (Table 3). Rates are extremely high, and there is evidence of a trend towards slightly greater rates in the surface than at deeper levels. Rates were greater at the upper site than further down the slope, but this could simply reflect sample variation. An unsaturated hydraulic conductivity curve for C horizon material is given (Fig. 1), and a curve for G.C.O.S. dike tailings sand, obtained under subproject VE4, is included for comparison. Of particular importance, is the extreme rapidity with which conductivity of Richardson sand declines between 30 and 60 mbars. For most purposes, a 'field

Table 1. Particle size distribution of sand samples from sites at Richardson Fire Tower.

Site	Horizon and Depth (cm)		% Sand Fractions					% silt 0.053-0.002 (mm)	% clay <0.0002 (mm)
			VCS (>1mm)	CS 1-0.5 (mm)	MS 0.5-0.25 (mm)	FS 0.25-0.105 (mm)	VFS 0.105-0.053 (mm)		
1	C	50	0.1	4.2	56.7	36.9	1.8	0.1	0.3
	C	600	0.2	4.5	40.3	39.7	9.2	5.3	0.9
2	Ae	0-2	0.3	5.7	38.0	45.9	7.3	2.3	0.5
	B	2-20	0.1	4.3	33.4	55.0	5.6	0.8	0.7
	B/C	20-30	0.0	0.6	8.6	79.4	10.8	0.2	0.4
	C	50	0.1	7.7	38.6	48.9	3.6	0.1	1.0
	C	600	0.1	8.9	68.1	21.2	1.2	0.3	0.2
3	C	50	0.1	3.8	38.7	45.8	9.7	1.7	0.2
	C	600	0.2	11.0	24.0	54.8	8.6	1.1	0.3
	C	1500	0.0	14.7	26.0	56.5	2.7	0.0	0.1

Table 2. Chemical analyses of sand samples from sites at Richardson Fire Tower.

Site	Horizon and Depth		pH	Organic Carbon(%)	Nitrogen (%)	C/N	$CaCO_3$ eq.%
1	C	50	6.3	-	-	-	0.0
	C	600	8.2	-	-	-	0.0
2	Ae	0-2	4.8	0.74	0.022	34.4	0.0
	B	2-20	5.8	0.08	0.003	25.3	0.0
	B/C	20-30	5.7	0.08	0.003	23.3	0.0
	C	50	5.9	0.02	0.001	15.9	0.0
	C	600	6.9	-	-	-	0.0
3	C	50	6.5	-	-	-	0.0
	C	600	8.1	-	-	-	0.0
	C	1500	8.1	-	-	-	0.0

Table 3. Saturated hydraulic conductivities in sand samples from sites at Richardson Fire Tower.

Site	Horizon	Conductivity cm/hr
1	C	40.1
2	Ae	43.5
	Bm	35.4
	C	31.3
3	Ae	57.6
	C	26.6

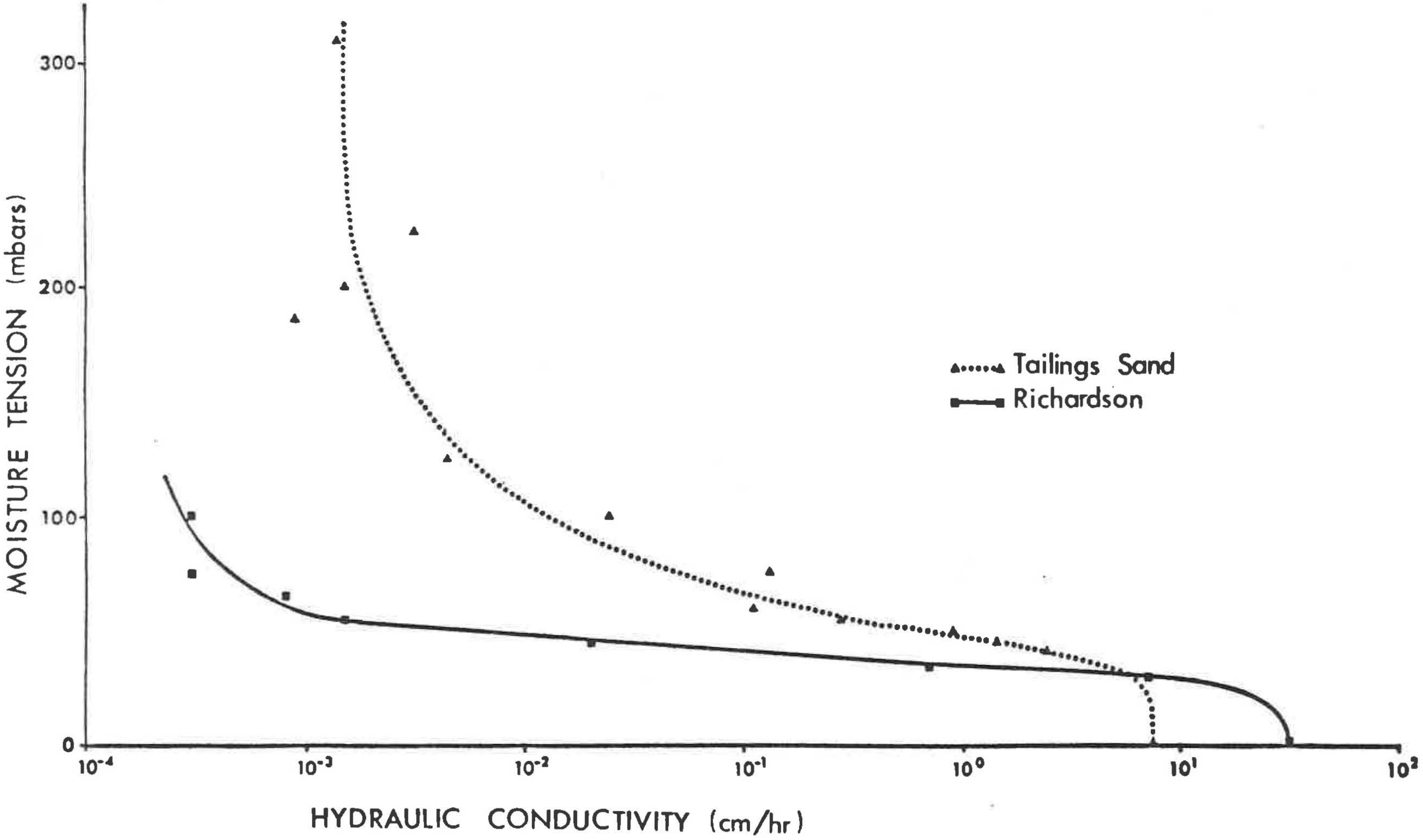

Figure 1. Relationship between hydraulic conductivity and moisture tension for C-tension for C-horizon material from site 2 at Richardson and for tailings sand from the G.C.O.S. dike.

capacity' can be considered to exist somewhere between 30 and 60 mbars, which agrees with information gained by others on sands (Salter et al. 1967, Webster and Becket 1971). The tailings sand, by comparison, has a lower saturated conductivity than Richardson sand, but the fall in conductivity with rise in tension is much less marked.

4.4.4 Moisture Retention

Curves for the middle site are shown (Fig. 2). If 50 mbars is taken as the tension at which rapid drainage of C horizon material ceases, then this corresponds to about 10% moisture by volume. Field moistures determined soon after rain showed this value was too high and a value of 6% which corresponds to 60 mbars is more correct. Since only about 0.2% moisture remains in this sand at high tensions, around 5.8% moisture is available to the vegetation, or 58 mm of water per metre depth of sand. This is low. However, at the same tension, the value for 0-5 cm material is much greater at around 95 mm m^{-1} while that for the Bm horizon is somewhere in between. So far there are indications that values for the top and lower sites differ little from those of the middle site.

4.4.5 Ground Temperatures

Ground temperatures for the middle site are available for one year (Fig. 3), while those for the upper and lower sites are only available since April 1976. At the middle site, the 0°C isotherm reached its deepest point (2.75 m) early in April, at the start of the thaw. Thawing of the ground was extremely rapid and appeared to be complete by early May. Rapid thawing is presumably encouraged, firstly by the SW aspect, secondly by the low moisture holding capacity of the sand

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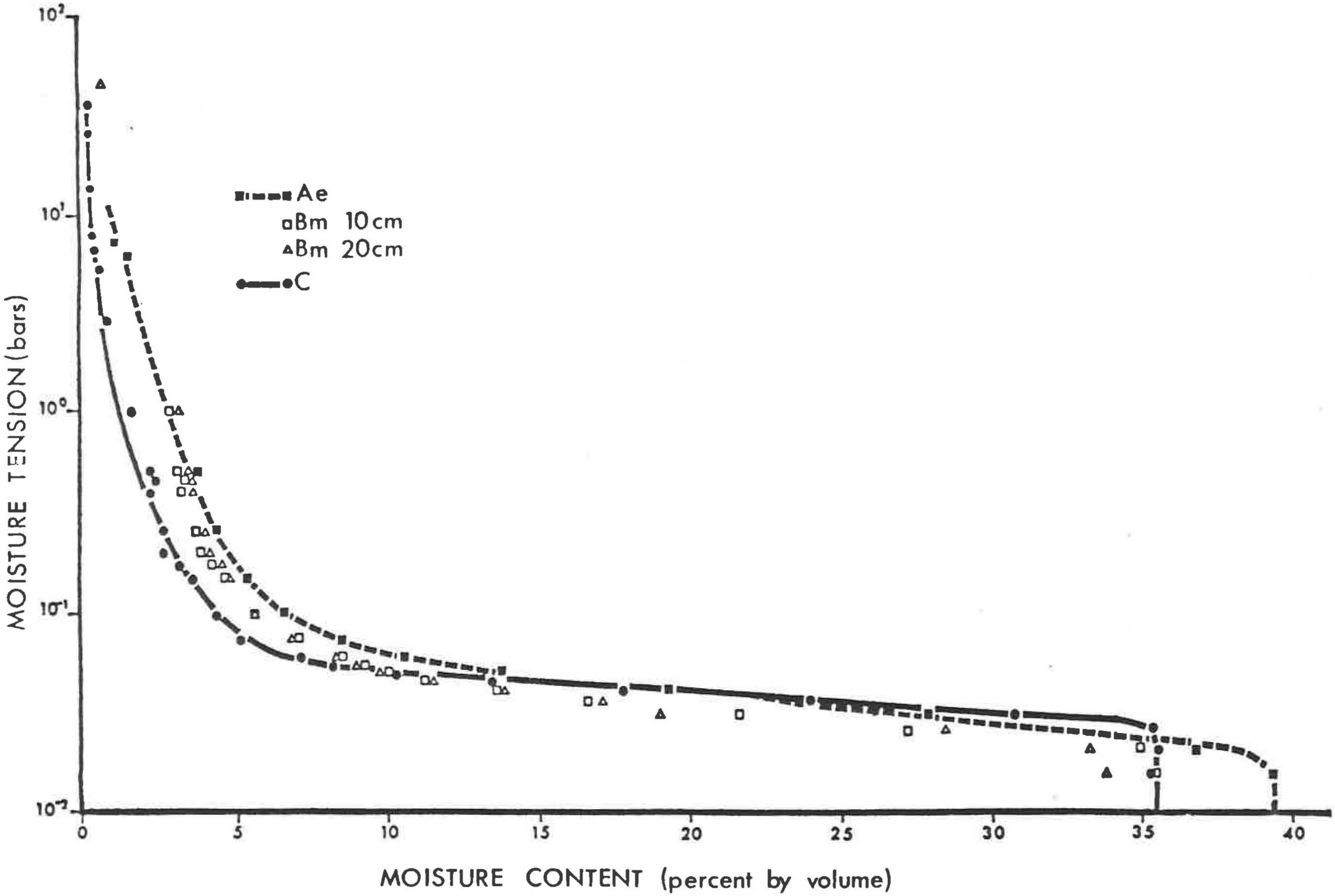

Figure 2. Moisture retention curves from soil samples from different depths at the middle site, Richardson.

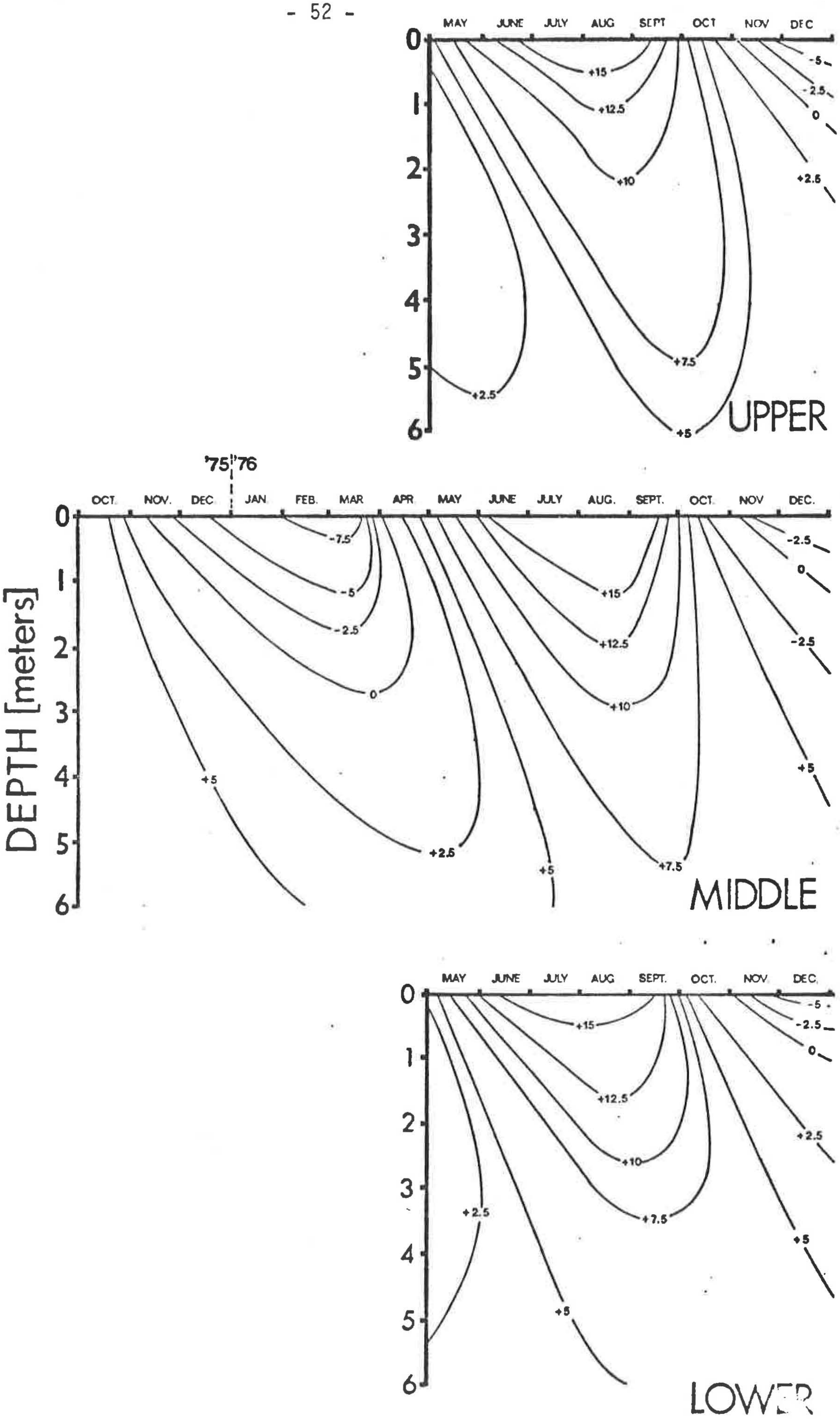

Figure 3. Isotherms in relation to time, and depth below ground at the three Richardson sites.

and consequent low heat capacity, and thirdly by a high saturated hydraulic conductivity which results in rapid infiltration of meltwater. Soil temperatures exceeded 15° C from early June until mid-October while continual freezing temperatures did not return until early November. Comparison of graphs for the three sites shows that the 15° C isotherm penetrated a little deeper at the middle site than at the other two sites. This is probably because canopy cover at the middle site is less than at the upper while the slope is steeper than at the lower site, so this site receives most incident radiation.

4.4.6 Moisture Tensions

Information on moisture tensions, particularly in the surface 50 cm, is sparse. Tensiometers failed to respond sufficiently rapidly (see section on Moisture retension) to give accurate readings at tensions greater than 100 to 200 mbars, and the equipment was not available to obtain much information with psychrometers. However some information can be gained from moisture results and the moisture retention curves. Conditions were dry through May and early June, and a tension of 18 bars was recorded at 10 cm depth on 12 May at the middle site. However the tension at 20 cm at this time was less than 1 bar. After mid-June, wet periods alternated with dry periods but psychrometer readings, together with neutron probe and gravimetric moisture values suggest that tensions greater than those in May did not occur. A summary of the information available is given in the appendix.

4.4.7 Moisture content

Moisture information was obtained from a combination of neutron probe and gravimetric results. Results for some selected dates are shown graphically (Fig. 4) for the three sites. Moisture levels below a depth of 200 cm fell slightly over winter, then after a spring rise, fell again over summer. Moisture levels at 600 cm remained relatively constant over the year at sites 2 and 3 while the profiles at site 1 are complicated by the presence of boulders, which are presumably the cause of very low moisture values at 400 cm and 500 cm.

The thaw period is of particular interest since a large amount of water is released over a short period while ground temperatures are below 0°C. Even though the thaw, being largely confined to the first 3 to 4 days of April, was extremely rapid, negligible surface runoff was observed, and it can be assumed that all the meltwater entered the soil. Changes in soil moisture immediately following the thaw were recorded both by gravimetric sampling and using the neutron probe. It became obvious from gravimetric information that neutron probe values within 100 cm of the surface soil were in error over much of this period, when a high contrast existed between moisture levels in the near-surface soil, which at times exceeded 30% by volume, and moisture in deeper layers which remained at 3 to 4%. Gravimetric results are therefore shown for the near-surface (Fig. 5) and neutron probe results for greater depths at the middle site. Gravimetric information shows that on 3 April, the meltwater was held

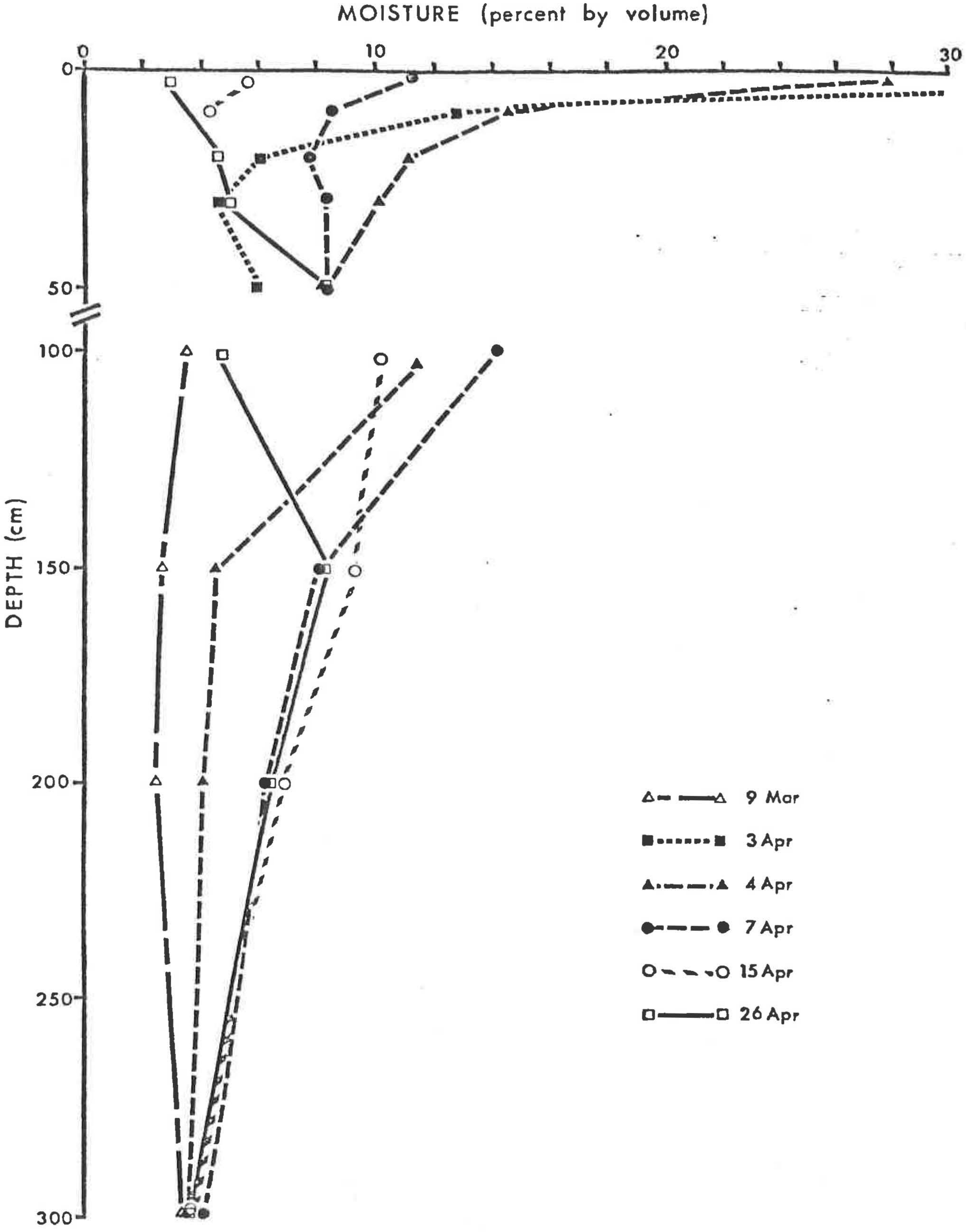

Figure 4. Moisture profiles on selected dates for the three sites at Richardson tower.

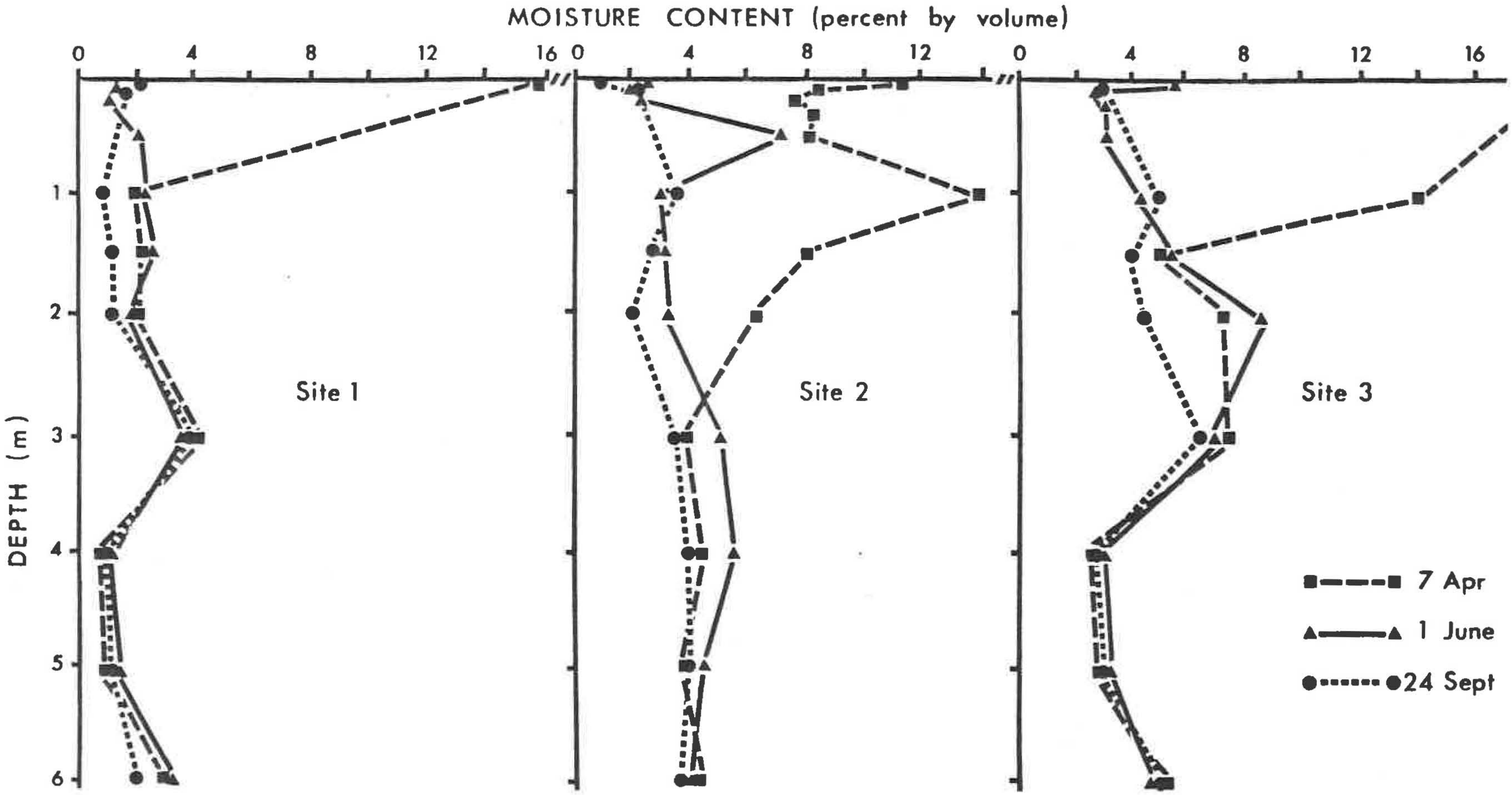

Figure 5. Moisture changes at the middle site obtained by gravimetric sampling following the thaw (above) and by use of the neutron probe before and immediately following the thaw (below).

in a near-saturated layer at the surface. By 4 April the moisture was distributed in the 0 to 50 cm layer while by 7 April moisture levels within 50 cm of the surface had returned to normal. At this time neutron probe information should again have become reliable, and it is reasonable to attribute the difference between values for 7 April and those prior to the thaw on 9 March to meltwater infiltration. Because values within 50 cm of the surface on 9 March must be adjusted to take account of the influence of snow, they have yet to be calculated.

On 7 April most of the meltwater was held between 100 and 150 cm of the surface, where temperatures had risen to between -1°C and 0°C. Since 7 April is the earliest date following the thaw for which reliable information is available over the whole depth range, this date is taken as a base for later water balance calculations. By 15 April a reduction in moisture had occurred at shallower depths than 150 cm and an increase below this depth, while between 15 and 26 April further reductions occurred within 150 cm of the surface, where temperatures were slightly above freezing while slight reductions occurred at depths greater than 150 cm. Information from the upper and lower sites was less complete, and any differences from the middle site could be attributed to a lesser amount of snow at the upper site and a slower rate of thaw at the lower site.

Changes in total water content within 6 cm of the surface, obtained from integration of moisture values, are shown for all three sites (Fig. 6) up until 28 November 1976. While the total amount of water is greatest at the middle site, and least at the

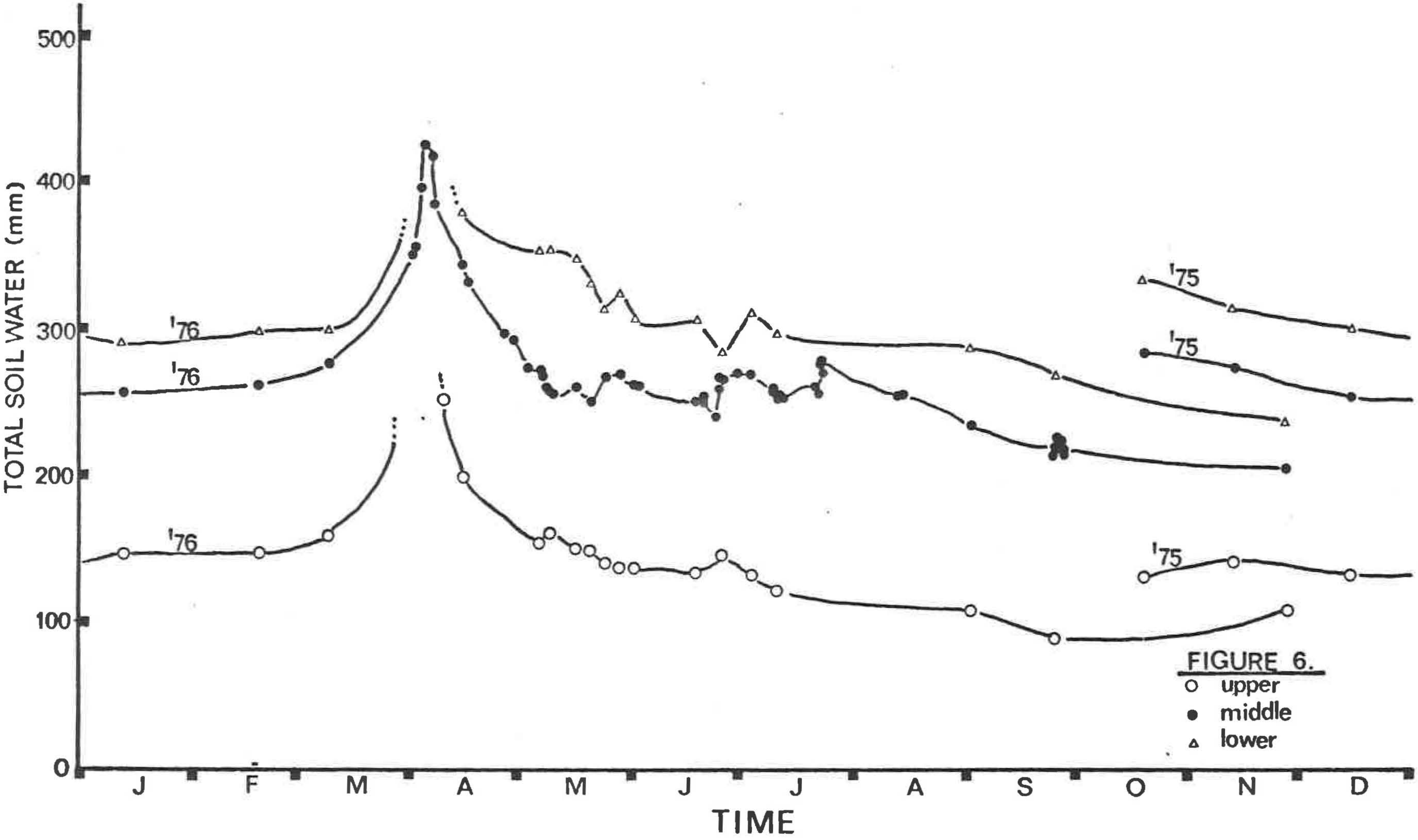

Figure 6. Changes in total water content within 6 m of the ground surface at the three Richardson sites.

lower site, seasonal changes parallel one another. Values in late winter may be slightly inflated because of effects of the snowpack on neutron probe readings, while detailed gravimetric information during the thaw in the first few days of April is only available for the middle site. At all three sites the total water content was less at the start of winter 1976-1977 than for the previous winter.

Various results are combined (Fig. 7) to show calculated cumulative loss (evaporation plus evapotranspiration plus deep flow), in relation to cumulative non-intercepted precipitation (see meteorological and lichen sections) and total water on 9 March in the snowpack. The absolute position of the cumulative loss curves could be incorrect because of errors at the start of the season, but the general slope should be reliable. The occasional drops in loss are impossible and are attributed to erratic readings.

4.4.8 Water Table

Water table levels have not been fully analyzed. However it was found that the absolute level of the water table varied little between wells. This supports the assumption that the hill contains no core of slowly permeable material.

4.5 CONCLUSIONS AND RECOMMENDATIONS

Both laboratory and field results have contributed to an understanding of moisture regimes within Jack pine covered sands of the A.O.S.E.R.P. study area. Following rain, the sands at Richardson drain rapidly to a moisture content of around 10% by volume in the

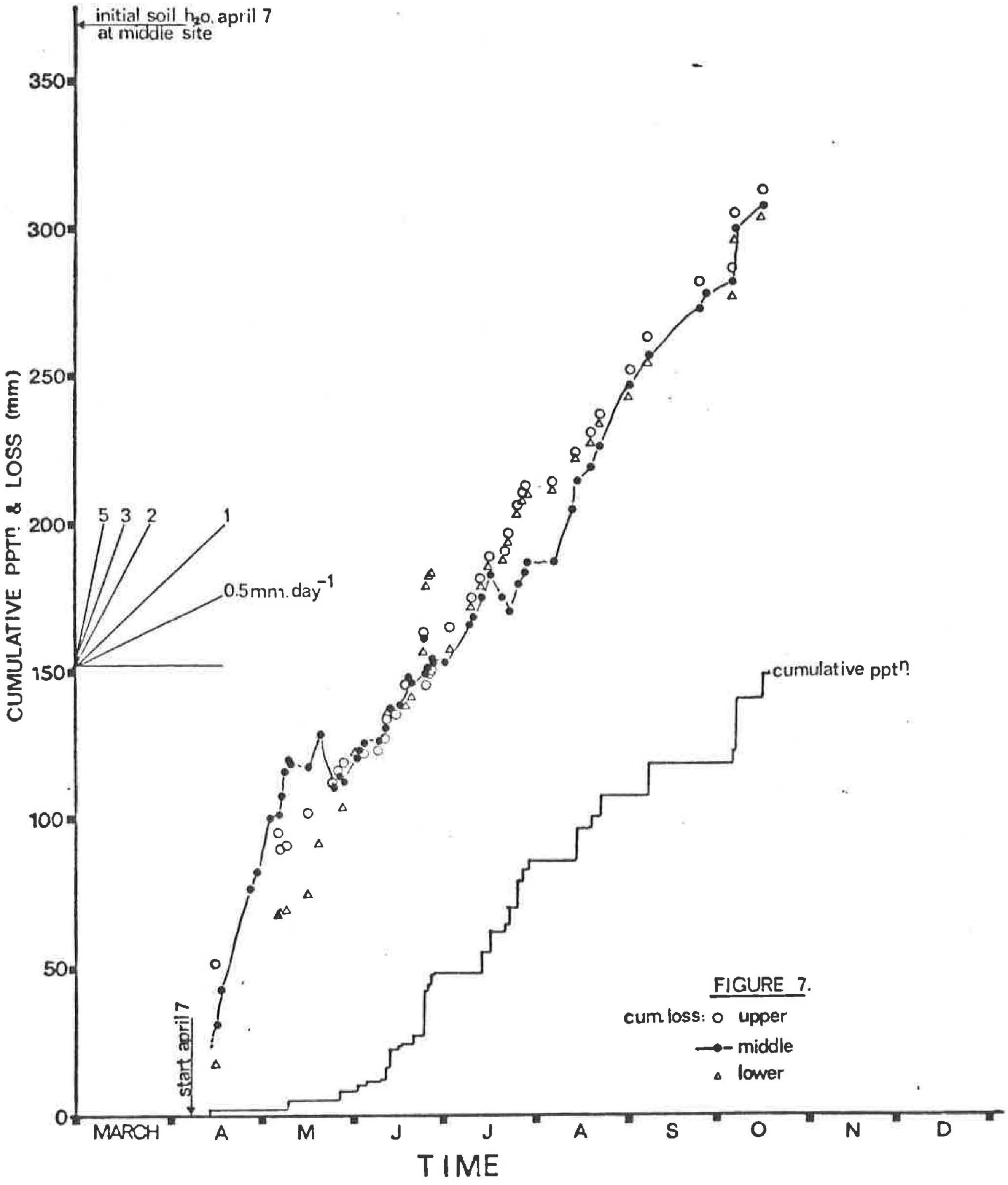

Figure 7. Cumulative total water loss within 6 m of the ground surface in relation to cumulative non intercepted precipitation. Slopes corresponding to various loss rates are shown (left).

thin Ae horizon and 6% beneath a depth of about 30 cm. This corresponds to 95 and 58 mm of available water respectively per metre depth. In spite of the low moisture-holding capacity of this sand, extreme periods of moisture stress were not recorded during spring and supper 1976.

The very rapid hydraulic conductivity at near saturated moisture levels ensures that even during spring thaw almost all moisture enters the ground, and there is little surface runoff, and therefore minimal erosion. Neither tensiometers in the field nor pressure plate measurements in the laboratory are very effective except at low tensions because of slow liquid movement over most of the unsaturated range resulting from low non-sand content. In addition, the narrow range and low content of moisture limits precision in following moisture changes with the neutron probe or by gravimetric sampling. Improved information on moisture tensions should be obtained by making increasing use of psychrometers, particularly in the near-surface soil, while better information on moisture changes in the near-surface soil should come either through increased gravimetric sampling, or preferably through development of an improved non-destructive method.

4.6 ACKNOWLEDGEMENTS

The work of George Davis who obtained most of the field readings and performed much of the data reduction, is gratefully acknowledged.

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4.8 APPENDIX

Table A-1. Soil Temperatures ($^{\circ}C$)

A. Upper Site

	Depth (cm)											
Date	1	2	5	10	20	50	100	150	200	300	450	600
PM May 5	17.4	16.6	13.1	9.4	6.6	3.6	2.0	0.6	0.1	0.4	1.8	3.0
AM 8	6.3	6.2	6.1	6.0	5.9	4.4	2.3	0.9	0.4	0.3	2.2	3.4
noon 9	10.2	10.1	8.4	6.6	5.0	4.2	2.7	0.9	0.3	0.4	2.0	3.2
AM 10	8.3	7.7	6.7	5.9	5.6	4.6	2.7	1.1	0.2	0.4	1.8	3.3
PM June 1	12.1	12.4	12.9	12.8	12.0	9.2	6.4	4.0	1.7	0.8	2.0	3.0
AM 2	10.6	10.5	10.0	9.8	10.2	9.1	6.7	4.3	2.1	0.8	1.9	3.1
AM 3	6.6	6.9	7.8	8.8	9.4	8.4	6.3	3.9	1.8	0.6	1.7	2.8
AM 30	15.1	15.2	15.1	15.2	14.8	12.5	9.6	7.7	6.0	4.4	3.0	3.1
AM July 21	13.6	13.8	14.0	14.4	14.4	12.9	11.0	9.7	8.3	6.3	4.1	3.3
PM 23	20.3	20.1	17.7	15.3	13.4	12.3	11.1	9.6	8.2	6.2	4.0	3.1
AM Aug.18	14.0	14.0	14.3	14.7	15.4	15.9	14.3	12.1	10.3	8.0	5.3	3.7
PM 20	15.3	15.3	15.0	14.8	14.3	13.6	13.1	11.9	10.2	7.8	5.1	3.6
AM Sept.26	7.5	7.5	7.4	7.7	8.7	9.8	9.8	9.7	9.3	8.5	6.6	5.0
PM Oct.28	6.0	5.7	4.5	3.6	3.0	3.0	3.8	5.4	6.6	7.4	7.0	5.9
Nov.26	-8.1	-7.8	-6.6	-5.2	-3.6	0.3	1.4	2.8	4.0	5.1	6.0	5.8
Jan. 7	-7.6	-7.5	-7.3	-7.0	-6.7	-5.1	-3.0	-0.5	1.0	2.7	4.2	5.0

Table A-1. (Continued)

B. Middle Site

Date	Depth (cm) 1	2	4	8	12.5	25	50	100	200	300	450	600
Oct.19, 75	5.7	5.6	5.3	4.4	4.5	5.1	5.9	6.6	7.5	8.2	8.1	7.2
Nov.13	0.1	0.1	0.1	0.2	0.4	0.6	1.4	2.4	4.6	6.6	7.2	7.2
Feb.19, 76	-8.9	-8.6	-8.5	-7.9	-7.8	-7.3	-6.0	-4.3	-0.4	+1.4	+3.0	+4.3
Mar. 3	-9.9	-9.9	-9.7	-9.2	-9.2	-8.6	-6.8	-6.1	-1.5	+1.1	+2.5	+3.9
PM Apr. 1	+0.1	+0.1	+0.1	0	+0.1	+0.1	-0.9	-2.0	-1.5	+0.4	+1.9	+3.3
AM Apr. 3	0	0	-0.1	-0.1	0	-0.1	-0.6	-0.5	-1.4	+0.4	+1.8	+3.3
PM 4	+1.7	+1.2	+0.7	-0.1	+0.1	+0.1	0	-0.1	-1.0	+0.4	+1.9	+3.2
AM 5	0	0	0	0	0	0	-0.1	-0.1	-0.7	+0.5	+1.9	+3.3
PM 15	8.9	8.5	8.2	4.1	3.1	1.8	0.7	0	0	0.5	1.8	3.1
AM 27	3.1	3.4	3.8	4.8	5.0	4.7	3.5	1.2	0.1	0.9	1.9	3.1
AM May 8	6.5	6.4	6.5	6.8	6.9	6.5	5.3	3.2	0.3	1.1	2.2	3.3
noon 9	8.3	7.3	6.7	5.6	5.3	5.3	4.9	3.2	0.1	0.8	1.9	3.0
AM 10	5.0	5.1	5.3	5.8	6.1	6.0	5.2	3.3	0.2	0.9	2.0	3.0

Note: In late May, new thermocouples were inserted at the middle site. Note amended depths after this date.

	Depth (cm) 1	2	5	10	20	50	100	150	200	300	450	600
PM June 1	11.4	11.5	13.5	14.1	13.8	10.8	9.0	7.3	5.7	3.7	3.1	3.2
AM 2	9.3	9.6	10.0	10.2	11.0	10.8	9.0	7.4	5.8	3.6	2.9	3.2
AM 3	6.8	8.3	8.5	9.7	11.0	10.5	8.8	6.7	6.0	3.8	2.9	3.1

Table A-1. (Continued)

B. Middle Site continued

	Depth (cm) 1	2	5	10	20	50	100	150	200	300	450	600
AM 30	18.6	18.3	17.5	16.9	16.5	15.2	12.7	10.2	8.5	6.3	4.7	3.7
AM July 21	14.9	15.1	15.9	16.5	16.9	16.0	14.1	12.5	11.0	8.5	6.3	5.0
PM 23	19.8	19.2	18.6	17.1	15.3	14.5	13.5	12.4	11.0	8.5	6.3	4.9
AM Aug. 18	14.9	15.1	15.6	16.2	17.2	18.2	17.2	14.9	13.1	10.1	7.5	5.7
PM 20	16.0	16.0	16.3	16.2	15.7	15.2	15.0	14.0	12.8	9.6	7.1	5.4
PM Sept.24	13.4	13.2	12.7	12.1	10.8	10.3	10.9	10.7	10.5	9.7	8.4	6.8
PM Oct. 28	6.5	6.2	5.0	4.3	3.4	3.2	3.9	-	-	-	-	-
Nov. 26	-6.3	-5.7	-4.6	-3.9	-3.2	-0.3	+1.2	-	-	-	-	-
Jan. 7	-5.8	-5.5	-5.2	-4.8	-4.4	-3.3	-1.2	+0.5	+1.4	+3.3	+4.6	+6.0

C. Lower Site

	Depth (cm) 1	2	5	10	20	50	100	150	200	300	450	600
AM May 8	6.2	5.8	5.4	5.3	5.3	4.4	1.9	0.7	0.2	1.4	2.3	3.3
noon 9	15.4	13.1	10.2	7.3	5.1	3.6	2.1	1.0	0.6	1.1	2.2	3.6
AM 10	8.3	7.1	6.0	5.2	5.1	4.2	2.1	0.5	0.3	1.1	2.2	3.0
PM June 1	11.4	11.9	12.3	12.6	12.1	9.8	7.0	5.7	4.1	2.5	2.1	2.8
AM 2	9.3	9.3	9.2	9.3	10.0	9.4	7.3	5.6	4.1	2.7	2.3	2.8
AM 3	7.7	7.9	8.3	9.1	9.8	9.3	7.1	5.6	4.3	2.6	2.2	2.8

Table A-1. (Continued)

C. Lower Site continued

		Depth (cm)											
		1	2	5	10	20	50	100	150	200	300	450	600
AM	30	14.9	15.1	15.1	15.3	15.3	13.6	10.6	8.7	7.4	5.4	3.8	3.5
AM	July 21	14.5	14.5	14.7	14.7	15.0	14.2	12.4	11.0	9.7	7.5	5.3	4.2
PM	23	21.7	21.1	20.1	18.3	15.5	14.2	12.1	10.9	9.6	7.5	5.3	4.2
AM	Aug. 18	14.7	14.7	14.5	14.7	15.2	15.7	14.5	12.9	11.4	8.7	6.2	4.7
PM	20	16.6	16.4	16.3	15.9	15.3	14.4	13.8	12.6	11.4	8.8	6.1	4.7
AM	Sept.26	8.3	7.7	7.2	6.9	7.4	8.7	9.4	9.7	9.7	9.2	7.9	6.5
PM	Oct. 28	4.4	4.2	3.9	3.3	2.8	2.9	4.0	5.1	6.4	7.7	8.0	7.3
	Nov. 26	-6.8	-6.5	-5.8	-4.9	-3.5	+0.1	+1.4	+2.6	+3.8	+5.2	+6.7	+7.1
	Jan. 7	-4.9	-4.8	-4.7	-4.5	-4.1	-2.7	-0.5	+0.6	+1.3	+2.9	+4.6	+5.6

Table A-2. Soil Water Tension (mbar) from tensiometers

A. Upper Site

Date		Depth (cm) 20	50	100	200	300
May	7	77	56	47	-	-
	9	141	85	56	-	-
	14	161	119	63	-	-
	18	248	136	84	-	-
	20	251	143	97	-	-
	24	254	147	77	165	29
	28	308	174	93	172	74
June	1	219	176	91	87	39
	3	317	206	106	125	64
	24	20	89	200	114	105
	25	50	139	197	121	99
July	3	293	286	134	126	88
	7	226	239	207	120	85
	10	259	252	206	134	84
	15	109	278	213	126	88
	19	138	307	203	120	74
	23	200	353	234	125	100
Aug.	13	399	311	196	111	32
	17	100	291	232	122	285
	20	209	340	247	127	72
	25	243	342	231	133	28
	30	277	373	239	131	65
Sept.	1	405	418	422	134	62
	24	436	466	268	138	91

Table A-2. (Continued)

B. Middle Site

Date		Depth (cm) 10	20	30	50	100	200	300
May	8	170	161	117	114	80	-	-
	10	347	186	358	72	49	-	-
	14	75	100	142	98	78	-	-
	18	163	132	145	96	83	-	-
	20	229	145	137	97	95	-	-
	24	359	104	119	77	62	35	14
	28	202	123	146	86	76	44	21
June	1	211	93	87	67	46	36	8
	3	45	110	122	92	76	39	10
	24	16	21	222	56	85	40	12
	25	39	35	33	50	89	41	13
July	7	222	98	65	64	57	45	27
	10	127	74	72	62	51	46	28
	15	49	58	45	57	53	44	23
	19	37	47	45	62	57	45	24
	23	25	40	36	56	59	48	28
Aug.	13	190	137	88	66	49	45	27
	17	53	56	51	66	53	47	23
	20	50	45	54	65	58	49	27
	25	45	53	50	64	58	46	22
	30	122	102	74	81	76	49	26
Sept.	1	143	90	70	72	70	50	26
	25	216	182	82	112	95	59	27

Table A-2. (Continued)

C. Lower Site

Date		Depth (cm) 20	50	100	200	300
May	7	54	79	105	-	-
	9	96	94	97	-	-
	14	64	90	92	-	-
	18	109	100	112	-	-
	20	74	92	112	40	-
	24	123	89	92	47	49
	28	181	104	108	52	73
June	1	130	89	84	50	64
	3	221	111	126	54	67
	24	18	122	113	61	70
	25	20	83	110	56	45
July	3	62	72	104	66	29
	7	94	77	106	67	-
	10	104	80	100	68	8
	15	89	83	106	72	68
	19	75	79	118	73	62
	23	28	65	98	74	49
Aug.	13	96	74	70	73	70
	17	46	78	75	71	57
	20	49	86	79	87	62
	25	33	79	93	89	55
	30	59	88	113	107	50
Sept.	1	71	91	107	97	40
	24	178	105	121	162	30

Table A-2. (Continued

D. Psychrometer Readings at Middle Site (bar)

	Depth (cm)				
Date	5	10	20	30	50
May 10	-	18	0.5	0	0
July 2	8	13	4	8	0
23	0	0	0	0	0
Aug. 17	2	9	0	2.5	0
Sept. 25	14	0	19	22	0

Table A-3. Soil Moisture (% vol). Neutron Prope (Plus Gravimetrically Determined in Parentheses).

A. Upper Site

	Depth (cm)											
Date	0.5	10	20	30	50	100	150	200	300	400	500	600
Oct. 19	-	-	6.2	5.3	3.8	1.7	1.9	1.6	3.3	1.0	1.1	2.2
Nov. 13	-	-	7.3	5.0	3.4	1.7	2.0	1.6	3.8	1.0	1.1	2.8
Dec. 15	-	-	10.5	5.6	3.3	1.4	1.4	1.4	3.0	1.0	1.0	2.6
Jan. 12	-	-	10.9	6.3	3.4	1.6	1.9	1.4	3.6	0.9	1.0	2.9
Feb. 18	-	-	11.9	6.1	3.4	1.6	2.0	1.5	3.4	1.0	1.0	2.9
March 9	-	-	12.7	6.6	3.8	1.8	2.1	1.7	3.5	1.1	1.0	3.0
April 2	-	-	28.4	13.1	7.9	2.0	2.3	1.9	3.7	1.2	1.2	3.2
5	-	43.7	35.4	18.7	8.4	2.0	2.4	2.0	4.0	-	-	-
	(19.4)	(10.8)	(9.6)	(4.7)	(4.7)							
6	-	41.0	36.4	21.9	9.8	2.0	2.4	1.9	3.7	-	-	-
7	-	34.9	34.0	24.4	17.3	2.1	2.5	1.9	4.0	1.1	1.2	3.0
15	-	12.0	13.3	11.1	9.0	3.0	2.4	2.0	3.8	1.1	1.3	31.
	(13.0	(10.2)										
May 6	-	3.3	5.1	5.2	4.7	3.2	2.7	2.0	3.7	1.1	1.2	3.1
7	(5.2)	2.9	4.8	5.0	4.7	3.0	2.8	2.2	4.0	1.1	1.3	3.1
9	(10.0)	3.9	4.7	5.0	4.6	3.2	2.9	1.9	3.9	1.1	1.3	2.9
16	-	3.4	4.4	4.1	3.9	2.8	2.8	1.9	3.9	1.1	1.3	3.0
20	-	2.5	3.6	3.8	4.1	2.6	2.7	1.9	4.1	1.2	1.3	3.2
24	-	1.7	2.9	3.2	3.6	2.6	2.8	1.8	3.8	1.0	1.3	3.0
28	-	2.1	2.7	2.8	3.2	2.5	2.7	1.8	4.1	1.0	1.2	3.0

Table A-3. (Continued)

A. Upper Site (continued)

Date		Depth (cm)										
		0.5	10	20	30	50	100	150	200	300	400	500	600
June	1	(6.2)	1.9	2.4	2.5	3.1	2.3	2.6	1.8	3.8	1.1	1.3	3.3
	18	-	1.4	1.6	1.7	2.2	1.9	2.2	1.8	3.8	1.2	1.4	3.3
	25	-	7.9	6.9	4.1	2.7	1.8	2.2	1.8	3.8	1.3	1.4	4.0
July	3	(6.9)	3.9	4.7	4.0	3.1	1.9	2.4	1.8	2.5	1.3	1.3	3.3
	10	-	1.8	2.4	2.7	2.4	1.7	1.8	1.7	3.5	1.2	1.3	3.0
Aug.	17	(5.8)	(3.0)	(1.6)	(1.2)	(1.7)	(2.5)						
Sept.	1	(4.6)	0.9	1.3	1.5	1.5	1.3	1.4	1.4	3.0	1.1	1.4	3.3
	24	(2.2)	0.4	0.6	1.1	1.4	0.9	1.2	1.2	2.9	1.0	1.2	2.0
Oct.	28	(8.9)	-	-	-	(1.3)	(4.1)						
Nov.	27	-	12.2	9.7	6.9	4.3	1.8	1.1	0.9	2.1	0.6	0.5	0.4

B. Middle Site

Date		Depth (cm)										
		0.5	10	20	30	50	100	150	200	300	400	500	600
Oct.	19	-	-	7.4	7.8	6.6	3.7	3.2	3.4	4.4	5.7	5.0	3.9
Nov.	13	-	-	8.5	7.3	6.7	3.7	2.9	3.2	4.1	5.3	4.8	4.0
Dec.	15	-	-	9.5	8.1	6.4	3.0	2.5	2.7	3.8	4.7	4.2	4.1
Jan.	12	-	-	10.2	8.4	6.5	3.1	2.3	2.7	3.5	4.9	4.3	4.2
Feb.	18	-	-	14.5	11.2	7.0	3.1	2.5	2.2	3.4	4.5	4.1	4.0
March	9	-	-	15.1	12.0	7.6	3.5	2.7	2.5	3.6	4.5	4.2	4.1
April	1	-	-	25.0	21.0	14.6	4.8	2.7	2.7	3.6	4.6	4.3	4.2
	2	-	-	27.7	22.3	18.9	4.4	2.7	2.5	3.2	4.7	4.3	4.3

Table A-3 (Continued)

B. Middle Site (continued)

Date		Depth (cm) 0.5	10	20	30	50	100	150	200	300	400	500	600
	3	(46.9)	-	33.5	29.1	27.7	7.1	3.1	4.1	3.6	4.4	4.1	4.1
			(12.8	(6.1)	(4.7)	(5.9)							
AM	4	(27.8)	15.1	22.4	28.7	29.0	11.3	4.3	-	-	-	-	-
			(14.5)	(11.1)	(10.1)	(8.2)							
PM	4	(28.3)	41.9	41.7	40.4	36.7	13.1	5.2	5.2	3.7	-	-	-
			(11.8)	(8.4)	(8.5)	(10.0)							
	5	-	10.1	16.8	24.1	30.6	12.4	8.4	5.3	3.6	-	-	-
	6	-	9.5	15.6	21.8	29.8	13.7	8.5	6.4	3.8	-	-	-
	7	(11.3)	7.5	12.2	16.7	26.3	14.2	8.2	6.4	4.0	4.5	4.2	4.4
			(8.5)	(7.8)	(8.3)	(8.2)							
	8	-	6.6	10.1	13.3	21.7	13.7	7.9	6.2	3.9	4.6	4.2	-
	15	(5.6)	3.8	5.9	7.6	8.3	10.1	9.2	6.8	3.6	4.6	4.1	4.1
			(4.2)										
	16	-	3.7	6.0	7.2	7.7	9.2	8.9	6.6	3.7	4.4	4.1	4.0
	26	(2.9)	3.0	4.9	6.2	6.4	4.7	8.4	6.5	3.9	4.2	4.0	4.0
			(4.3)	(4.6)	(5.0)	(8.3)	(3.6)						
	29	-	2.5	4.9	5.8	6.1	4.4	7.0	6.6	3.9	4.6	4.0	4.0
May	3	-	2.2	4.0	5.4	5.8	4.2	5.1	6.2	3.9	4.4	4.0	4.2
	6	-	2.1	4.0	5.3	3.6	3.9	4.7	6.2	4.2	4.4	4.1	4.2
	7	-	2.0	3.7	5.0	5.6	3.9	4.5	5.7	4.0	4.5	4.2	4.1
	8	(1.5)	1.7	3.4	4.6	5.2	3.5	4.2	5.5	4.2	-	-	-
			(2.5)	(2.6)	(2.3)	(3.7)	(3.6)						

Table A-3. (Continued)

B. Middle Site (continued)

	Depth (cm)											
Date	0.5	10	20	30	50	100	150	200	300	400	500	600
9	(6.3)	2.7	4.3	4.9	5.4	3.6	3.8	5.2	4.0	4.5	4.0	4.0
10	(4.6)	2.4	3.9	4.8	5.5	3.8	4.1	4.9	4.0	4.4	4.0	-
		(1.8)										
16	-	3.1	4.6	5.6	5.5	3.7	3.6	4.1	4.7	4.5	4.2	4.2
20	-	2.4	4.1	4.9	5.1	3.4	3.3	3.7	5.0	4.7	3.8	4.0
24	-	2.3	3.7	4.5	5.0	3.3	3.5	3.8	5.5	5.4	4.3	4.2
28	-	2.2	3.8	4.6	4.9	3.5	3.3	3.4	5.4	5.7	4.3	4.7
June 1	(2.5)	1.9	3.4	4.0	4.5	3.1	3.2	3.4	5.2	5.7	4.6	4.1
		(2.0)	(2.4)		(7.2)							
2	-	1.7	2.9	3.8	4.4	3.6	3.2	3.4	5.1	5.5	4.7	4.1
18	-	1.8	2.8	3.5	4.0	3.1	2.7	3.1	4.8	5.6	4.9	4.0
20	-	1.9	2.9	3.5	3.9	3.1	3.0	3.0	5.1	5.6	4.9	4.1
23	-	1.6	2.5	3.5	3.8	2.8	2.7	2.9	4.7	5.5	4.6	4.0
24	-	7.1	8.5	8.1	4.8	2.8	2.9	3.0	4.7	-	-	-
25	-	5.1	7.2	7.7	6.4	2.9	2.7	3.0	4.6	5.4	4.7	4.1
29	-	5.0	6.5	7.7	7.1	3.1	2.7	2.9	4.7	5.3	4.6	4.2
30	-	4.0	6.2	7.0	8.0	3.1	2.7	-	-	-	-	-
July 3	(2.3)	3.4	5.3	6.5	6.9	3.5	2.8	2.9	4.8	5.4	4.8	4.2
		(2.7)	(2.1)		(6.0)							
9	(4.2)	2.9	4.2	5.5	5.6	3.3	2.6	-	-	-	-	-
10	(2.6)	2.4	3.7	5.1	5.4	3.3	2.6	-	-	-	-	-
11	(4.1)	2.4	4.0	4.9	5.5	-	-	-	-	-	-	-
12	(1.6)	2.4	3.9	4.8	5.5	3.3	2.7	-	-	-	-	-

Table A-3. (Continued)

B. Middle Site (continued)

Date	0.5	10	20	30	50	100	150	200	300	400	500	600
						Depth (cm)						
13	(6.0)	4.8	6.2	-	5.4	3.2	2.7	-	-	-	-	-
20	(4.6)	3.8	5.5	6.6	6.9	3.5	2.6	2.6	4.5	5.2	4.7	4.3
		(5.2)	(3.4)	(2.7)	(3.3)							
21	(10.6)	10.0	9.9	8.8	7.1	3.5	2.6	2.4	4.4	-	-	-
22	(6.7)	6.6	8.4	8.9	8.0	3.4	2.6	2.5	4.3	-	-	-
		(6.3)	(6.2)	(5.0)	(4.0)							
Aug. 12	(0.6)	2.2	3.8	5.3	6.3	4.6	2.7	2.5	4.3	-	-	-
14	-	6.3	7.6	7.2	6.3	4.4	2.7	2.5	4.2	4.5	4.4	4.1
17	(2.7)	(5.3)	(4.7)	(4.6)	(5.0)	(5.1)						
Sept. 1	(3.0)	3.4	5.0	6.0	6.0	4.0	2.7	2.3	3.7	4.4	4.3	4.2
		(4.8)										
24	(1.1)	2.2	3.8	4.6	5.0	3.5	2.7	2.1	3.6	4.0	4.0	4.2
		(2.6)										
25	(1.4)	2.0	3.5	4.3	4.7	3.4	2.6	2.1	3.6	-	-	-
26	(0.9)	2.2	3.4	4.8	4.8	3.4	2.7	-	-	-	-	-
27	(0.9)	2.0	3.7	4.8	4.9	3.6	2.8	2.1	3.6	4.1	4.2	4.0
		(2.2)										
Oct. 28	(7.0)	-	-	-	(5.5)	(6.0)						
Nov. 27	-	8.2	8.9	8.9	6.1	4.2	3.7	2.2	2.5	2.4	2.3	-

Table A-3. (Continued)

C. Lower Site

Date	Depth (cm) 0.5	10	20	30	50	100	150	200	300	400	500	600
Oct. 19	-	-	10.1	9.6	8.0	5.5	4.7	6.6	8.0	2.8	3.3	4.8
Nov. 13	-	-	9.2	7.7	6.7	5.1	4.2	6.1	7.9	2.8	3.3	5.0
Dec. 15	-	-	11.3	8.9	6.7	4.2	4.4	5.6	6.4	3.0	3.2	5.0
Jan. 12	-	-	11.2	8.3	6.3	4.4	3.6	5.3	7.0	2.6	3.0	4.7
Feb. 18	-	-	12.8	9.2	6.8	4.3	4.2	4.7	7.0	2.8	3.0	4.6
March 9	-	-	12.7	9.3	6.8	4.6	4.6	5.0	6.7	2.7	3.0	4.1
April 2	-	-	25.4	13.2	7.0	4.8	4.5	7.0	6.8	2.8	3.1	5.1
5	-	29.9	34.1	30.7	26.8	5.1	4.9	7.3	7.0	-	-	-
6	-	27.7	32.8	31.3	27.9	6.5	5.0	7.1	7.1	2.9	3.1	5.0
	(34.6)	(17.8)	(11.4)	(10.3)	(9.2)							
7	-	14.8	19.7	21.1	23.6	14.2	5.1	7.4	7.3	2.9	3.2	5.2
15	-	4.6	7.1	8.3	8.7	14.0	8.9	6.6	6.9	3.1	3.2	5.2
	(7.0)	(6.4)										
May 6	-	1.8	3.8	5.1	5.7	6.6	11.5	9.5	6.9	2.9	3.2	5.3
7	-	1.6	3.5	5.2	5.5	6.2	11.2	9.7	7.2	2.9	3.2	5.2
9	(6.4)	3.1	4.6	5.4	5.3	6.1	10.3	9.6	7.2	3.0	3.3	5.2
16	-	4.6	6.7	7.5	6.6	4.9	7.9	10.2	6.9	3.1	3.3	5.3
20	-	3.3	5.2	6.2	6.0	5.0	6.9	10.0	7.1	2.9	3.1	5.1
24	-	2.4	4.5	5.6	5.5	4.7	6.4	9.4	7.1	3.0	3.3	3.0
28	-	3.0	4.9	5.4	5.3	4.3	-	-	-	-	-	-
June 1	(5.4)	2.8	4.6	5.1	4.9	4.4	5.4	8.6	7.1	3.0	3.1	5.0
		(2.8)	(3.1)	-	(3.2)							

Table A-3. (Continued)

C. Lower Site (continued)

	Depth (cm)											
Date	0.5	10	20	30	50	100	150	200	300	400	500	600
18	-	2.9	4.8	5.2	5.0	4.4	4.8	7.6	7.7	3.0	3.3	5.4
25	-	6.0	8.9	10.0	9.4	3.5	3.8	5.6	6.3	2.6	2.5	5.1
July 3	(6.7)	4.0	6.2	7.6	7.9	5.0	4.1	6.4	7.4	2.9	3.3	5.5
		(4.3)	(4.6)	-	(5.7)							
10	-	2.9	4.7	5.7	6.3	4.8	4.1	6.4	7.5	3.0	3.4	5.2
Aug. 17	(5.7)	(5.6)	(5.8)	(6.1)	(5.3)	(5.9)						
Sept. 1	-	3.4	5.8	6.8	6.7	5.7	4.1	4.9	6.9	3.0	3.1	5.3
24	(3.0)	2.4	4.3	5.5	5.9	5.0	4.0	4.5	6.5	2.9	3.3	5.2
		(2.9)										
Oct. 28	(8.1)	-	-	-	(6.4)	(4.4)						
Nov. 27	-	8.2	8.9	8.9	6.1	4.2	3.7	2.2	2.5	2.4	2.3	-

Table A-4. Water Table (Meters below surface, October 1975 - September 1976)

Period	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr(1-4)	Apr(5-8)
Gully	1.54	1.65	1.79	1.87	1.93	1.96	1.99	1.82*
Lower Site	13.50	13.49	13.55	13.56	13.60	13.61	13.60	13.58

Period	Apr(15-18)	Apr(26-30)	May(1-15)	May(16-31)	June(1-15)
Gully	1.81	1.82	1.78	1.74	1.74
Lower Site	13.60	13.60	13.62	13.65	13.65

Period	June(16-30)	July(1-15)	July (16-31)	Aug(1-15)	Aug(16-31)	Sept.
Gully	1.78	1.77	1.83	1.80	1.88	1.93
Lower Site	13.64	13.64	13.65	13.63	13.64	13.66

* Max. meter level on Apr. 8 = 1.30 m below surface

5. PLANT PHYSIOLOGY

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5.1 INTRODUCTION

The plant ecophysiological research on the Jack pine forest at the Richardson Fire Tower is designed to understand the physiology of plants growing on stable sand slopes and to supply the necessary parameters for development of a soil-plant-atmosphere model of heat and water fluxes. This model will help characterize the behavior of natural vegetation on stabilized sand and allow the prediction of vegetation performance for dike management. The present study also constitutes a base line for extention into and comparison with communities influenced by pollutants such as SO_2. A basic assumption in this study is that water is a major controlling factor in the long-term stability of vegetation on sand. Plant ecophysiological research has thus initially concentrated on the water relations of the major shrub and tree species with the emphasis on Jack pine, *Pinus banksiana* Lamb. Mineral nutrition is also recognized as an important limiting factor on sand, and will need to be incorporated into models of the system.

5.2 RESUME OF CURRENT STATE OF KNOWLEDGE

Extensive literature searches have revealed a paucity of information on the physiological responses of conifers (particularly *Pinus banksiana* or *P. contorta*) in northern latitudes even though considerable silvicultural information is available. The studies that have been reviewed to aid in the design and orientation of the ecophysiological part of this project are either descriptive or purely qualitative and thus able to supply only limited quantitative information of value. The following are a few of the studies most pertinent to the present research.

Descriptive studies of the root systems of Jack pine growing in sand have been conducted by Cheyney (1932) and Bannan (1940). In general, the root system of Jack pine growing on dry sandy soil is very wide spreading and not very deep (although deeper than *Picea mariana* or *P. glauca*). Several studies have been conducted on the nutrient composition of various Jack pine components (Morrison 1972, 73, 74) or the rate of transfers to the forest floor (Foster and Gessel 1972, Foster 1974). The addition of large amounts of sulfur to the soils in the Ft. McMurray area will alter nutrient cycling, and these studies may serve as a comparison. The cold hardiness of Jack pine has been studied by Yeatman and Holst (1972) and Glerum (1973). In general, Jack pine is very hardy, but differences in provenances do exist and must be taken into consideration when selecting seeds for reforestation in the north (e.g. Logan, 1971).

Many studies have been conducted on the growth response of Jack pine and lodgepole pine seedlings to environmental factors. These include nutrient regime (Cochran 1972, Calvert and Armson 1975, McClain and Armson 1975), air temperature (Cochran 1972), soil temperature (Heninger and White 1974), soil moisture (McClain and Armson 1975), and rooting volume (Endean and Carlson 1975, Hocking and Mitchell 1975). Studies of more direct applicability to the present research include those estimating water movement in stems of lodgepole pine using heat-pulse velocity measurements (Mark and Crews 1973, Swanson 1975) and radioisotopes (Owston et al. 1972). Photosynthetic studies include those of Dykstra (1974), Legge et al. (1976), and Logan (1971). Various aspects of the water relations of Jack pine and lodgepole pine are treated by Dykstra (1974), Legge et al. (1976), and Lopushinsky and Klock (1974). These studies, while useful, do not go into the water relations in sufficient detail. For example: Lopushinsky and Klock (1974) only report transpiration of a percent of maximum, and Dykstra (1974) worked only with greenhouse seedlings which may or may not behave like trees in the field.

5.3 STUDY AREA

The project study area or Richardson Fire Tower site is located at Lat. 57° 53' N, Long. 111° 02' W (subdivisions 15 and 16, Sect. 30, Twp. 102, R6 W4 and subdivisions 1 and 2, Sect. 31, Twp. 102, R6 W4). The ecophysiological research was conducted on a 72 m high sand hill (2.3: 1 rise, 19° slope, and 20° S of W aspect). A more complete description and map is provided in an earlier section of the report. (Site Description pages 6-8).

5.4 MATERIALS, METHODS, AND SOURCES OF DATA

5.4.1 Research Approach

The research approach combines field and laboratory-controlled environment studies of the physiological responses of major shrub and tree species in the project study area (Richardson Fire Tower site), with a concentration on Jack pine. This work is oriented to provide 1) necessary input parameters for development of a soil-plant-atmosphere model of heat and water fluxes to predict vegetation performance for dike management, and 2) base line data for comparison with sites exposed to atmospheric emissions such as SO_2. The field studies were initiated in late fall, 1975, and continue to date. The approach has been to examine plant responses intensively over periods of one to several days at biologically significant times of the year: midwinter, pre-thaw, snow melt, needle flush, midsummer, needle cast, herb die-back, fall dormacy. This allows a comparison of diurnal and seasonal changes in plant responses. A basic assumption has been that moisture (as well as nutrient) stress constitutes a major problem for any long term, stable community on sand. Thus, the main emphasis of both field and laboratory studies has been on plant water relations. Physiological processes such as photosynthesis, that are influenced by changes in the plant's water status have or will be studied as is necessary to understand the development and significance of internal water deficits.

5.4.2 Photosynthesis

Net assimilation of carbon dioxide was determined on cut branches of Jack pine collected from the project study area in November and December, 1975. Samples were stored in a moist, dark environment near $0^{\circ}C$ during transport to the laboratory, and readings started within 48 hr of sampling time. The needled portion of each branch was sealed in a plexiglass cuvette (van Zinderen Bakker 1974) connected to an open gas analysis system placed in a plant growth chamber (model M 12, Chagrin Falls, Ohio) supplied by a rheostat-regulated 1000 W quartz-iodide lamp, was measured in the photosynthetically active range (PAR = 400-700 nm) with a Lambda Quantum Sensor Model LI-185. Leaf temperature was monitored with .003 in (3 mil) copper-constantan thermocouples (Omega Engineering), and controlled at high light levels with a Peltier cold plate (Thermoelectrics Model TCP2). Carbon dioxide flux was measured differentially with a Beckman Model 215 infrared gas analyzer, and net assimilation expressed on a needle dry weight basis.

5.4.3 Water Potential and Water Content

Leaf (needle) water potential (ψ_L) and xylem water potential (ψ_{xylem}) are used to evaluate water deficits in Jack pine. Water potential is a measure of the free energy status of water in a system and is usually expressed in negative pressure units of bars or atmospheres (1 bar = 0.987 atm). The components of leaf water potential can be written as:

$$\psi_L = \psi_P + \psi_\tau + \psi_\pi$$

where ψ_L = leaf water potential
ψ_P = turgor potential
ψ_τ = matric potential
ψ_π = osmotic potential

Xylem water potential also includes component potentials:

$$\psi_{xylem} = P - \psi_s^{xylem}$$

where ψ_{xylem} = xylem water potential

P = the combined gravitational and frictional potentials

ψ_s^{xylem} = the combined solute and matric potentials (Boyer 1969).

The ψ_s^{xylem} component of the transpiration stream in most plants is constant or negligible, and xylem water potentials can be estimated from pressure chamber determinations of P. Xylem water potential estimates (also referred to as xylem pressure potentials or xylem tensions) are generally in fairly close agreement with leaf water potential measurements, particularly at high water potentials (Ritchie and Hinckley 1975).

Water moves through the soil-plant-atmosphere system along a gradient of decreasing (more negative) water potentials. This is controlled by the level of soil water potential, the atmospheric demand due to radiation, vapour pressure, and temperature, and the plants ability to exercise control over transpiration by stomatal closure. More negative plant water potentials indicate increasing internal water deficits. Increasing internal water deficits imply increasing stress although plant species vary as to the degree that normal physiological processes are impaired or stressed by a given level of water deficit.

Leaf water potentials and component potentials were measured with Spanner type thermocouple psychrometers after Mayo (1974). Branches were collected in the field and sealed in containers until psychrometric samples could be taken (within 30 minutes). Psychrometers were filled with 2 mm sections of needles from separate age classes and transported to Edmonton for equilibration in a constant temperature bath. Leaf water potentials (ψ_L) were measured within approximately 24 hr. The psychrometer chambers were then immersed in liquid nitrogen (-196°C) to rupture cell membranes and the tissues remeasured to determine turgor (ψ_P) and combined osmotic and matric potentials ($\Psi_{\pi + \tau}$). Psychrometric data was difficult to obtain under field conditions so the limited readings were used primarily to supplement the more extensive xylem water potential determinations. Xylem water potentials were estimated with a Scholander pressure chamber (PMS Instrument Co.). Branches were collected as with psychrometric samples and read within 30 minutes. Holding cut conifer branches in a high humidity container for periods up to 1 hr does not introduce errors in measurement (Ritchie and Hinckley, 1975). Water content samples of needles and stem segments were dried at 40-50°C in the field to kill the tissue and later dried to constant weight at 70°C in the laboratory.

5.4.4 Transpiration and Leaf Resistance

Transpiration rates of needled branches were measured using a dew point hygrometer (EG & G Model 880). The technique involves the measurement of the increase in absolute humidity of an air stream passing over a transpiring branch enclosed in a plexiglass cuvette (Slavik 1974). Leaf area of needles was determined using the method of Thompson and Layton (1971). Transpiration rate may be used to calculate the diffusive resistance to water vapour of the needles. Transpiration resistance is the sum of the resistance situated in the needles and in the boundary layer of air at the plant's surface:

$$R_T = R_L + R_a$$

where R_T = transpiration resistance

R_L = leaf resistance

R_a = boundary layer resistance

Adequate ventilation in the cuvette reduces the boundary layer resistance to a minimum constant value so that R_T approximates R_L and reflects the degree of stomatal control over transpiration. A portable ventilated diffusion porometer (Gresham et al. 1975) has also been built and field tested and will be used to increase the stomatal resistance measurement capabilities.

5.5 RESULTS

5.5.1 Photosynthesis

Cut branches of Jack pine collected under freezing conditions began positive net assimilation of carbon dioxide within 24 to 48 hr. Maximum rates of photosynthesis (1.4 mg CO_2 g^{-1} hr^{-1}) were found in tissue collected in November (Fig. 1). Light saturation occurred at approximately 800 μ E m^{-2} sec^{-1}, an intermediate light level. Optimum temperature for photosynthesis of branches collected in December was between 8 and 18°C (Fig. 2). Dark respiration was maintained at temperatures as low as -8°C, and increased with increasing leaf temperature. Positive net assimilation was measured from below 0°C to + 28°C.

5.5.2 Seasonal Water Potential and Water Content

Psychrometric data on leaf water potentials (ψ_L) and component potentials (ψ_P and $\psi_{\pi + \tau}$) of Jack pine from the Richardson Fire Tower site are listed in Table 1. Xylem water potentials (ψ_{xylem}) measured on the same branches with a Scholander pressure chamber are also presented. Leaf water potentials varied between -7.1 and -24.9 atm. while ψ_{xylem}

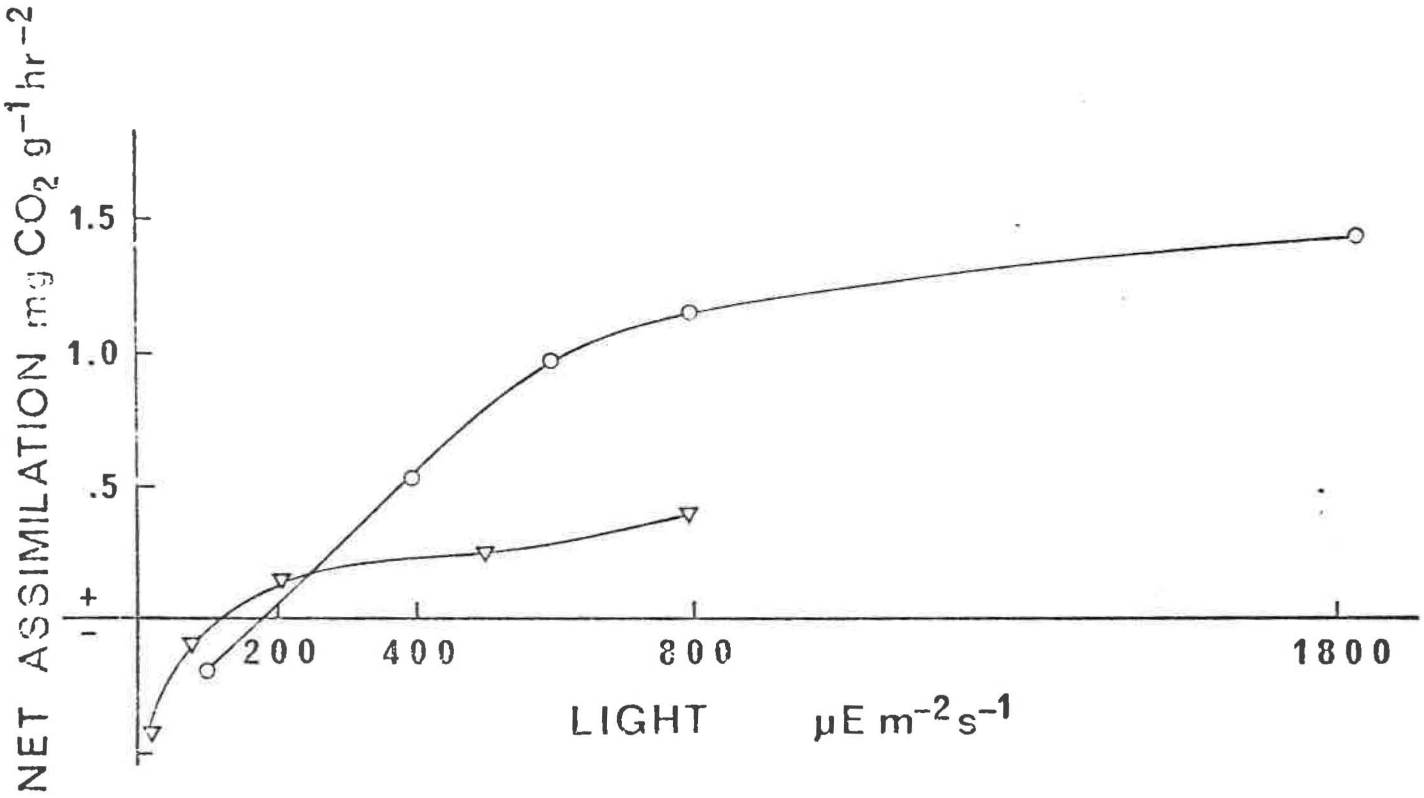


Figure 1. Net assimilation of cut branches of *Pinus banksiana* in relation to irradiance. Measured at leaf temperatures 23-25°C (November branches) ○ , and 10-12°C (December branches) ▽ .

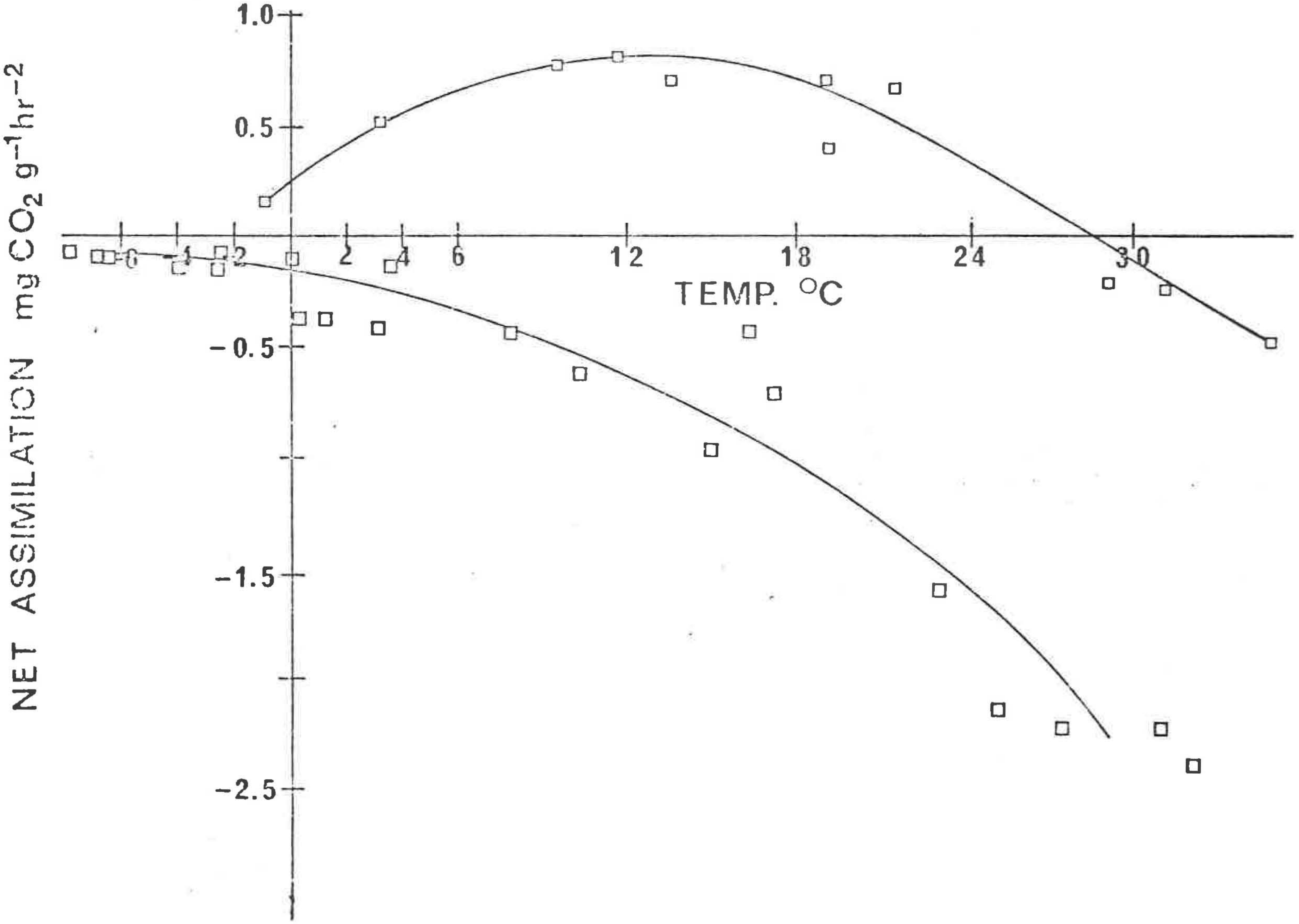


Figure 2. Net assimilation and dark respiration of cut branches of *Pinus banksiana* in relation to temperature. Net assimilation measured at 800 μE m^{-2} sec^{-1} on branches collected in December.

Table 1. Seasonal leaf water potentials (ψ_L), osmotic plus matric potentials ($\psi_{\pi + \tau}$), turgor potentials (ψ_P), and xylem water potentials (ψ_{xylem}) of *Pinus banksiana* at the Richardson Fire Tower site during 1975-76. Values listed are means ± 95% confidence limits in atmospheres.

Date	ψ_{xylem}	ψ_L	$\psi_{\pi + \tau}$	ψ_P	Notes
13/XI/75	-6.3[a]	-10.5 ± 3.3	-22.9 ± 3.0	12.4 ± 4.1	75 needles only, 0630 hr
15/XII/75	-4.8 ± 1.4	-11.4 ± 3.0	-23.8 ± 4.2	12.3 ± 4.2	75 needles only, 0830 hr
12/I/76	-5.4 ± 0.6	-7.1 ± 2.5	-23.5 ± 2.5	16.1 ± 2.9	75 needles only, 1005 hr
20/II/76	-9.5 ± 0.6	-8.4 ± 1.6	-23.1 ± 3.0	14.8 ± 3.0	75 needles only, 1430 hr
4/IV/76	-5.7 ± 0.4	-7.9 ± 2.1	-23.3 ± 3.5	15.4 ± 3.3	75 needles only, 0645 hr
16/IV/76	-5.0 ± 0.5	-11.4 ± 6.0	---	---	75 needles only, 0510 hr small sample
11/V/76	-6.6[a]	-11.4 ± 2.0	-23.0 ± 2.0	11.9 ± 2.2	72-75 needles, 0630 hr
3/VI/76	-10.4[a]	-14.1 ± 2.5	-24.2 ± 3.1	10.1 ± 2.8	72-75 needles, 1200 hr
27/IX 76	-16.9[a]	-22.5 ± 2.2	-29.0 ± 1.6	7.6 ± 2.0	72-76 needles, 1200 hr
27/IX/76	-16.9[a]	-19.1 ± 1.7	-29.4 ± 1.4	10.3 ± 2.1	75-76 needles
27/IX/76	-16.9[a]	-24.9 ± 2.7	-28.7 ± 3.3	5.1 ± 2.2	72-74 needles

[a] All psychrometric samples taken from one branch, therefore only one Scholander reading.

varied between -4.8 and -16.9 atm. Xylem water potentials are generally not significantly different from ψ_L except at lower water potentials (e.g., September). The discrepancy in readings is due in part to a difference in what is actually being measured (ψ_L = needles; ψ_{xylem} = needled branch). Osmotic plus matric potentials were quite constant throughout the year (-22.9 to -29.4 atm.), and turgor remained consistently high even through the winter. The data from September indicates that the older needles are physiologically drier (significantly lower ψ_L and ψ_P) than the younger needles. No such difference was apparent in the May and June data, perhaps due to a smaller sample size.

The seasonal progression of xylem water potentials at midslope on the study hill is indicated in Fig. 3 (data from the hill top and bottom are included in the Appendix). Values remained high (-3 to -10 atm.) throughout the winter with little diurnal change between dawn and midday readings. The magnitude of the diurnal variation increased suddenly after the spring thaw period, and decreased again with the onset of fall dormancy in October. Mean summer (May to September) maximum (dawn) and minimum (midday) ψ_{xylem} values varied between -5 to -7 atm. and -11 to -14 atm., respectively. The absolute maximum and minimum values measured at this site were -3.4 and -16.2 atm. Figure 3 also indicates that a general decrease in ψ_{xylem} (and increase in water deficits) occurred during the summer. Figure 4 represents the combined data from the hill transect (mean of hill top, midslope, and hill bottom positions) with the absolute maximum and minimum values recorded on the different sampling dates. A general decrease in ψ_{xylem} through 1976 and an increase in the variation during the summer months is also evident in the combined data. The maximum values were generally recorded

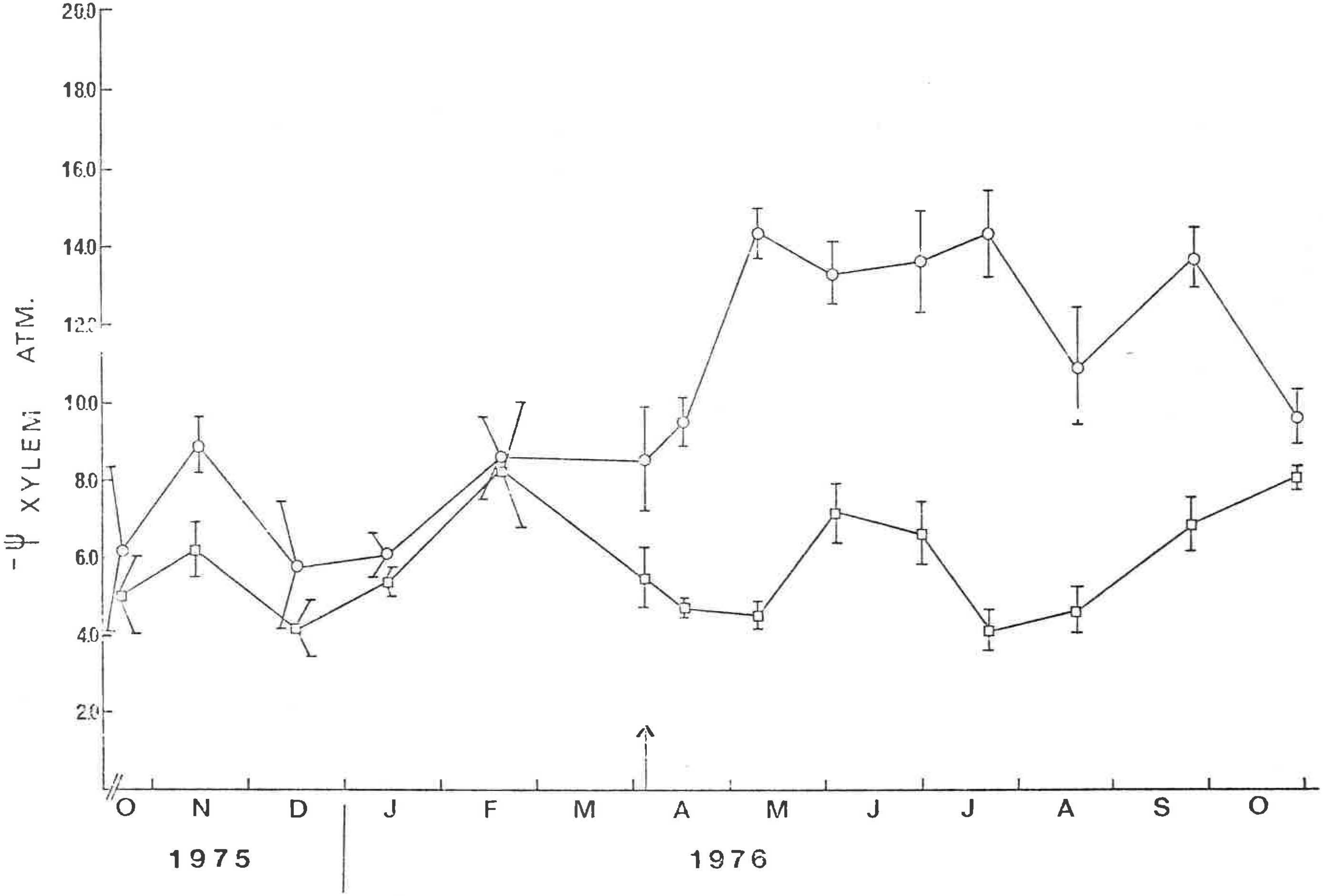


Figure 3. Seasonal courses of maximum (dawn) and minimum (midday) ψ_{xylem} of *Pinus banksiana* at midslope on the study hill at Richardson Fire Tower during 1975-76. Vertical bars represent 95% confidence intervals, and the vertical arrow indicates snow release.

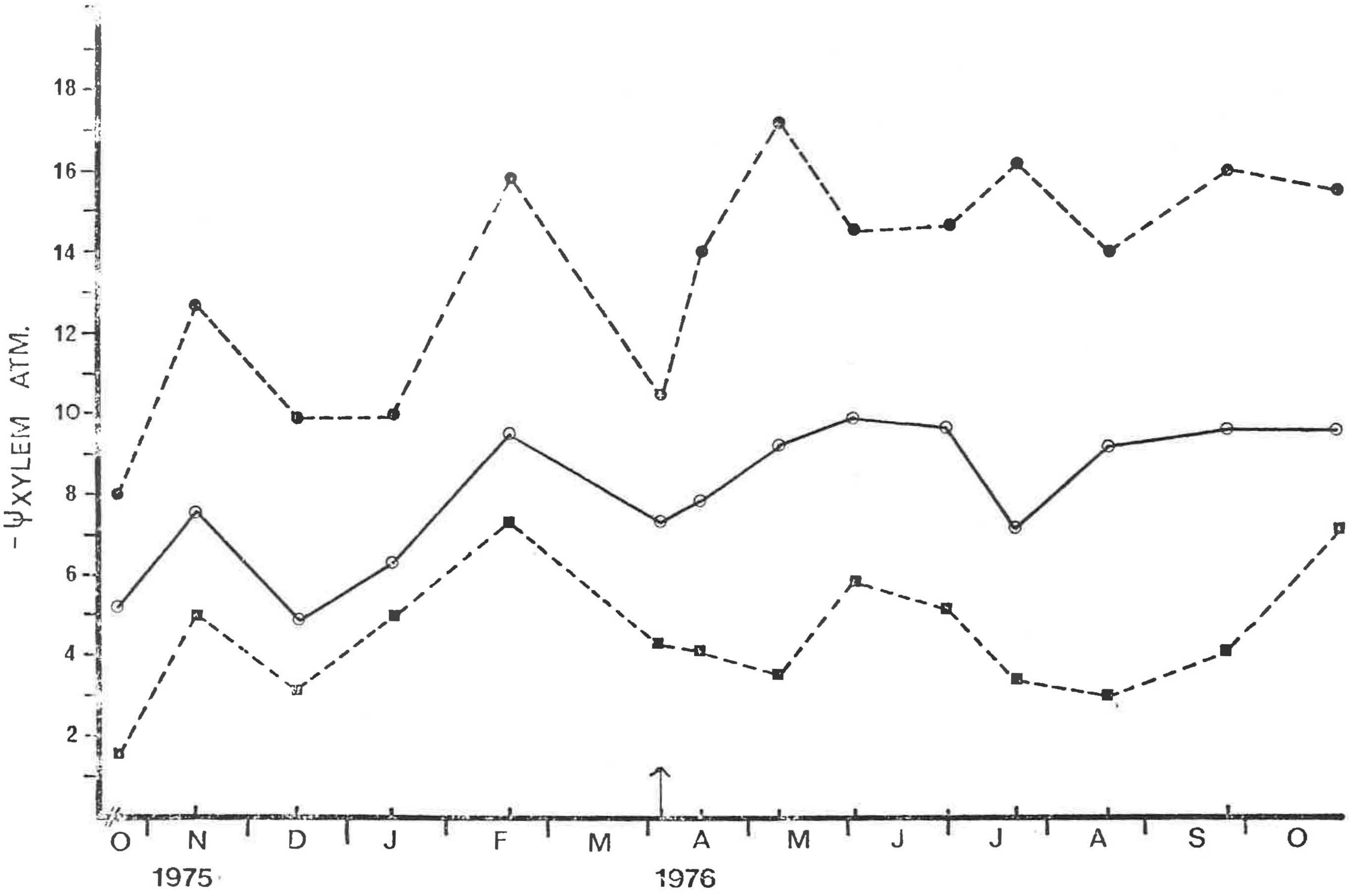
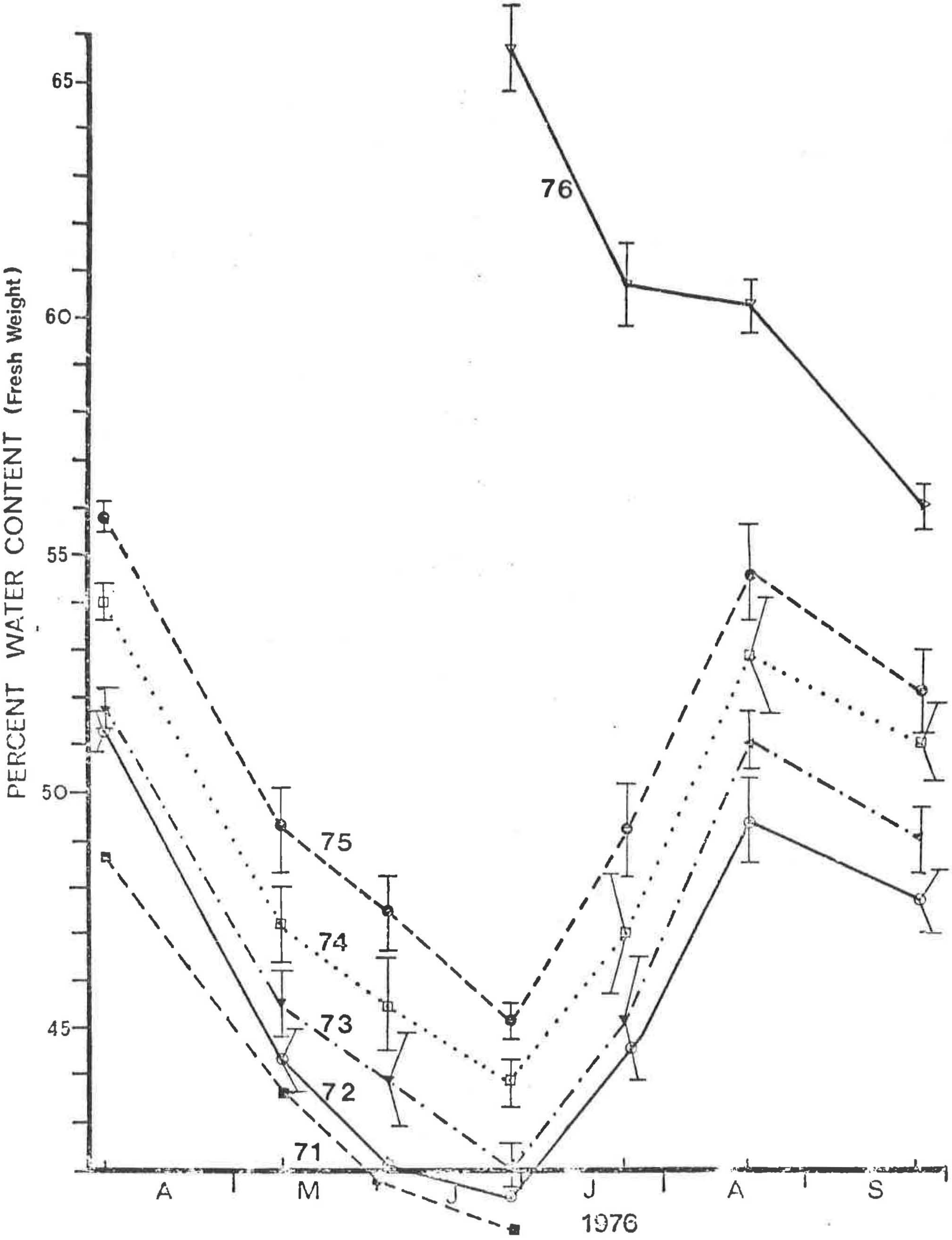


Figure 4. Seasonal courses of mean and absolute maximum and minimum ψ_{xylem} of *Pinus banksiana* on the hill transect at Richardson Fire Tower during 1975-76. The vertical arrow indicates snow release.

at the more mesic midslope and hill bottom positions, and the minimum values at the drier hill top position. The absolute maximum and minimum values recorded on the hill transect were -1.5 and -17.2 atm., respectively. Values to -18.2 atm. were measured at other sites on the hill during the summer.

Water contents of all needle age classes (current years needles excluded) decreased during the early summer months to a low in late June, but increased again to approach the spring high by late August (Fig. 5). The current years needles (1976) began to expand in late June and decreased in water content throughout the summer. The water contents of all needles on a needled branch (composite sample) follows the same trend as each of the older age classes (Fig. 6) due to the small contribution in total biomass of the 1976 needles (Fig. 7). The percentage contribution of the different needle age classes to the total needle leaf area follows approximately the same trend as total needle dry weight. Water contents of needles decreased with increasing needle age with the greatest difference between the 1976-75 age classes. Needled branches commonly have at least a few needles four to five (sometimes six) years old, the water contents of which are usually not significantly different (partially due to small sample size in older age classes).

The shift in water contents during the summer appears to be followed by a concomitant shift in the relationship between water contents and ψ_{xylem} (Fig. 8 and 9). Needles that are drier (water contents) in midsummer are not necessarily drier physiologically because of the maintenance of high xylem water potentials at lower water contents. This summer shift in ψ_{xylem} and water contents was not anticipated and will need further study for proper explanation. However, the data does



gure 5. Mean water contents (fresh weight) of different needle age classes of *Pinus banksiana* at Richardson Fire Tower during 1976. Vertical bars represent 95% confidence intervals.

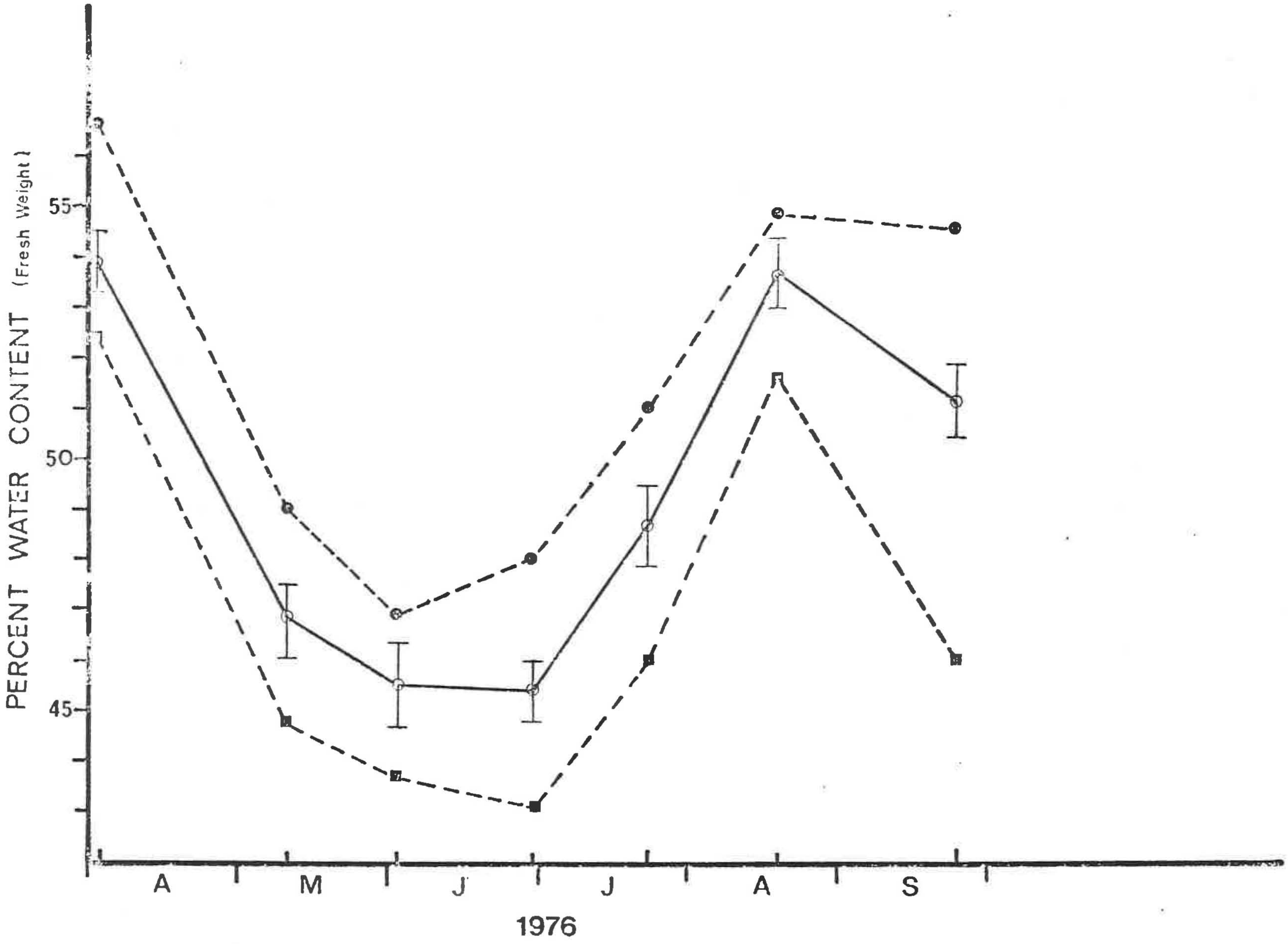


Figure 6. Mean and absolute maximum and minimum water contents (fresh weight) of all needles on needled branches of *Pinus banksiana* at Richardson Fire Tower during 1976. Vertical bars represent 95% confidence intervals.

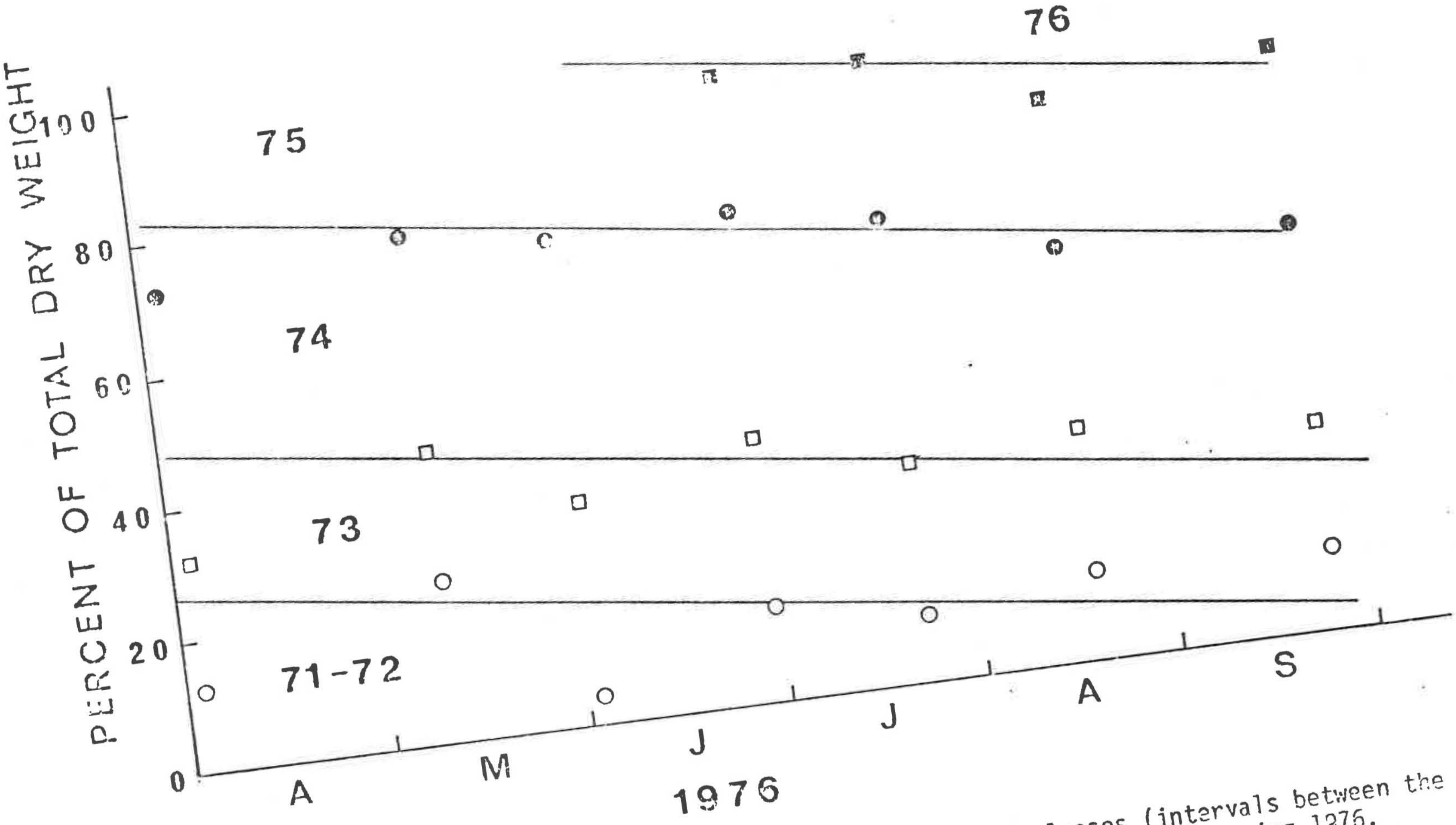


Figure 7. Change in percentage contribution of different needle age classes (intervals between the lines) to total needle dry weight of *Pinus banksiana* at Richardson Fire Tower during 1976.

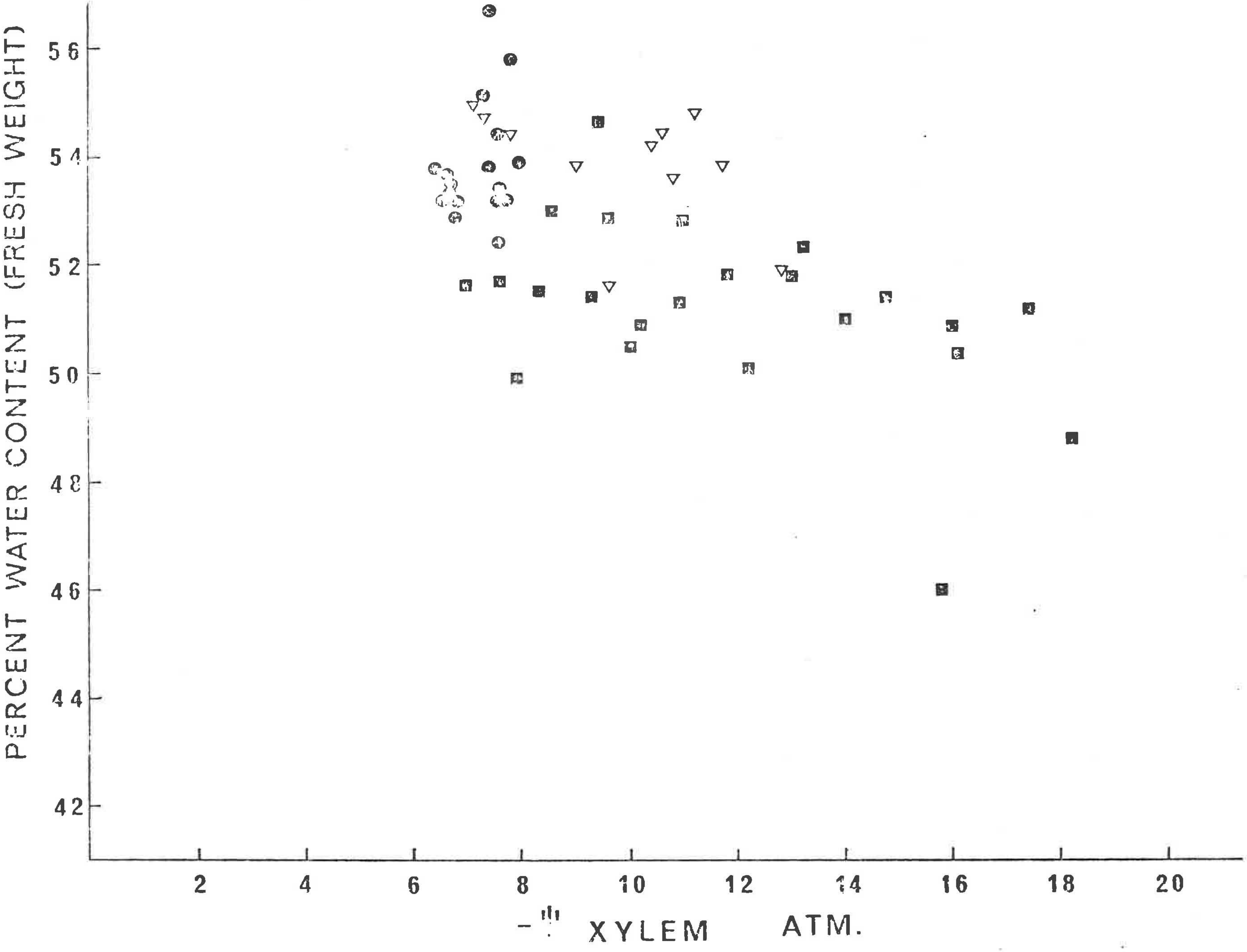


Figure 8. ψ_{xylem} vs. needle water content (fresh weight) of *Pinus banksiana* at Richardson Fire Tower for the periods 2-4 April ⊕ , 16-20 August ▽ . and 24-27 September ▣ , 1976.

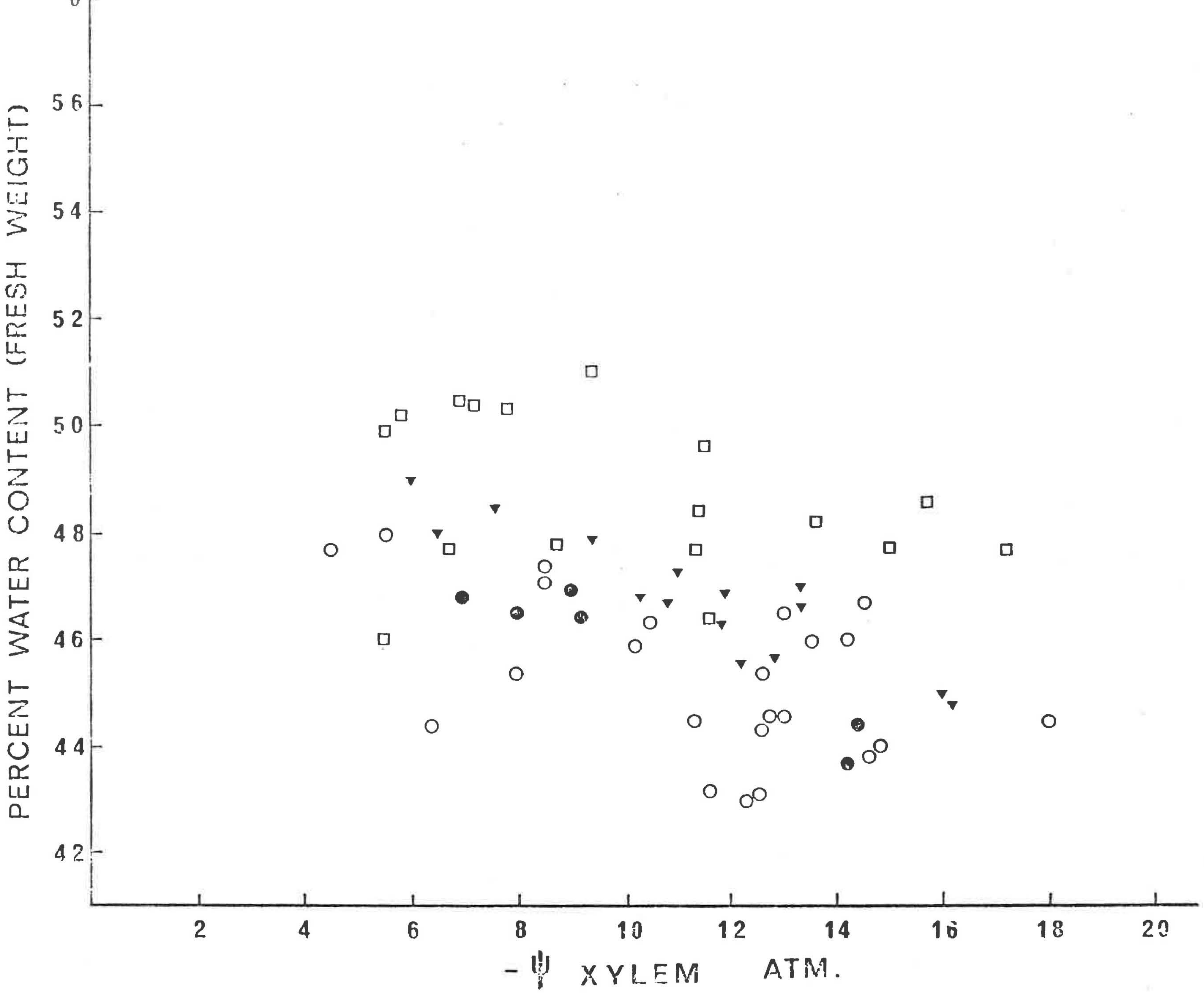


Figure 9. ψ_{xylem} vs. needle water content (fresh weight) of *Pinus banksiana* at Richardson Fire Tower for the periods 9-10 May ▼, 2-3 June ◐, 29-30 June ○, and 20-23 July □, 1976.

imply that the measurement of water contents alone does not adequately portray the plants physiological water status.

Figures 10, 11, and 12 illustrate the diurnal progression of ψ_{xylem}, transpiration, and leaf resistance of Jack pine during the intensive study periods of 3-4 April, 29-30 June, and 24-27 September, 1976. Data from the other intensive study periods are included in the Appendix. The April study was conducted during the snow release period. Soil temperatures to 50 cm depth remained within 1°C of freezing while pine needle temperatures were often elevated to 10-15°C. Midday transpiration rates were less than 0.1 ug cm^{-2} sec^{-1} with corresponding leaf resistances of approximately 100 sec cm^{-1}. These values indicate that the stomata were fully closed. Xylem water potentials remained nearly constant, varying between -6.5 and -8.0 atm. over the 30 hr period, providing additional evidence that the plant's water status did not vary significantly.

The uniformity of the plant responses in April contrasts sharply with the large diurnal changes in ψ_{xylem}, transpiration, and leaf resistance that occurred in late June and September. Xylem water potentials in both cases showed a large diurnal fluctuation of over 10 atm. with rapid recovery within a few hours of sunset, indicating that soil moisture was not limiting.

Transpiration rates varied from low night levels less than 0.1 ug cm^{-2} sec^{-1} to high midday levels near 1.4 ug cm^{-2} sec^{-1} in June and 0.6 ug cm^{-2} sec^{-1} in September. Transpiration rates closely paralleled ψ_{xylem}, increasing concomitantly with decreasing xylem water potentials. The low leaf resistance values of 10-15 sec cm^{-1} measured

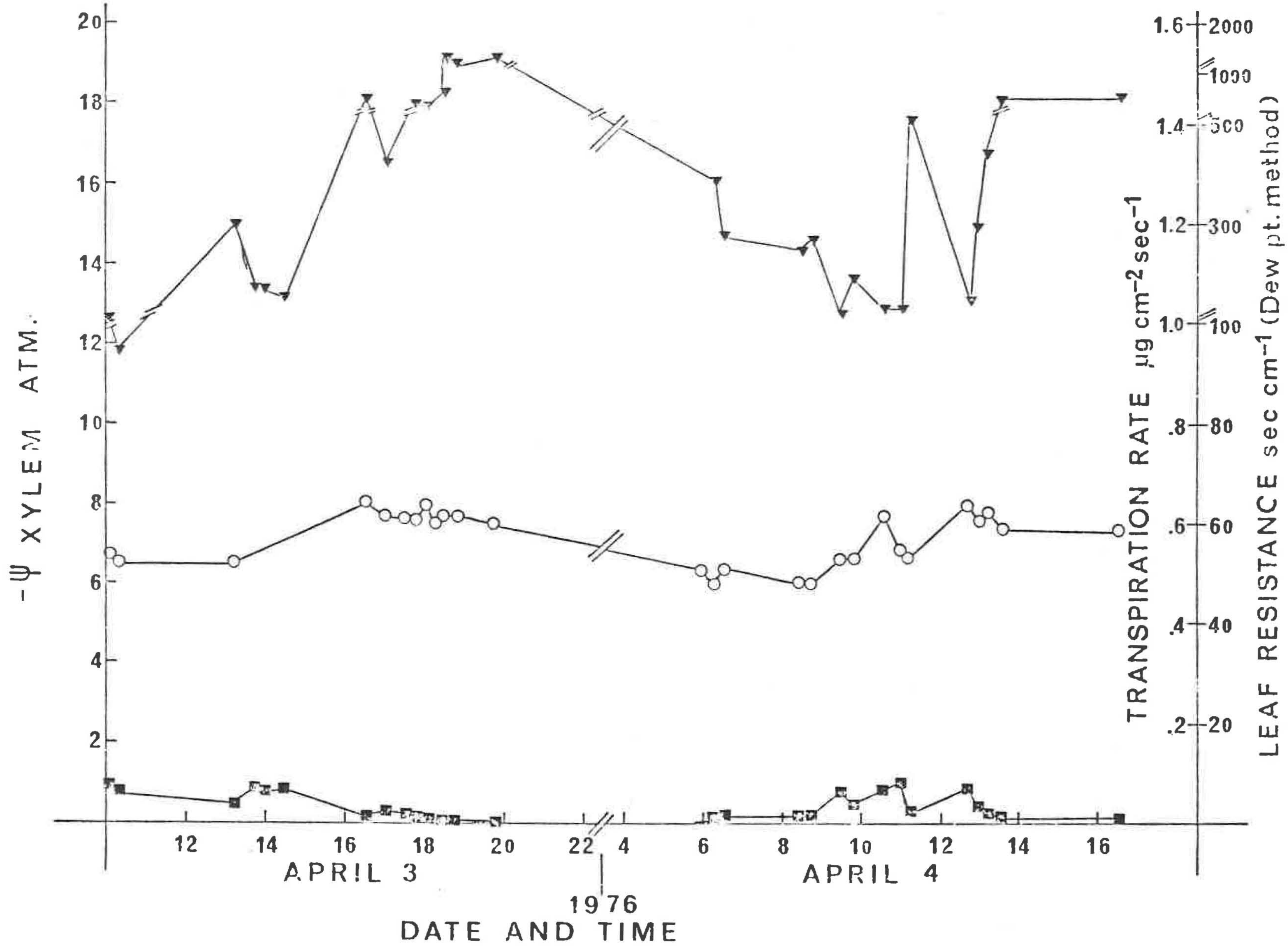


Figure 10. Diurnal courses of ψ_{xylem} ○, transpiration ■, and leaf resistance ▼ of *Pinus banksiana* at midslope on the study hill at Richardson Fire Tower on 3-4 April, 1976.

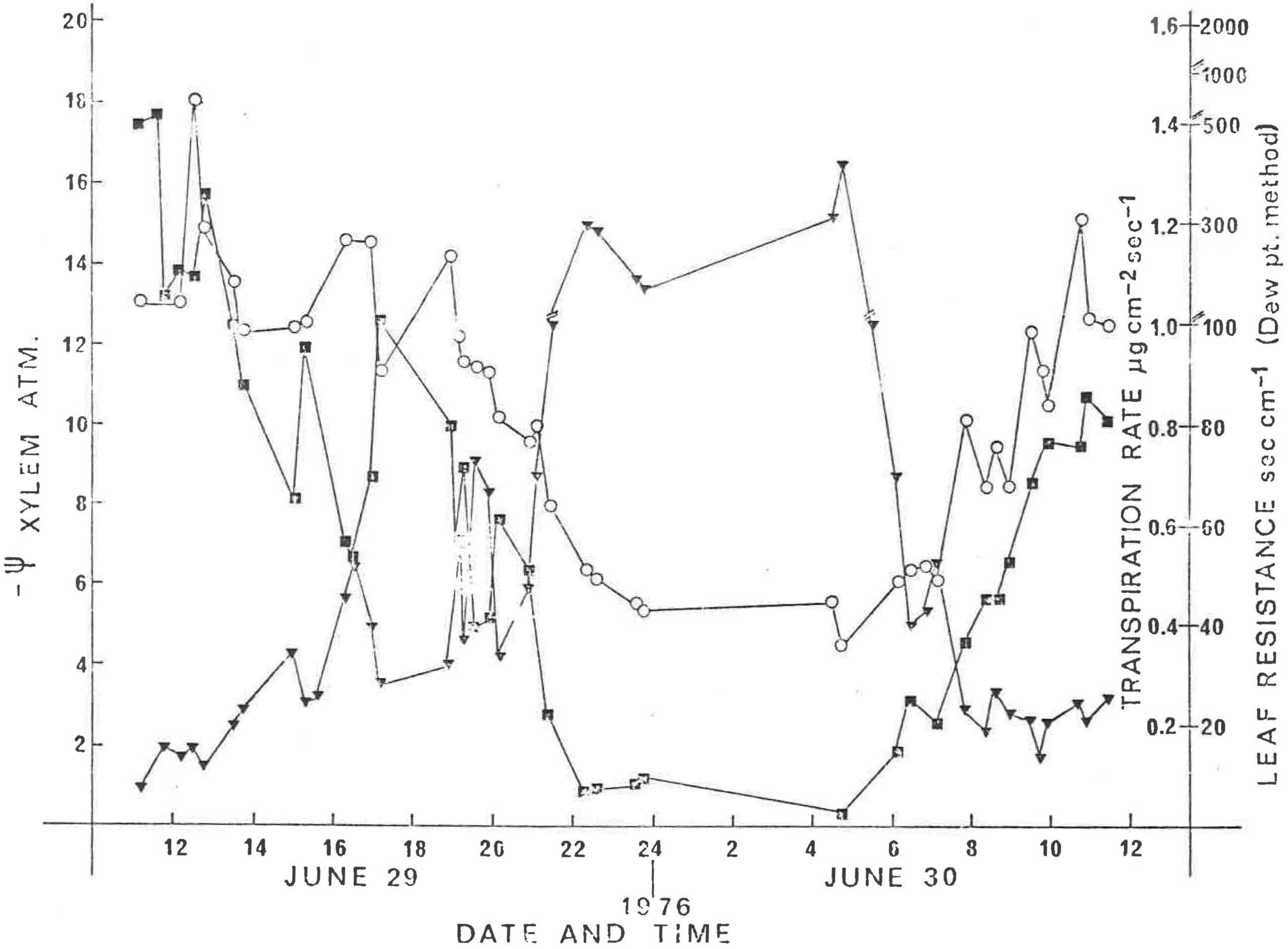


Figure 11. Diurnal courses of ψ_{xylem} ○, transpiration ⊞, and leaf resistance ▼ of *Pinus banksiana* at midslope onthe study hill at Richardson Fire Tower on 29-30 June, 1976.

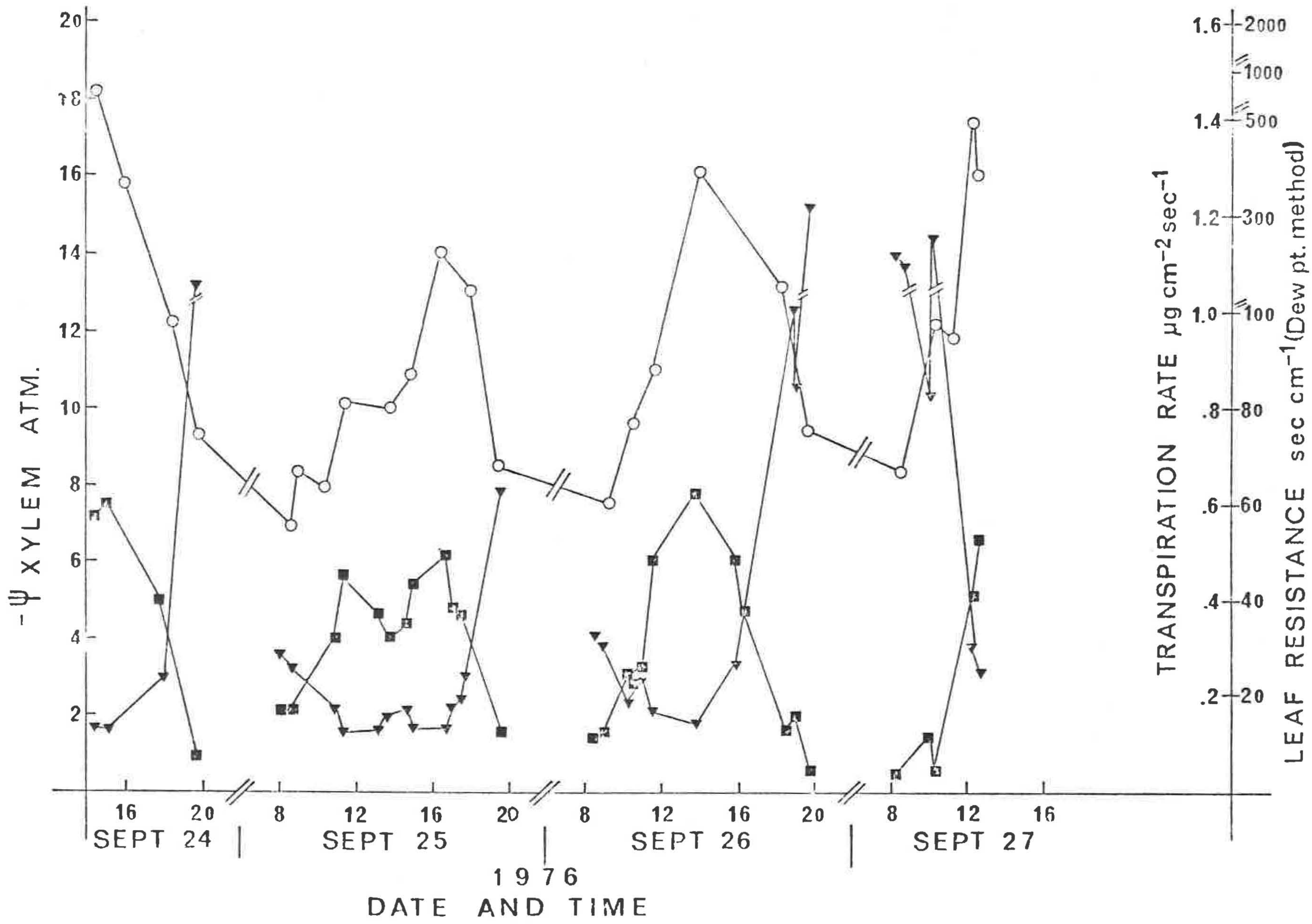


Figure 12. Diurnal courses of ψ_{xylem} ○ , transpiration ■ , and leaf resistance ▼ of *Pinus banksiana* at midslope on the study hill at Richardson Fire Tower on 24-27 September, 1976.

during midday represent fully open stomata. It should be noted that these resistances are determined for a vegetated branch that includes all age classes of needles. The high night values greater than 100 sec cm^{-1} represent closed stomata and are similar to the lowest values obtained during April.

Figures 13 and 14 show the change in transpiration and leaf resistance with the change in radiation and ψ_{xylem} for the 29-30 June study period. The nature of the response was slightly different in early and late summer than in midsummer and the composite data from these different periods is presented in the Appendix. There was a nearly linear increase in transpiration with a decrease in ψ_{xylem} over the range of -5 to -18 atm. This indicates that the stomata remained open, transpiration was not limited, and the pine trees were not appreciably water stressed at xylem water potentials (water deficits) down to -18 atm. Maximum transpiration rates occurred in midday when xylem water potentials were lowest. Figure 14 indicates that the stomata became fully open (with minimum leaf resistance values) at 0.2 to 0.4 $mE\ m^{-2}\ sec^{-1}$ PAR. Higher radiation levels resulted in increased water loss (and thus increased water deficits) probably as a result of elevated needle and air temperatures and high evaporative demands.

Partial midday stomatal closure is evident between 1400 and 2000 hr on 29 June (Fig. 11), when transpiration (and leaf resistance) fluctuated even though radiation levels remained high. This results in some of the scatter observed in Fig. 13 and 14. Figure 15 indicates that the stomata at these times were responding largely to the

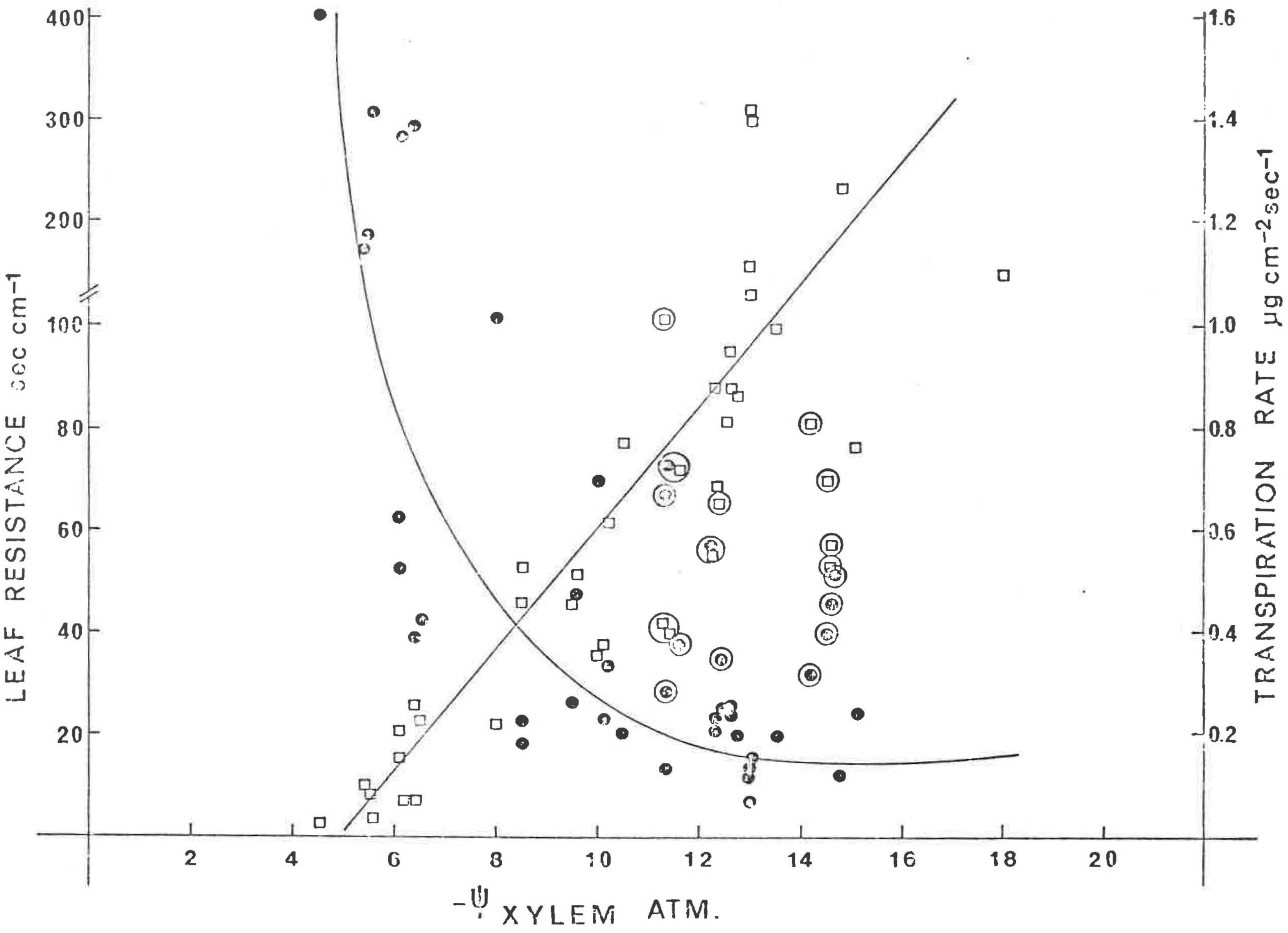


Figure 13. Transpiration □ and leaf resistance ● of *Pinus banksiana* vs. ψ_{xylem} for the period 29-30 June, 1976, at Richardson Fire Tower. Circled values represent stomatal closure at high vapour pressure deficits and are excluded from the curves.

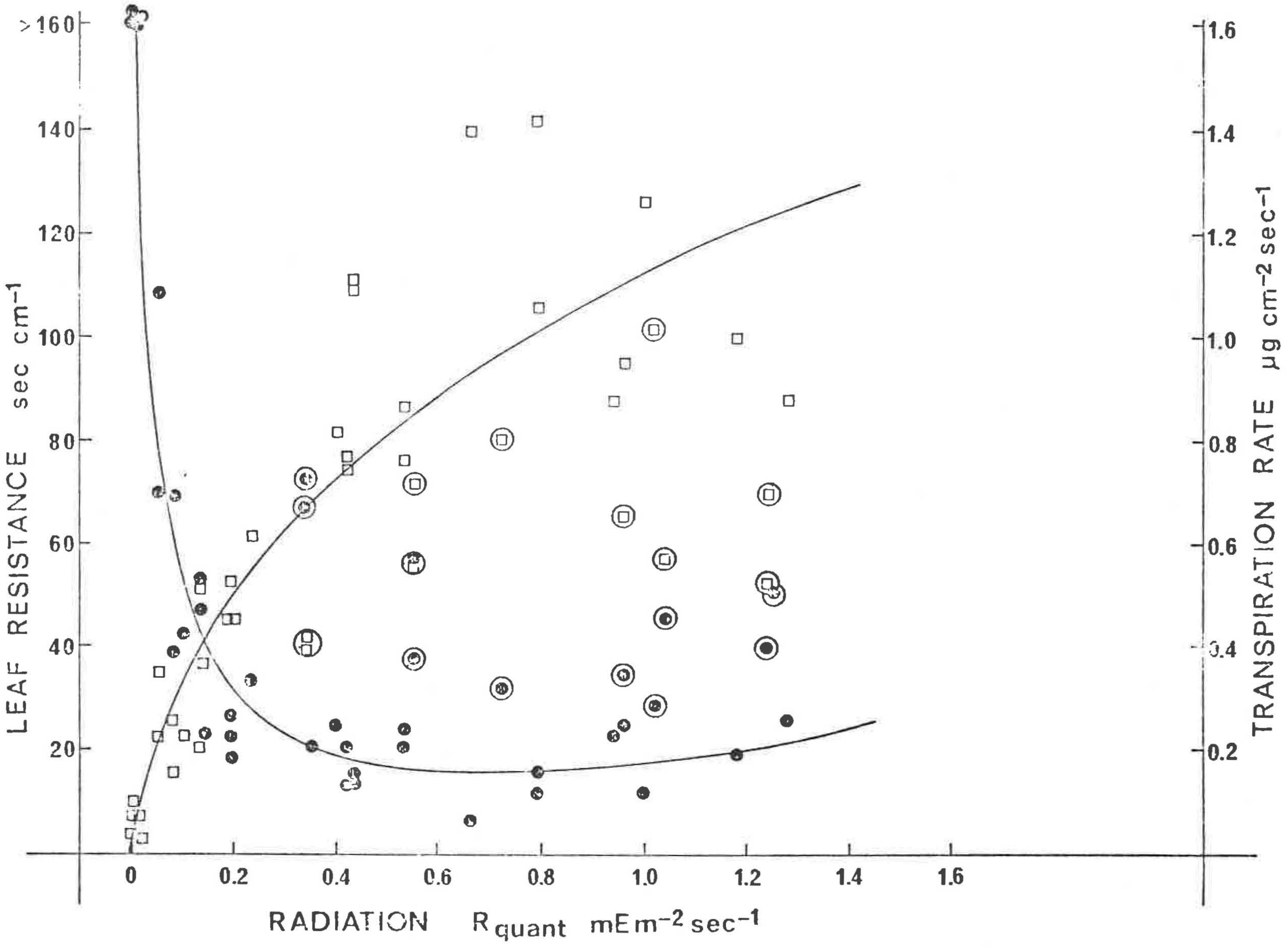


Figure 14. Transpiration □ and leaf resistance ● of *Pinus banksiana* vs. radiation for the period 29-30, 1976, at Richardson Fire Tower. Circled values represent stomatal closure at high vapour pressure deficits and are excluded from the curves.

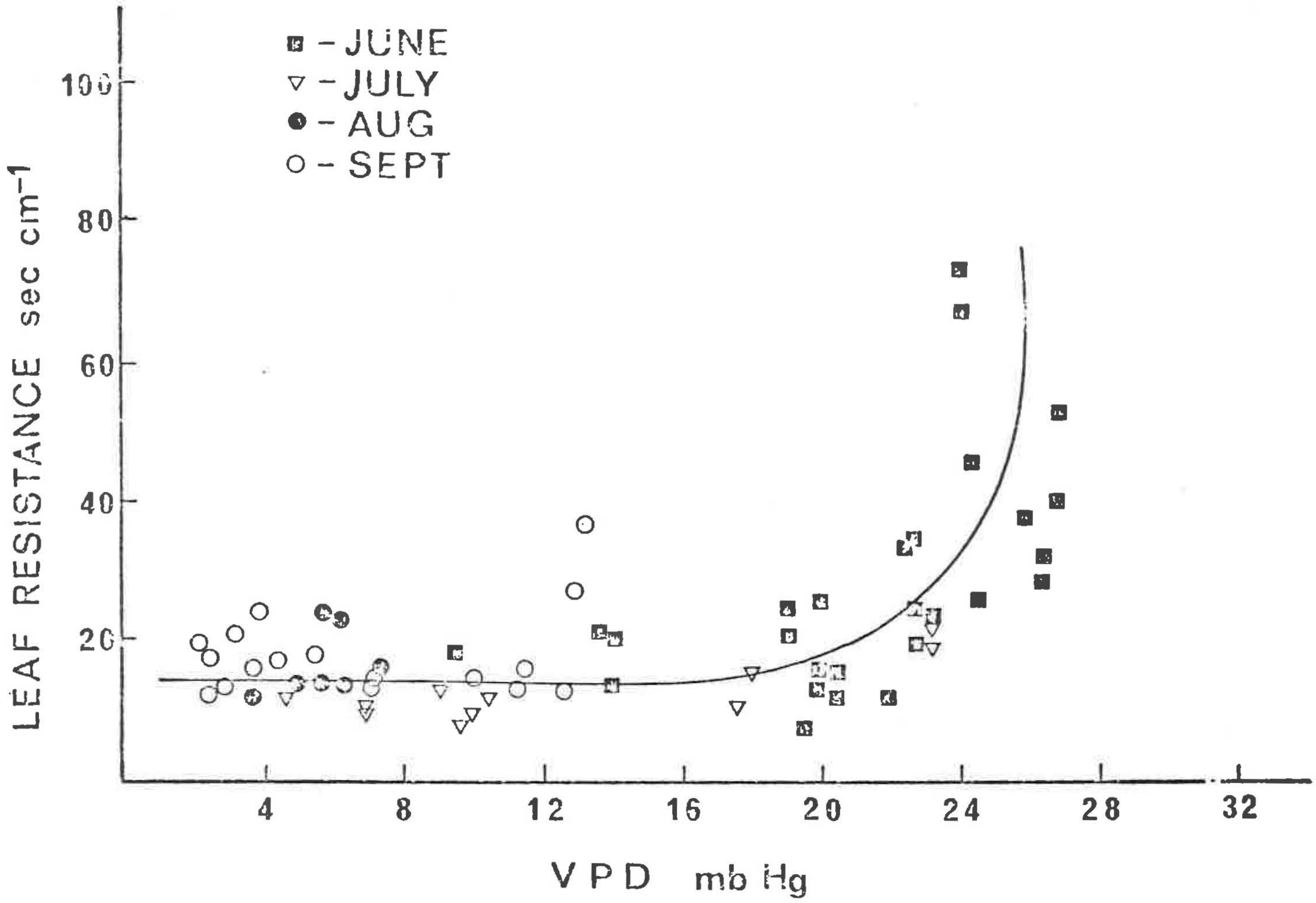


Figure 15. Leaf resistance of *Pinus banksiana* vs. vapour pressure deficit for the periods 29-30 June ▣, 20-23 July ▽, 16-20 August ●, and 24-27 September ○, 1976, at Richardson Fire Tower. Only values with R quant. >0.2 mEm^{-2} sec^{-1} are plotted.

evaporative demands of the air. At VPD levels of 22-26 mb Hg, stomatal resistance increased even though light and water (as indicated by ψ_{xylem}) were not limiting. The relationship between ψ_{xylem} and VPD is not as clear. Xylem water potentials generally decreased with increasing VPD (Fig. 16), but the scatter in the data tends to suggest not only a seasonality in the response (in line with the ψ_{xylem} VS water content relationships in Fig. 8 and 9), but also that ψ_{xylem} is influenced by other factors besides VPD.

5.6 DISCUSSION

The maximum rates of photosynthesis recorded on winter hardened cut branches of Jack pine (1.4 mg CO_2 g^{-1} hr^{-1}) are comparable to early post-dormant rates for black spruce (van Zinderen Bakker 1974) but are considerably lower than the November rates of 7-11 mg CO_2 g^{-1} hr^{-1} for Jack pine reported by Logan (1971). However, trees in the latter case were growing at Lat. 46°N and probably had not entered dormancy as deeply as trees at the Richardson Fire Tower site at Lat. 58°N. Photosynthetic rates were also measured on cut branches of Jack pine collected at the Richardson site by Legge et al. (1976) to serve as background data for comparison with *Pinus banksiana* X *P. contorta* hybrids near the Amoco Windfall gas processing plant, Whitecourt, Alberta. Early fall (1 Sept.) rates for Jack pine from the Richardson site (3.02 mg CO_2 dm^{-2} hr^{-1} $\approx$ 3 mg CO_2 g^{-1} hr^{-1}) were comparable with lodgepole pine samples collected in Jasper Natl. Park (12 Aug.) but were higher than at the Whitecourt site. Sulfate-sulfur content of needles was lower on samples from the Richardson site than either Jasper or Whitecourt. Data of this type will serve as important base line information for sites exposed to atmospheric emmissions such as SO_2

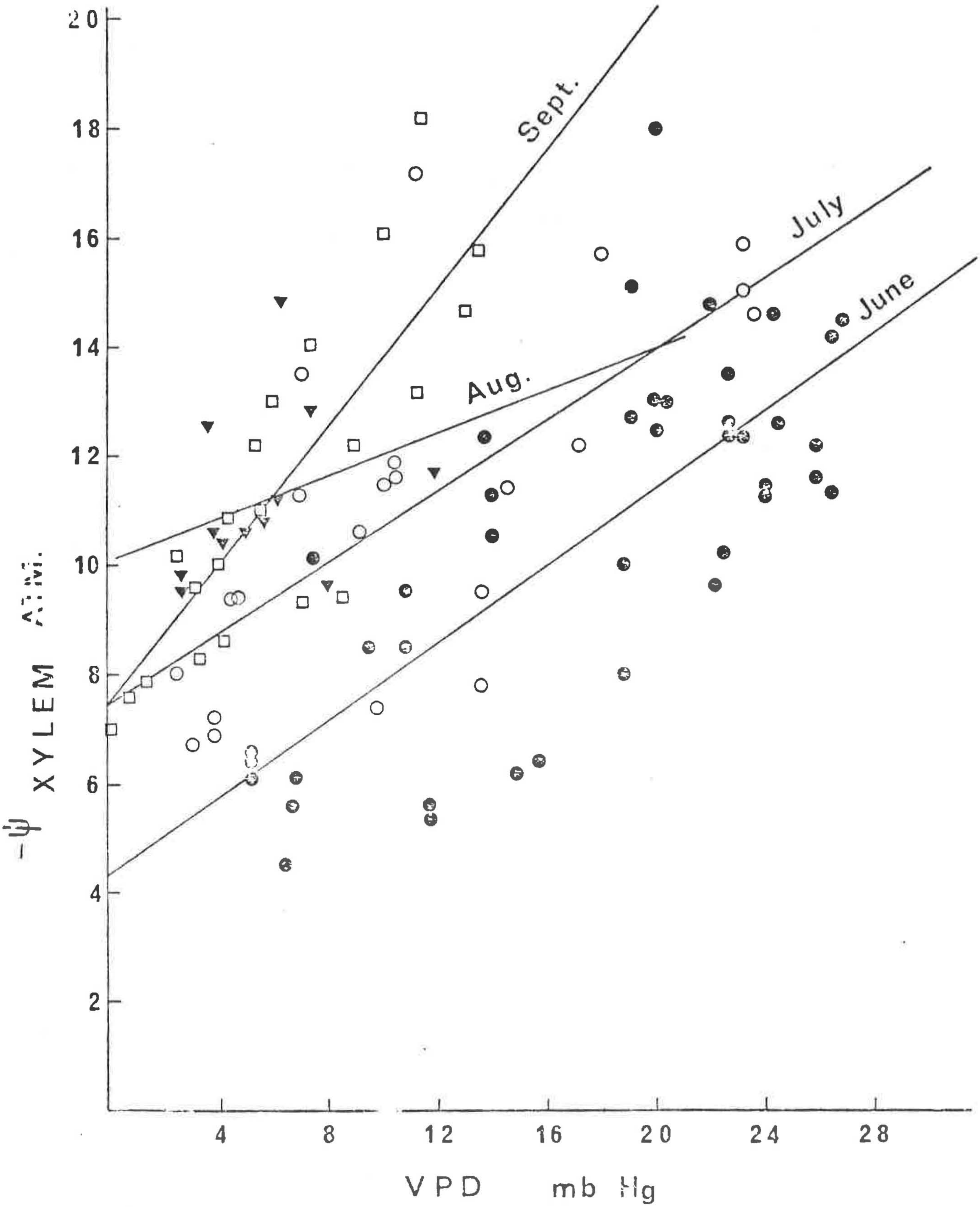


Figure 16. ψ_{xylem} of *Pinus banksiana* vs. vapour pressure deficit for the periods 29-30 June ●, 20-23 July ○, 16-20 August ▼, and 24-27 September □, 1976, at Richardson Fire Tower.

The rapidity with which winter hardened cut branches of Jack pine began positive net assimilation when brought into the laboratory (one-two days) was not anticipated considering the five days for a similar response by black spruce (van Zinderen Bakker 1974). This tends to suggest that Jack pine could show a positive net assimilation in late winter or spring when air temperatures are at or above freezing. It also suggests that the plants may experience severe water stress during these periods when air temperatures are elevated, the soil is still frozen, and there is no replenishment of water lost during gas exchange through open stomata.

Seasonal measurements of leaf and xylem water potentials and April measurements of ψ_{xylem}, transpiration, and leaf resistance failed to substantiate any stomatal activity of Jack pine during these late winter or spring periods. Psychrometric data indicates that $\psi_{\pi + \tau}$ remained constant and ψ_p remained high (12-16 atm.) throughout the winter. Xylem water potentials also remained high and relatively constant until after snow melt. Measurements during April showed that the trees remained dormant during the spring thaw and avoided the development of large water deficits. These data indicate that winter or spring water stress in Jack pine probably did not occur.

The diurnal variation (winter and summer) of ψ_{xylem} values in this study are similar to that reported for *Pinus banksiana* X *P. contorta* hybrids at Whitecourt by Legge et al. (1976), although trees at this latter site tended to develop more negative xylem water potentials. The summer water deficits of Jack pine at Richardson (ψ_{xylem} minimum = -16 to -18 atm.) would be devastating to many temperate region agronomic species. Boyer (1976) states that " ..... virtually all the work that was done in the first half of this century agrees that even modest desiccation can have large inhibitory effects on photosynthetic activity." More recent work simply confirms this. Boyer (1976) also states that leaf enlargement in such plants as maize, soybeans, and sunflower is reduced to 25% or less of controls when ψ_{leaf} decreases to -4.0 bars. These levels of ψ_{xylem} probably represent a sub-lethal stress for Jack pine, the significance of which will have to be determined by laboratory studies. Recovery of midday water deficits occurred rapidly after sunset probably due to the high soil moisture through the summer. A dry year may not occur during the study period and the model of heat and water fluxes will help to predict the water deficits that would occur during years with reduced precipitation and soil moisture. Failure to anticipate such extreme environmental conditions (or the plant's responses to such environmental conditions) could prove catastrophic to any revegetation program.

Water contents of needles showed a shift during the summer matched by a shift in the ψ_{xylem}- water content relationship. This response needs further study but does indicate that a single type of measurement is inadequate to describe a plant's water status and that this status may change seasonally. Seasonal differences in stomatal responses (as indicated by leaf resistance and transpiration) as a function of radiation (PAR) and ψ_{xylem} was also noticed. Transpiration was less in early and late summer at a given level or PAR or ψ_{xylem} than in midsummer. This may be due to a number of factors including sluggishness of stomatal response at early stages of fall or post-winter dormancy, lower temperatures and vapour pressure deficits at these times, or to the high transpiration rates (relative to older needles) of the rapidly growing current year's needles in midsummer.

The stomatal response of Jack pine is influenced largely by the level of radiation, the atmospheric evaporative demands, and the water status of the tissue. The stomata open to full aperature (and thus a minimum leaf resistance) at relatively low light levels. This agrees with data presented by Federer and Gee (1976) for three hardwood species. High VPD levels result in stomatal closure even though radiation or soil water is not limiting. Water stress (as indicated by ψ_{xylem}) does not result in stomatal closure or an increase in leaf resistance down to a water deficit of -18 atm. This is in complete contrast to the study of Dykstra (1974) that reports an increase in stomatal resistance of lodgepole pine seedlings with a decrease in tree water potentials beginning at -3 bars. Lopushinsky and Klock (1974) also report a decline in transpiration of lodgepole pine seedlings with a decrease in soil water potentials beginning at -2 bars. The results of our study agree with Legge et al. (1976) who shows the maintenance of a low leaf resistance in *Pinus banksiana* X *P. contorta* hybrids over a broad range of xylem water potentials with an indication of stomatal closure at -18 to -20 bars. Xylem water potentials apparently did not become low enough during our summer intensive study periods to result in stomatal closure. The ability of Jack pine to maintain open stomata and CO_2 flux for photosynthesis at increasing water deficits may be an adaptation to a xeric environment. Laboratory studies in stress physiology will need to be conducted to determine at what point water becomes limiting.

5.7 CONCLUSIONS

(a) Soil moisture did not appear to be a limiting factor for Jack pine at the Richardson Fire Tower site during the 1976 study period (Soils Section page 40). Precipitation was relatively frequent and sufficient to keep ψ_{soil} high most of the summer (Meteorology Section page 12).

(b) Jack pine avoided spring drought by remaining dormant (with closed stomata) during the periods when the soils were still frozen but radiation and air temperatures were sufficent for photosynthesis.

(c) Xylem water potentials did not reach levels sufficiently negative to cause stomatal closure during the 1976 growing season.

(d) Stomatal resistance above 0.2 mE m^{-2} sec^{-1} (PAR) was controled largely by vapour pressure deficits.

(e) Jack pine did not appear to be seriously moisture stressed (as indicated by stomatal closure due to low ψ_{xylem}) during the 1976 study period. However, atmospheric evaporative demands caused ψ_{xylem} to reach -16 to -18 atm. and high vapour pressure deficits resulted in stomatal closure. Thus, even in years of favorable precipitation and soil moisture, low water potentials can develop in plants growing on sand in the Ft. McMurray region. The choice of species for revegetation must include a consideration of their growth and survival at low water potentials (see NEED FOR FURTHER STUDY).

(f) As expected, Jack pine seems well adapted to the sandy soils of the region.

5.8 IMPLICATIONS AND RECOMMENDATIONS

Matters of General Scientific Importance

(a) The strong dependence of Jack pine stomatal response upon vapour pressure deficits has not been reported. This phenomena is also not generally acknowledged in the literature.

(b) The maintenance in Jack pine of rather stable osmotic and turgor potentials throughout the year has not been reported, nor does this seem to happen in other species (e.g., black spruce).

(c) The maintenance of consistently low leaf resistances with decreasing xylem water potentials is opposite of reports for lodgepole pine seedlings.

(d) The responses of stomata during the spring breaking of dormancy have not been intensively studied.

Matters Relating Specifically to Oil Sands Development

(a) A matter of major importance is the fact that even in a relatively wet year with soil moisture generally adequate, xylem water potentials of -16 to -18 atm. developed. This means that any potential species for revegetation must be drought hardy.

(b) The implications of what might happen in a dry (but reasonably possible) year have been explored by modelling and suggest that extreme water deficits can develop. Testing a revegetation program particularly using introduced species during a few relatively wet years gives no indication of how the plants will respond to extreme moisture stress during dry years.

(c) Jack pine is obviously adapted to sandy soils, but its tolerance to atmospheric pollutants such as SO_2 is relatively unknown.

NEED FOR FURTHER STUDY

(a) The implications of the field studies and modelling must be pursued in the laboratory. Artificial stressing of Jack pine is necessary to determine lethal limits and the effects of increasing moisture stress upon photosynthesis and respiration. Questions such as "What levels of xylem water potentials cause stomatal closure in Jack pine?" need answering.

(b) Further field testing of parameters suggested by the model are needed. This would be particularly useful should 1977 have a dry-hot summer when much of (a) could be determined in the field.

(c) A completion of the canopy geometry studies is necessary.

(d) Studies need to be initiated with grasses (and other available species) on the G.C.O.S. dike so that modelling can be extended to include other potential revegetation species.

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5.11 APPENDIX

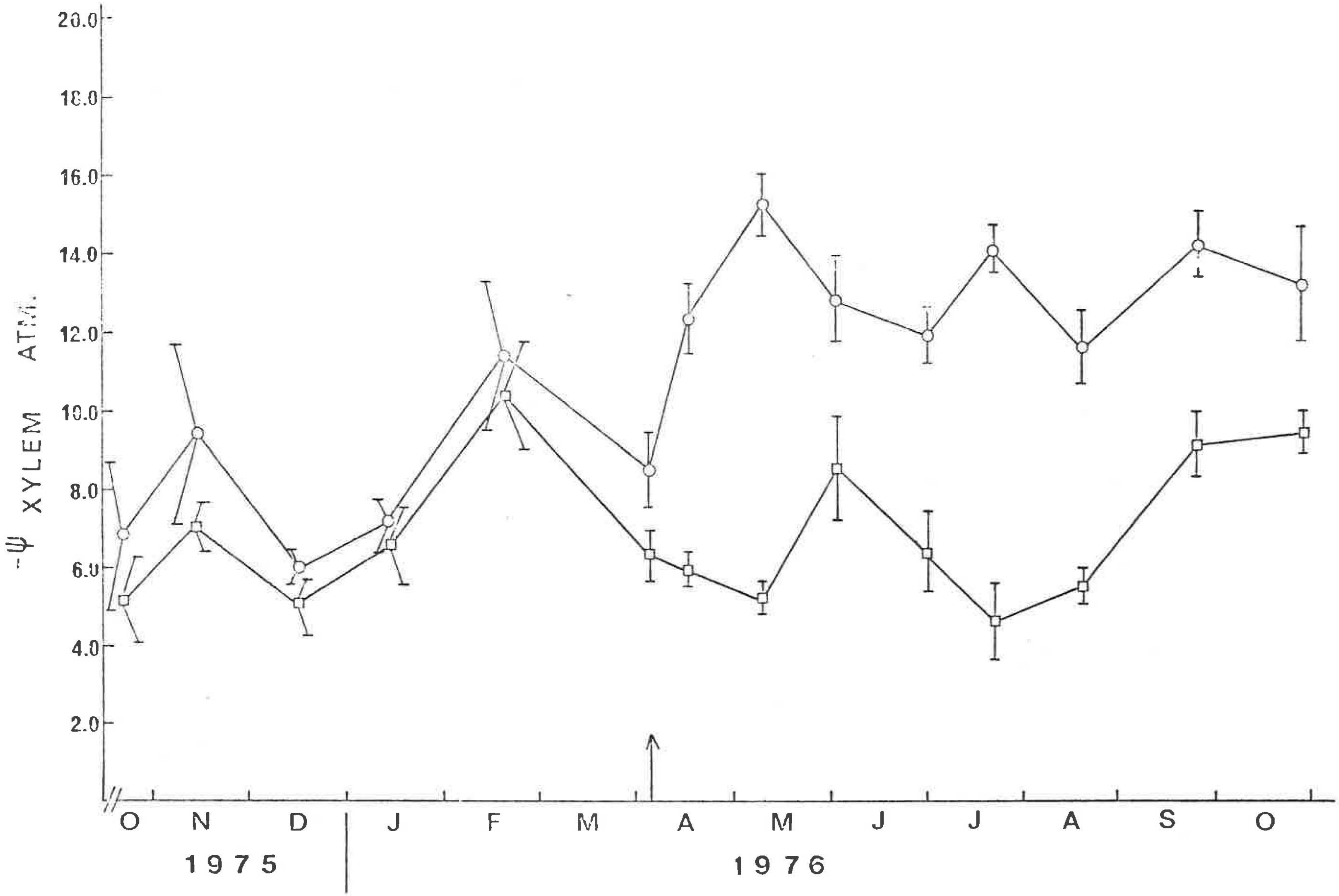

Figure A-1. Seasonal courses of maximum (dawn) and minimum (midday) ψ_{xylem} of *Pinus banksiana* at topf of the study hill at Richardson Fire Tower during 1975-76. Vertical bars represent 95% confidence intervals, and the vertical arrow indicates snow release.

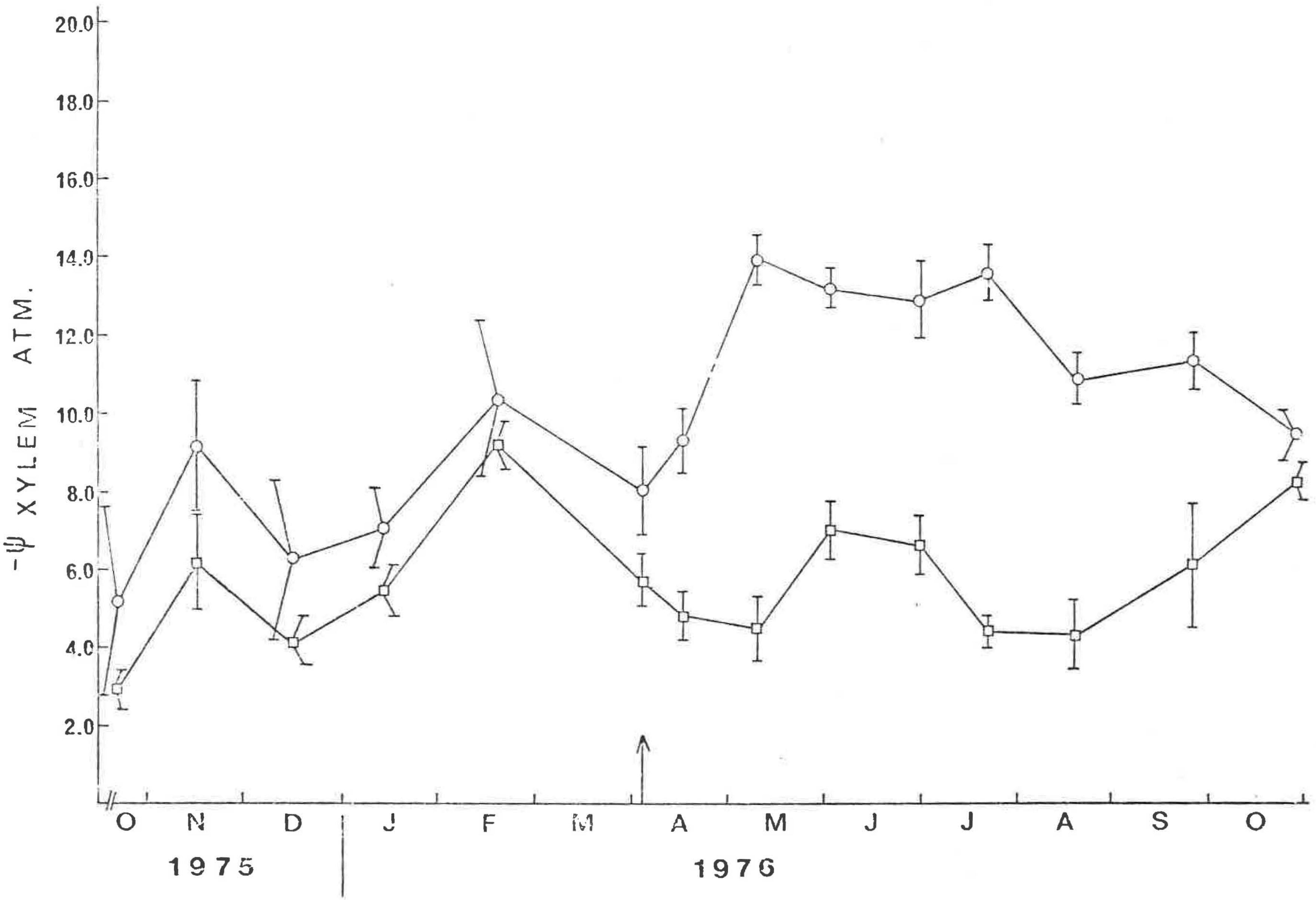

Figure A-2. Seasonal courses of maximum (dawn) and minimum (midday) ψ_{xylem} of *Pinus banksiana* at the bottom of the study hill at Richardson Fire Tower during 1975-76. Vertical bars represent 95% confidence intervals, and the vertical arrow indicates snow release.

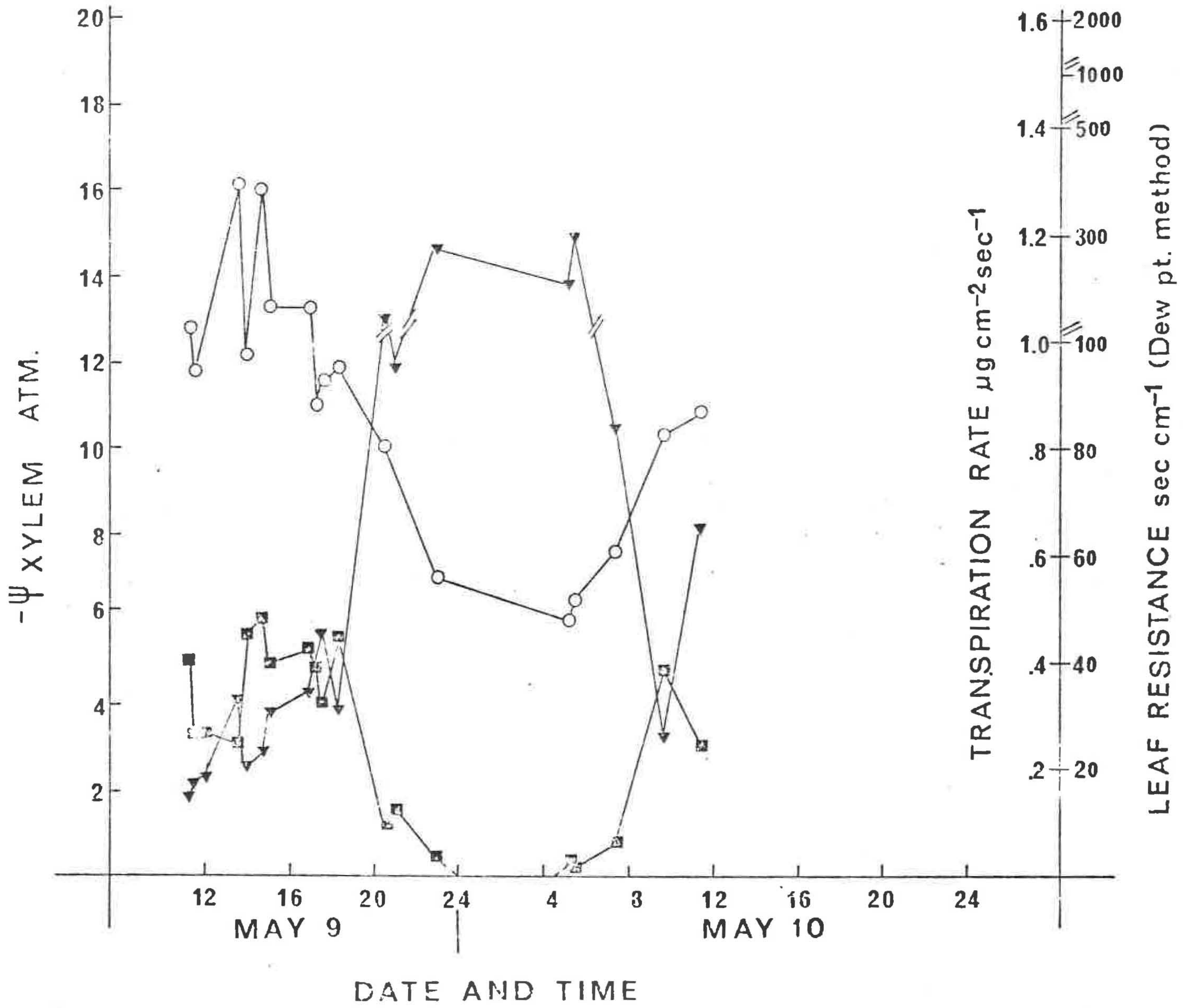

Figure A-3. Diurnal courses of ψ_{xylem} ○ , transpiration ■ , and leaf resistance ▼ of *Pinus banksiana* at midslope on the study hill at Richardson Fire Tower on 9-10 May, 1976.

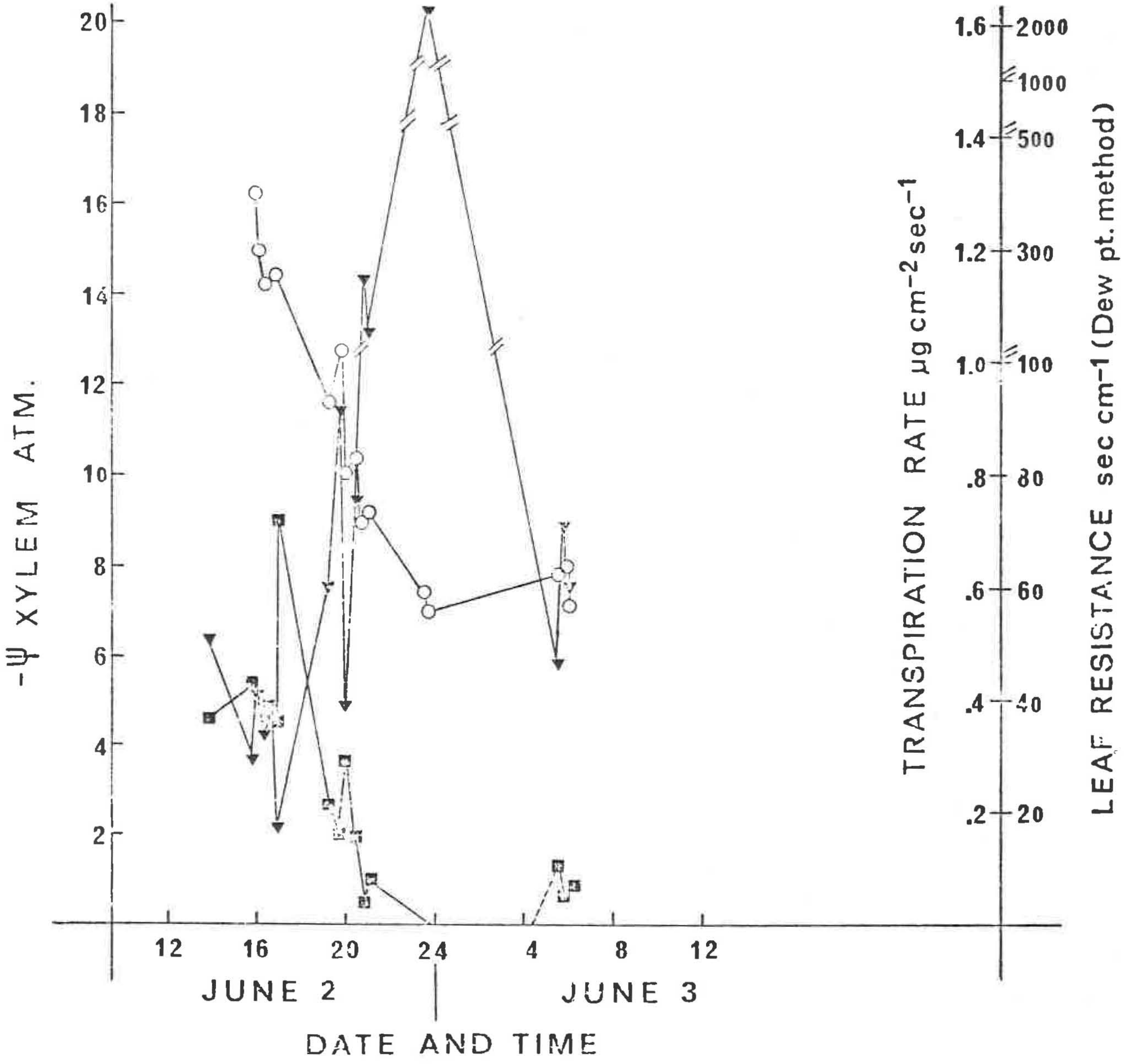

Figure A-4. Diurnal courses of ψ_{xylem} ○, transpiration ■, and leaf resistance ▼ of *Pinus banksiana* at midslope on the study hill at Richardson Fire Tower on 2-3 June, 1976.

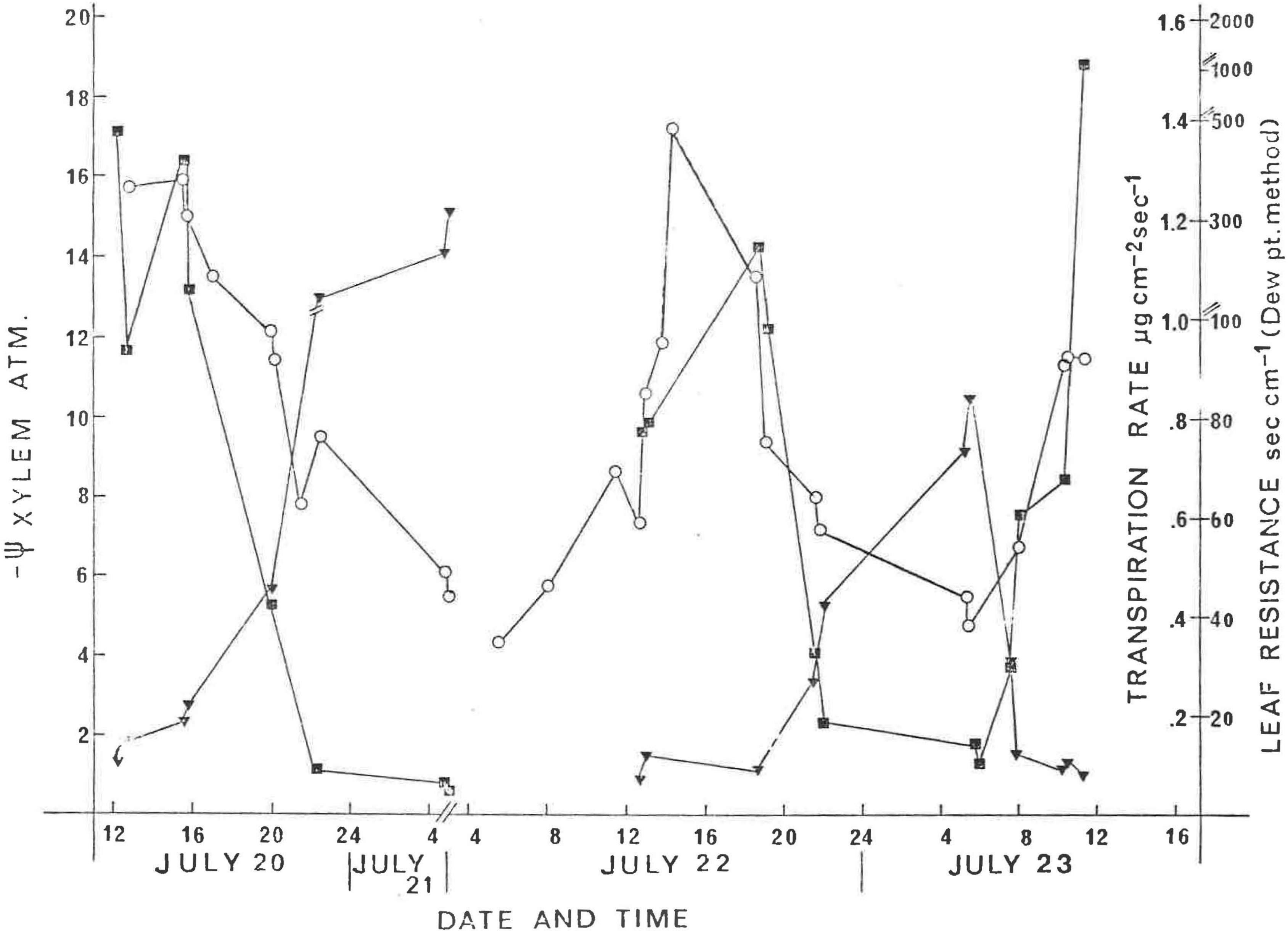

Figure A-5. Diurnal courses of ψ_{xylem} ○, transpiration ■, and leaf resistance ▼ of *Pinus banksiana* at midslope on the study hill at Richardson Fire Tower on 20-23 July, 1976.

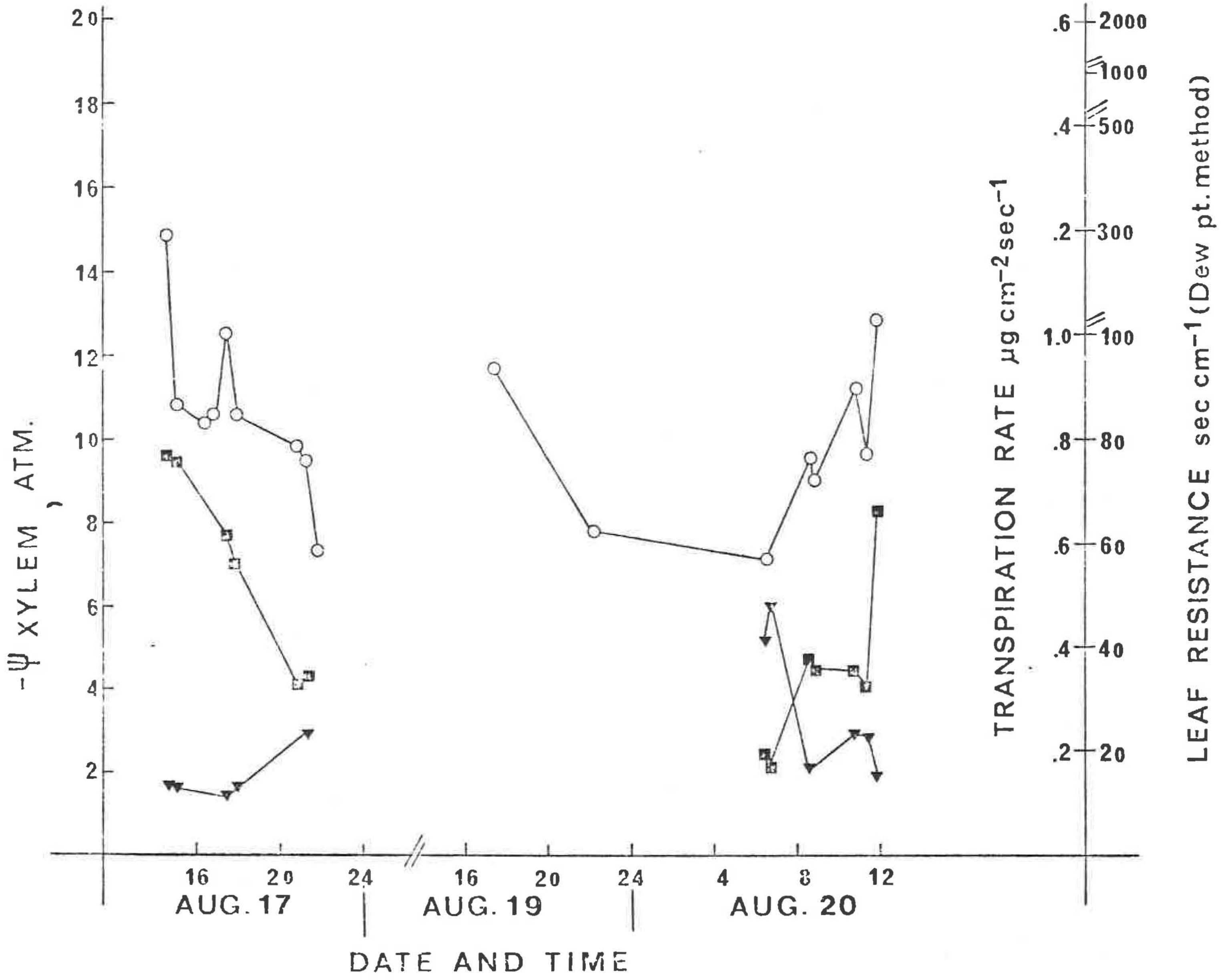

Figure A-6. Diurnal courses of ψ_{xylem} ○ , transpiration ■ , and leaf resistance ▼ of *Pinus banksiana* at midslope on the study hill at Richardson Fire Tower on 17-20 August, 1976.

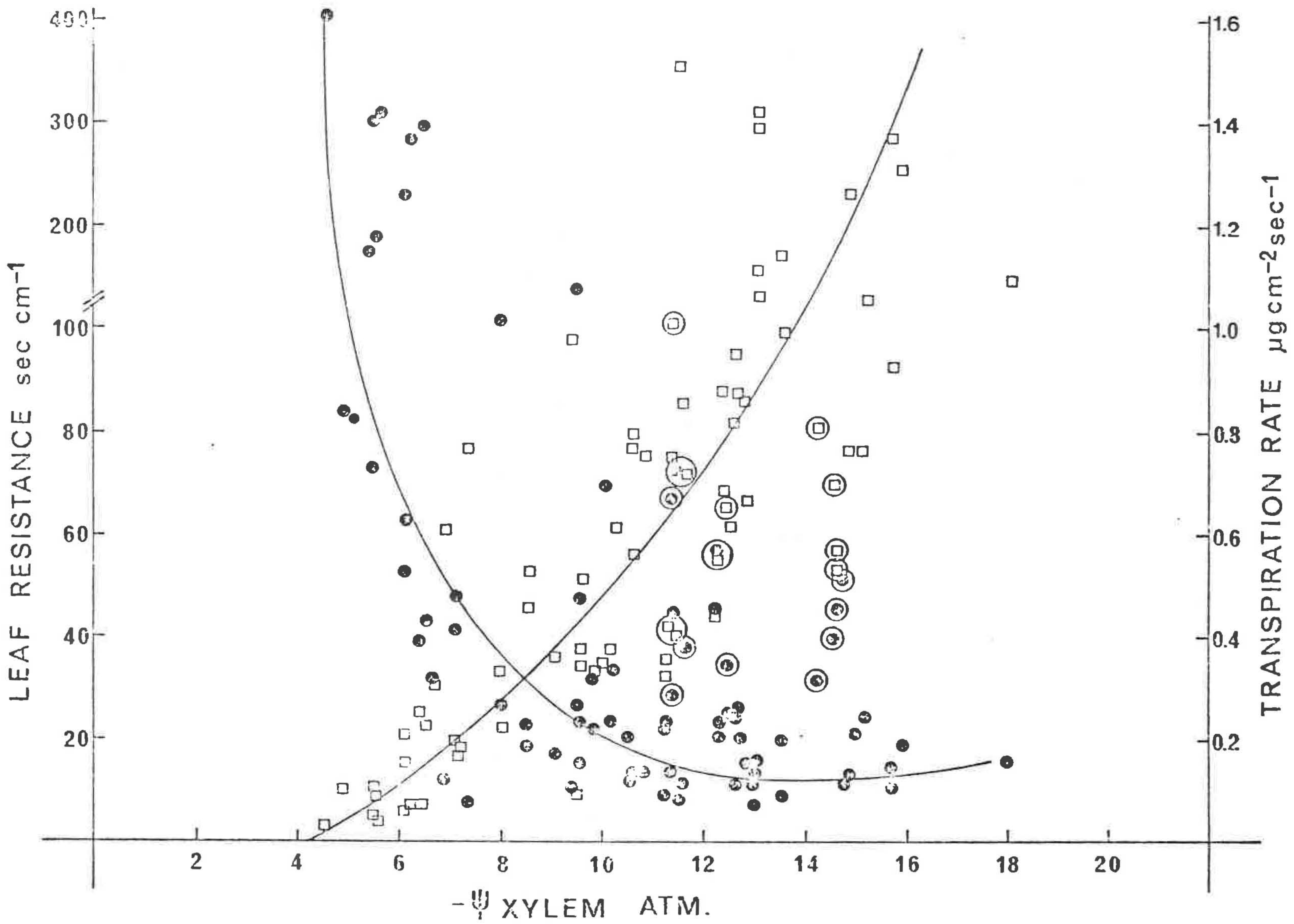

Figure A-7. Transpiration □ and leaf resistance ● of *Pinus banksiana* vs. ψ_{xylem} for the periods 29-30 June, 20-23 July, and 17-20 August, 1976, at Richardson Fire Twoer. Circled values represent stomatal closure at high vapour pressure deficits and are excluded from the curves.

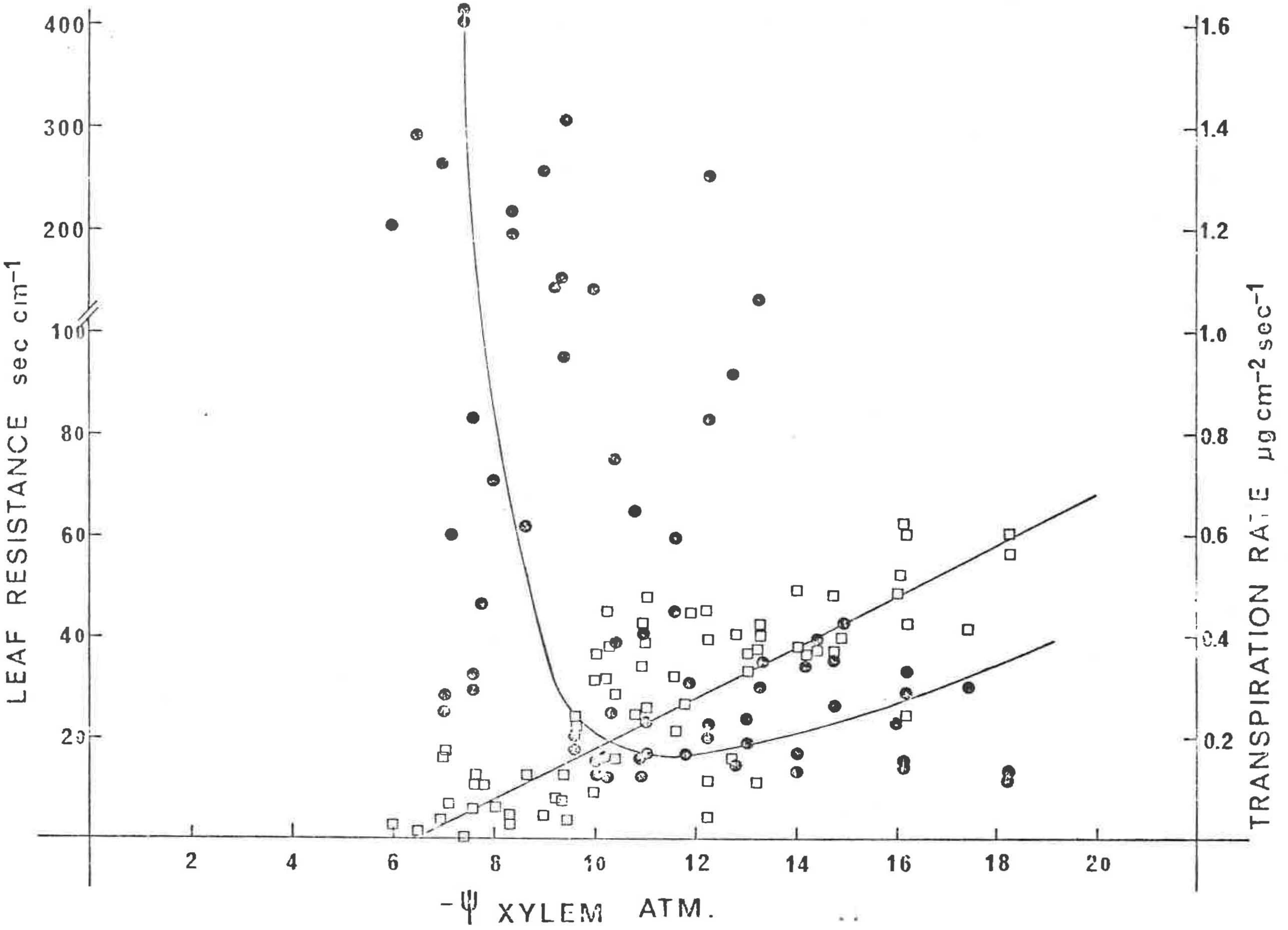

Figure A-8. Transpiration □ and leaf resistance ◉ of *Pinus banksiana* vs. ψ_{xylem} for the periods 9-10 May, 2-3 June, and 24-27 September, 1976, at Richardson Fire Tower.

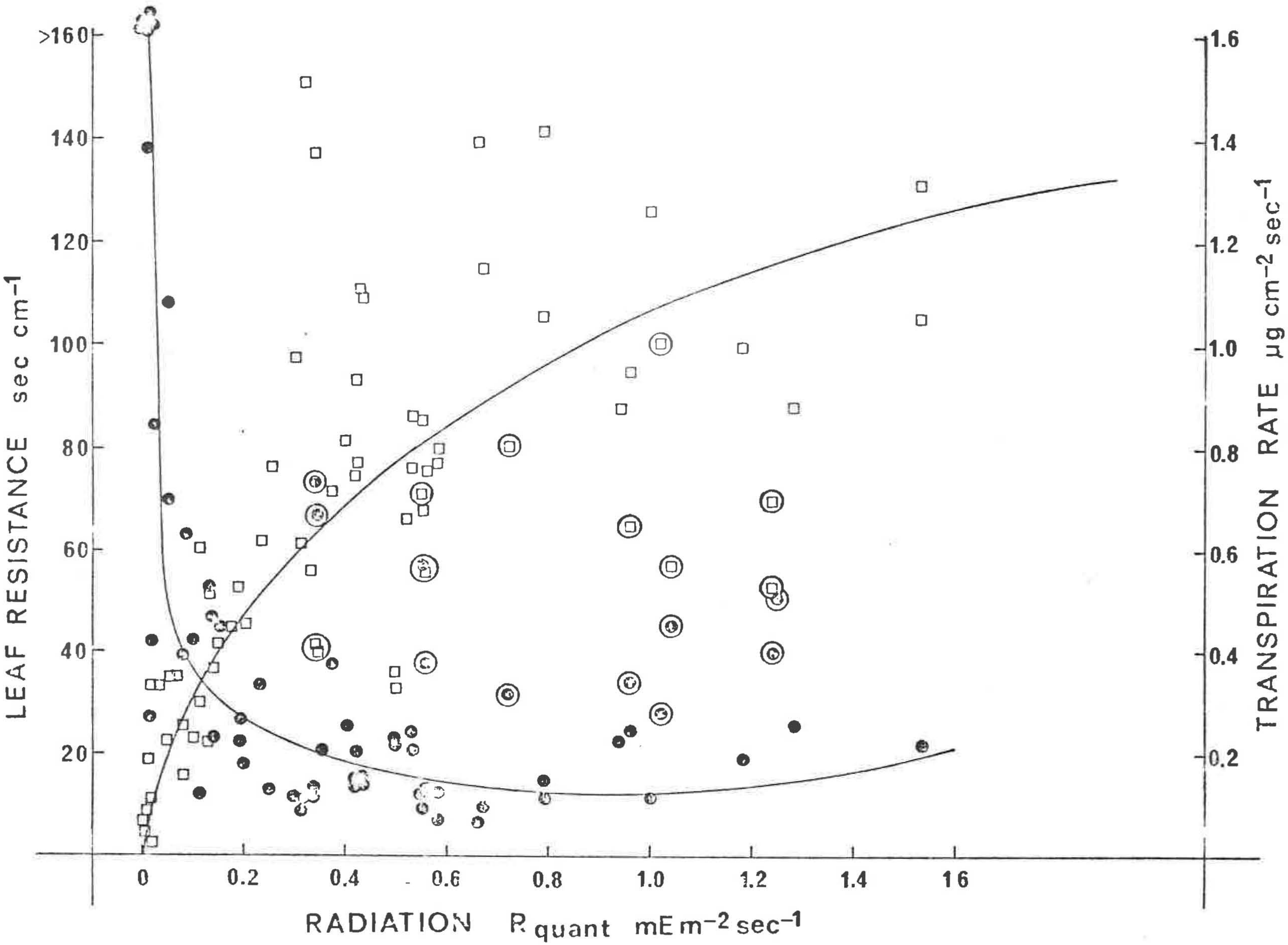

Figure A-9. Transpiration □ and leaf resistance ◉ of *Pinus banksiana* vs. radiation for the periods 29-30 June, 20-23 July, and 17-20 August, 1976, at Richardson Fire Tower. Circled values represent stomatal closure at high vapour pressure deficits and are excluded from the curves.

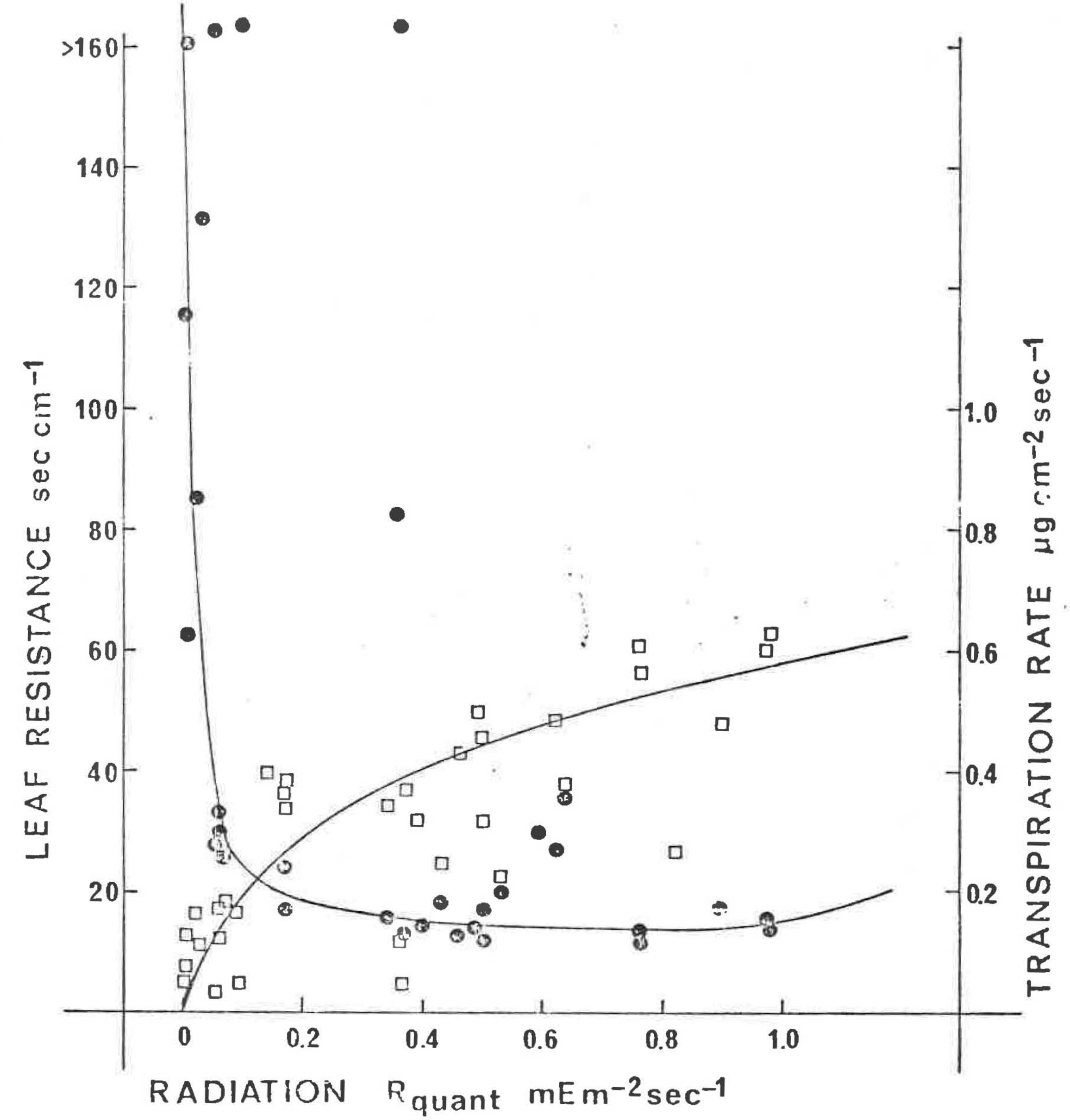

Figure A-10. Transpiration □ and leaf resistance ● of *Pinus banksiana* vs. radiation for the period 24-27 September, 1976, at Richardson Fire Tower.

6. HEAT PULSE VELOCITY INVESTIGATIONS IN JACK PINE

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6.1 INTRODUCTION

The purpose of these investigations was to gain some background experience in applying heat pulse velocity (HPV) techniques to measuring transpiration in *Pinus banksiana*. I wanted some idea of the magnitude of HPV readings within Jack pine and some estimate of the radial variability with depth in individual trees and between trees. I also wanted a measure of the sapwood area as indicated by moisture content change at the sapwood-heartwood interface.

A second purpose was to obtain a few individual tree HPV-transpiration estimates for comparison with simultaneous stomatal measurements, and areal HPV-transpiration estimates for comparison with simultaneous evapotranspiration modelling, energy and mass budgeting studies by other investigators in the area.

6.2 METHODS

Three individual trees numbered 1, 2 and 3 were instrumented with five sets of heat pulse sensors at radial depths from the cambium of 5, 10, 15, 20 and 25 mm. Ten other trees, one tree in each of two groups of 5 trees were instrumented with one set of HPV sensors as each of the radial depths indicated above. Increment borings were obtained from each of the trees - a total of 13 cores. These cores were sealed in soda straws for transportation back to the Edmonton laboratory for moisture content determination. The trees instrumented were in plots 28, 46-48 and 51-53, surrounding the middle met. power. (see page 131)

Heat pulse velocity readings were taken at approximately hourly intervals from 0700-2200 hr, 25 Sept. 1976. A few readings were taken between 0800-1200 hr, 26 Sept. All sensors were removed from the trees between 1300-1400 hr, 26 Sept.

The cores were sectioned into 1 cm increments and dry weight moisture content of each core segment determined by oven drying at 75°C for 48 hr.

6.3 RESULTS

6.3.1 Moisture Contents

The overall level of xylem moisture content was low compared to that I have encountered in lodgepole pine. Maximum moisture content, 67%, occurred in the first 1 cm of sapwood and declined to 23% between the 3rd and 4th cm depth, indicating heartwood thereafter. Phloem moisture content was much higher at 156%.

[illegible]

6.3.2 Sapwood Area

The depth to heartwood averaged 2.3 cm for the 13 trees studied (range 1.1 to 4.0 cm). Weighting areas for each heat pulse sensor were calculated as if this thickness were 2.5 cm. These areas are given in Table 1.

6.3.3 Transpiration

Transpiration, as defined here, is given by equation (1).

$$T = 1.6 \sum_{n=5}^{n=25} (HPV_n \times Au) \quad cm^3/hr \qquad (1)$$

This value will not necessarily correlate directly with a given hour's evaporation at the leaves because of stem storage buffering. However, the values averaged over 24 hr should be close. All data is given in the appendix along with hourly and periodic values for individual tree and areal transpiration expressed in mm. Areal transpiration was calculated with equation (2).

$$\text{Areal } T = 6100\ T/10{,}000 \quad mm \qquad (2)$$

where: T is expressed in l/hr

6100 = number of trees/ha

6.4 DISCUSSION

This small sample indicates that the radial and between tree variation in heat pulse velocities in Jack pine are similar to those encountered in other pinus species. It appears that no new techniques would need to be developed to utilize the heat pulse method for estimating transpiration in this species. However, the 1.6 constant in equation (1) above was empirically derived from *P. radiata*. This constant is related to the areas sensed by a particular heat pulse probe geometry and the relative thermal diffusivity of the xylem wood in the axial and tangential directions. Its use here ought to be justified in light of the low wood moisture content before the calculated transpiration values are taken at face value.

caps

Table 1. Area weights for calculating xylem sap flow from heat pulse velocity sensors at 5, 10, 15, 20 and 25 mm depths.

	Area Weight, cm^2 for Depth					Basal
Tree(s)	5	10	15	20	25	Area
1	15.7	8.5	6.9	5.3	3.8	43.0 cm^2
2	17.3	9.6	8.0	6.4	4.9	51.5
3	15.7	8.5	6.9	5.3	3.8	43.0
4-8	22.2	12.8	11.3	9.7	8.1	81.7
9-13	14.9	7.9	6.4	4.8	3.2	39.6

6.5 APPENDIX

Table A-1. Heat pulse value (HPV) and estimated transpiration rates, 25-26 September, 1976.

		HPV along radius from outer bark (mm) PSC = 1.6					Transpiration	
Day/ Hour	Trees	5	10	15 (cm/hr)	20	25	Tree cc/hr	Area mm/hr
25/07	1	3.3	3.5	3.6	4.1	2.7	221	.14
	2	4.1	3.4	4.2	3.1	2.1	268	.16
	3	1.5	2.6	3.1	3.5	2.7	153	.09
07-08	All						214	.13
25/08	1	3.4	3.9	1.8	3.1	2.5	200	.12
	2	1.8	3.4	2.2	3.1	2.4	181	.11
	3	1.8	2.8	0.8	2.1	2.7	126	.08
08-09	All						169	.10
25/10	1	3.0	2.2	4.3	2.3	2.6	188	.11
	2	3.0	2.1	2.7	2.2	2.7	194	.12
	3	2.6	2.7	3.0	1.7	2.6	165	.10
10-11	All						182	.11
25/11	1	3.4	2.9	4.4	4.4	2.4	225	.14
	2	3.5	5.0	3.2	4.4	3.0	283	.17
	3	2.7	3.9	1.1	3.1	3.7	182	.11
11-12	All						230	.14
25/14	1	8.3	6.5	7.3	6.6	4.0	458	.28
	2	6.2	8.0	5.6	6.0	4.4	462	.28
	3	4.5	5.4	4.4	3.4	3.7	286	.17
	4-8	3.5	5.2	5.1	3.1	3.2 E	413	.25
	9-13	3.6 E	7.9	4.6	4.0	4.4	262	.16
14-15	All						376	.23
25/16	1	10.1	8.4	12.6	7.5	3.8	594	.36
	2	9.1	9.9	7.7	9.3	8.8	667	.41
	3	6.2	8.2	6.2 E	4.2	4.7	400	.24
	4-8	5.5	4.7	7.6	4.7	5.9	578	.35
	9-13	3.8	12.0	5.7	4.2	5.6	362	.22
16-17	All						520	.32
25/17	1	12.6	8.2	10.7	8.6	5.1	650	.40
	2	10.2	12.4	9.0	9.6	6.1	734	.45
	3	6.1	8.5	5.9	5.8	5.6	417	.25
	4-8	5.4	5.2	5.6	5.0	6.0	555	.34
	9-13	5.9	14.2	7.0	5.5	6.2	466	.28

Table A-1 (continued).

17-18	All						564	.34
25/18	1	10.7	9.5	6.9	7.2	4.9	565	.34
	2	8.6	10.3	7.1	7.8	6.3	616	.38
	3	5.8	7.2	4.5	4.3	4.5	357	.22
	4-8	4.4	4.0	3.3	3.4	4.4	408	.25
	9-13	4.5	13.6	7.0	5.0	4.2	411	.25
18-19	All						471	.29
25/19	1	3.4	3.1	4.2	2.3	2.7	210	.13
	2	4.3	4.9	3.3	4.0	3.1	302	.18
	3	3.8	4.7	3.7	3.4	3.5	250	.15
	4-8	2.4	3.3	3.6	3.0	3.6	311	.19
	9-13	2.9	3.7	3.0	3.1	3.3	187	.11
19-20	All						252	.15
25/21	1	2.2	1.1	2.6	2.1	2.5	132	.08
	2	2.5	3.5	2.4	2.8	2.5	202	.12
21-22	All						167	.10

Arithmetic model: $T = 1.6 \sum_{n=5}^{n=25} (HPVn \times Au)$ cm^3/hr

Area cm^2

Trees	5	10	15	20	25	Σ	Dia	TBA
1	15.7	8.5	6.9	5.3	3.8	40.2	7.4	43.0
2	17.3	9.6	8.0	6.4	4.9	46.2	8.1	51.5
3	15.7	8.5	6.9	5.3	3.8	40.2	7.4	43.0
4-8	22.2	12.8	11.3	9.7	8.1	64.1	10.2	81.7
9-13	14.9	7.9	6.4	4.8	3.2	37.2	7.1	39.6

Day/ Hour	Trees	5	10	15	20	25		cc/hr		mm/hr	
26/08	1	2.3	1.9	2.7	0.9	2.0	cm/hr	133	cc/hr	.08	mm/hr
	2	2.5	2.9	1.9	2.2	1.7		174		.11	
	3	2.1	0.0	1.8	1.6	0.0		86		.05	
	4-8	1.3	1.4 E	1.4	0.0	2.4		131		.08	
	9-13	2.2	1.0	2.0	0.0	0.0		86		.05	
08-08	All							122		.07	
26/10	1	5.3	6.1	5.7	5.3	3.7		346		.21	
	2	4.5	5.4	4.1	3.0	2.9		313		.19	
	3	2.1	4.2	3.8	2.1	3.2		189		.12	
	4-8	1.9	2.1	2.0	1.9	2.6		210		.13	
	9-13	2.6	5.2	3.8	3.5	2.7		207		.13	

Table A-1 (continued).

10-11	All						253	.15
26/11	1	7.4	6.0	5.2	6.0	4.2	401	.24
	2	6.7	9.3	6.8	6.4	5.0	520	.32
	3	4.9	6.8	4.9	4.4	4.3	333	.20
	4-8	5.4	4.7	7.0	3.4	4.8	530	.32
	9-13	2.8	7.8	5.0	5.0	4.5	278	.17
11-12	All						412	.25

End of HPV Data

Summary

Day	Hour of Data		T/Tr/hr	mm/hr	Period Hours	mm/ period		
25	0700	0800	214	.13	1	.13		
	0800	0900	169	.10	1	.10		
	1000	1100	182	.11	2	.22		
	1100	1200	230	.14	1	.14		
	1400	1500	376	.23	3	.69		
	1600	1700	520	.32	1	.32		
	1700	1800	564	.34	1	.34		
	1800	1900	252	.15	1	.15		
	2100	2200	167	.10	2	.20	2.29 mm	0700-2200
26	0800	0900	122	.07	1	.07		
	1000	1100	253	.15	2	.30		
	1100	1200	412	.25	1	.25	.67 mm	0800-1200

7. TREE GEOMETRY AND OPTICAL PROPERTIES OF LEAVES

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7.1 INTRODUCTION

A number of studies concerning tree spacing, canopy geometry, optical properties of needles, and light quality within the forest stand have been carried out. These are gathered together in one section so as to be more accessible to the reader.

These measurements have been taken to provide specific information (inputs) for the water and energy balance models. The radiation penetration and interception model requires information on the mean distance between trees and its variability, on tree size and canopy geometry, and on the optical properties of the needle clumps (especially with respect to short wave and near infrared radiation). The transpiration model requires needle element distribution and surface area.

7.2 RESUMÉ OF CURRENT KNOWLEDGE

Reports of studies of various species were examined to determine the best method of characterizing the canopy geometry (e.g., Norman and Jarvis 1974, Gary 1976). None of these were thought to be entirely applicable to the Richardson site. For example: the study by Norman and Jarvis (1974) was made on a plantation with uniformly spaced trees and assumptions were made about branch symmetry which were not appropriate

(Gary 1976). These studies were used as the basis for the method developed.

Tests to characterize the spacing of forest trees have been carried out in many forests (e.g., Clark and Evans 1954) but the results from elsewhere are not directly applicable to the Richardson site.

Ross (1975) provides a good general summary of the optical properties of vegetation. Jarvis et al. (1976) has gathered together the relevant information for coniferous forests. Measurements have been made on *Pinus resinosa, P. sylvestris* and *P. ponderosa,* but no previous work has been done for *P. banksiana.* It was expected, from the work cited above, that the transmissivity and reflectivity of needles would be much greater in the near infrared (>700 nm) than in the visible range of the spectrum.

As a result of the studies of optical properties of leaves cited in the preceeding paragraph it is to be expected that the spectral intensity within a forest would be different than that just above the stand. There are numerous studies proving that this is the case (e.g., Feyman 1968, Federer and Tanner 1966, Yocum et al. 1964). These studies all show a sharp increase in radiation inthe near infrared region (>700 nm) relative to the shorter wavelengths. This altering of the spectral composition can effect energy budget calculations, as well as have considerable effect upon plant development (Mohr 1972).

7.3 METHODS AND MATERIALS

7.3.1 Tree Geometry

A system was devised (based upon the references cited) to measure the geometry of one or more trees as accurately as possible. ~~This~~ These data will be used to design a more extensive sampling method to characterize the stand. The method used is as follows:

i. The tree is considered to be made up of elements which are one of the following:

- a) vegetated portion of a branch including all age classes of needles
- b) live unvegetated portion of a branch
- c) dead branch
- d) a cone
- e) or the main stem.

The geometric measurements were made to describe the positioning of these elements in space.

ii. A main stem (trunk) section, with attached branches, approximately 1 m in length was removed from the top of the tree. True south was marked on the section just prior to removal. The tree was subsequently harvested piece by piece from the top down.

iii. The stem section (with branches) was fixed upright on a table on which lines were drawn so that the tree stood in the center of a circle divided into 360° (2°, intervals). See Fig.1A for a diagram of the tree and table. The stem section was oriented so that north was at 0°. This placed the stem section as close as possible to its position as it had been on the tree.

iv. The element azimuth (true north = 0°) was determined by holding a compass mounted on a 360° protractor above the element center and orienting it such that zero and the needle lined up. (See Fig. 1A)

v. The table azimuth (i.e., the direction of the element center from the main stem) was determined by dropping a plumb line to the table from the center of the element (Fig.1A &B). In the example (Fig. 1), the element has an azimuth of 315°and a table azimuth of 45°.

vi. The distance from the center of the element to the table was measured with the plumb line and the distance along the table to the stem was measured with a meter stick. These measurements (iv, v, vi) located the element in space with regard to north and south and the main stem.

vii. In addition to the above, the following measurements were made:

a) the angle of the element (0 to 360°) was determined with a weighted protractor positioned along side the element such that 0 was toward the point of attachement and the protractor was oriented in the same azimuth as the element. In Fig. 1B the angle was 100° (nearly straight up);

b) the element length and midpoint diameter were measured;

c) needle subsamples were taken for needle fresh weight, dry weight, and area by age class.

viii. Every element was placed in a labeled bag and brought back to the laboratory, dried to a constant weight at <u>ca.</u> 75°C and the dry weight determined.

7.3.2 Tree Spacing

The randomness (or nonrandomness) of tree spacing was tested using the method of Clark and Evans (1954). This was done in the same plots where radiation penetration studies were made (Section 2).

Two plots, 10 x 20 m, containing 188 trees were studied. Fifty trees, dbH > 1 cm, were selected at random. The distance from each of the selected trees to its nearest neighbor was measured. An index of randomness was determined by using:

$$R = 2\bar{r}\sqrt{p}$$

where p = the mean tree density
$\bar{r}$ = the mean nearest neighbor distance
R = the index of randomness where 1 is expected for random spacing.

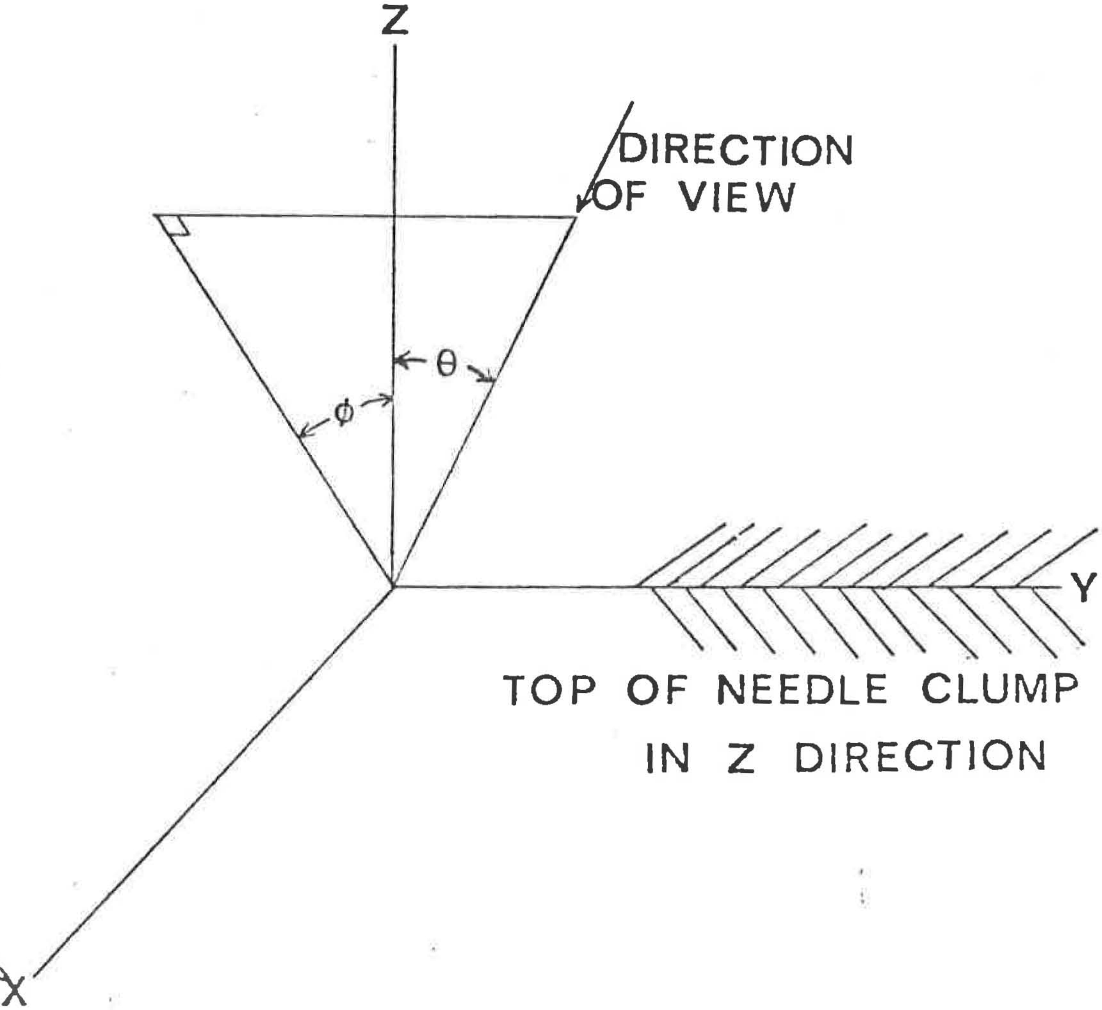
7.4.3 Projected Area of Needled Elements

Representative needled elements were mounted such that they were held at predetermined angles. They were then photographed against a graph paper background. Figure 2 illustrated the coordinate system used. A 35 mm camera, 450 mm focal length, was used to photograph the elements from a distance of ca. 3 m. The graph paper was 8 to 15 cm behind the element. It was assumed that at these distances parallax was not a problem. Projected needle area was then determined from 16 x 24 cm prints by two methods: a) manual planimetry, and b) by the use of a Spatial Data Systems Ltd. microdensitometer (Model 703-32). The latter equipment used by the courtesy of the Alberta Environment, Alta. Remote Sensing Center.

Total needle surface area was determined by the method of Thompson and Layton (1971).

7.4.4 Needle Transmissivity

Fresh Jack pine needles were tightly packed side by side between two plates of glass such that no visible gaps could be seen.



Binding / Margin

The spectral transmission of radiation (from a mixture of fluorescent and incandescent lamps) by this "sandwich" was determined between 400 and 1550 nm using an ISCO spectroradiometer. The transmission characteristics of the glass plates alone compared with the plates and needles to determine needle transmissivity.

[illegible]

7.4.5 Canopy Effect upon Radiation Spectral Intensity

The effect of the forest canopy upon radiation spectral intensity was determined by taking spectroradiometer readings (ISCO, Lincoln, Neb.) at the top of the Fire Tower hill and then walking down into the forest and repeating the measurements. Readings were taken within the forest near the top, midslope and at the bottom of the hill. The reported readings were taken on a bright, uniformly cloudy day so as to avoid direct sun.

7.4 RESULTS AND DISCUSSION

7.4.1 Tree Geometry

The data from the tree harvested as described earlier have not been fully analyzed. However, the vertical frequency distribution of needled branches and the frequency distribution of the table azimuth of needled branches are shown in Fig. 3. Gary (1976) found no departure from radial symmetry in a lodgepole pine stand in Wyoming. It is quite obvious that this is not the case with the Fire Tower hill Jack pine stand. The tree studied has a very asymmetric crown. This is likely due to the presence of the hill and the nearness of trees on the northeast. This data confirms what was already suspected and complicates the sampling to characterize the stand (i.e., not only will trees have to be sampled, but their relationship to other trees and the hill will have to be described).

The vertical distribution of needled branches (Fig. 3) does not seem to differ significantly from the lodgepole pine stand studied by Gary (1976).

Once the data are fully analyzed they will be used to design a more extensive procedure to characterize the stand. The effects of canopy asymmetry will be explored with the model.

7.4.2 Tree Spacing

The randomness index (R) for live and dead trees was R = 0.999 and for live trees only R = 1.044. In both cases there is clearly no departure from randomness of spacing in the plots sampled. The mean tree density in the same plots was 0.94 m^{-2}.

7.4.3 Projected Needle Area

Figure 4 shows a comparison of projected needled element areas determined by planimeter and by microdensitometer. There is considerable variability between the methods and these will need to be resolved in future work. For the present only the microdensitometer results are discussed.

The ratio of projected element area to needle surface area plotted as a function of the viewing coordinates is shown in Fig. 5. Confidence intervals are indicated for the points representing $\phi = 0$. It is clear that no confidence can be placed in the variation with ϕ but that we can clearly see the effect of θ.

7.4.4 Needle Transmissivity

Transmissivity data are shown in Fig. 6. The two sets of data shown are from entirely different needle samples. It is clear that transmissivity is very consistant. In the visible portion of the spectrum

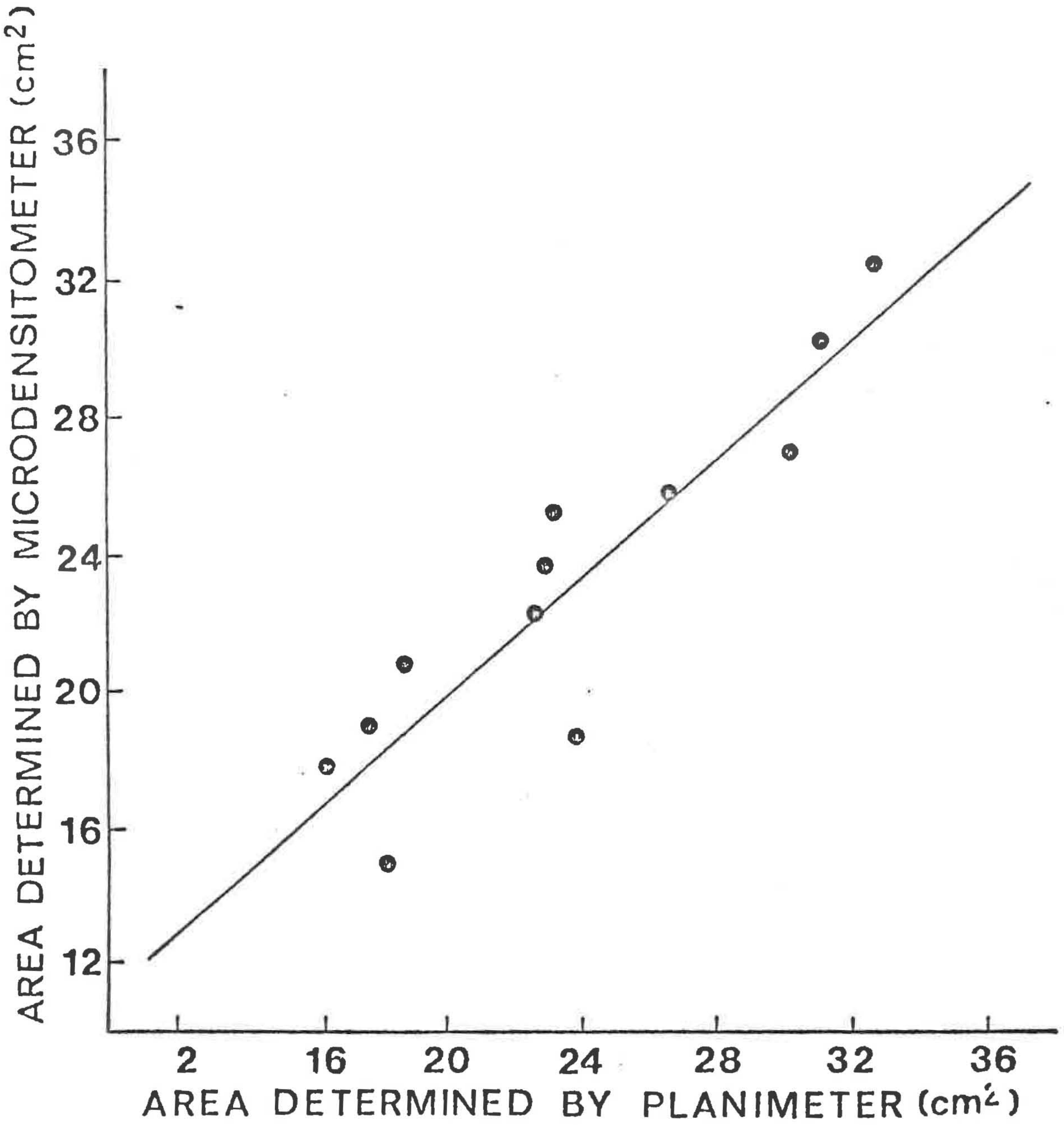


Fig. 4. A comparison of projected needle clump areas determined by two methods of photograph analysis.

Margin

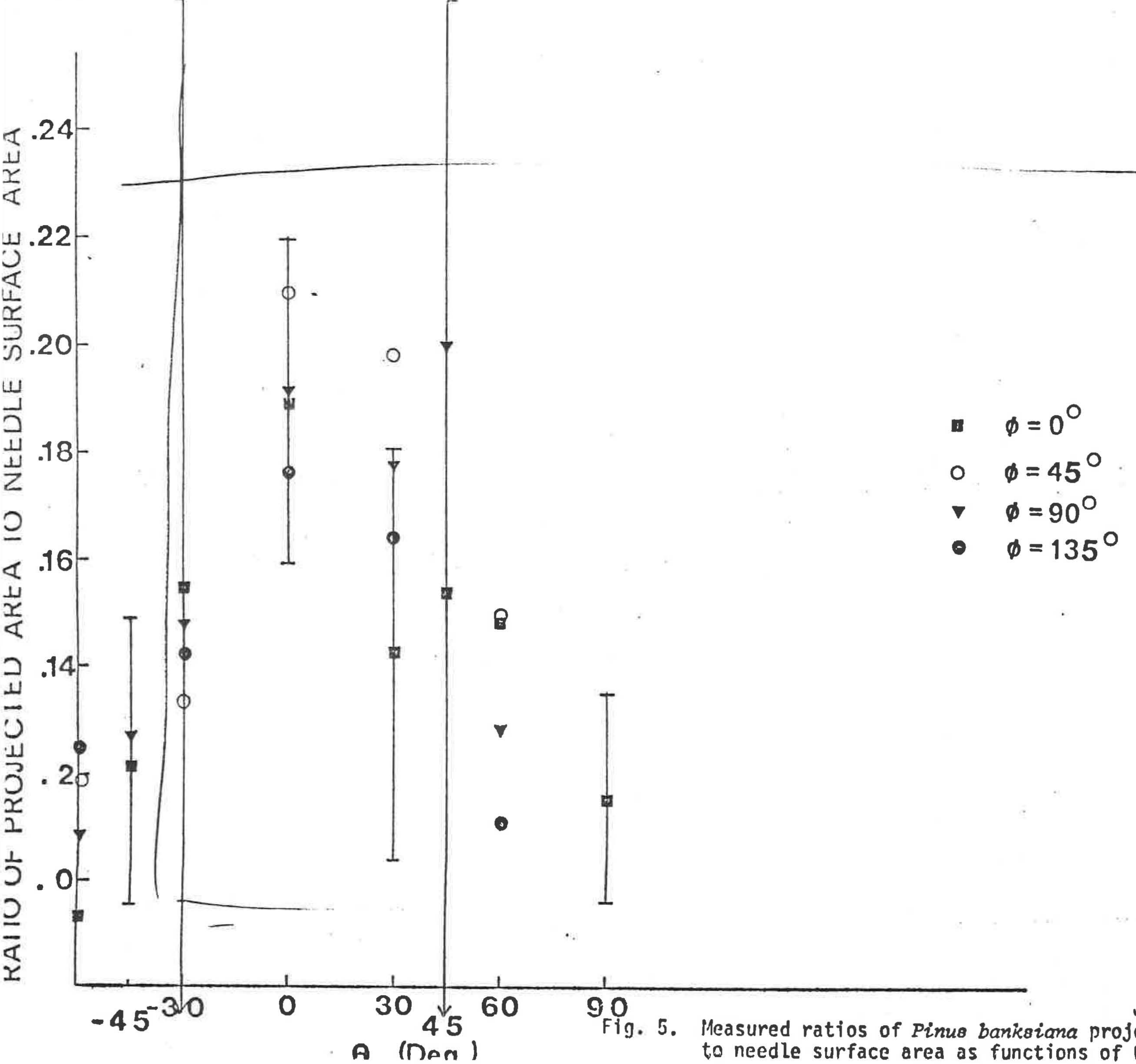


Fig. 5. Measured ratios of *Pinus banksiana* projected needle clump area to needle surface area as functions of θ and ∅. The bars indicat

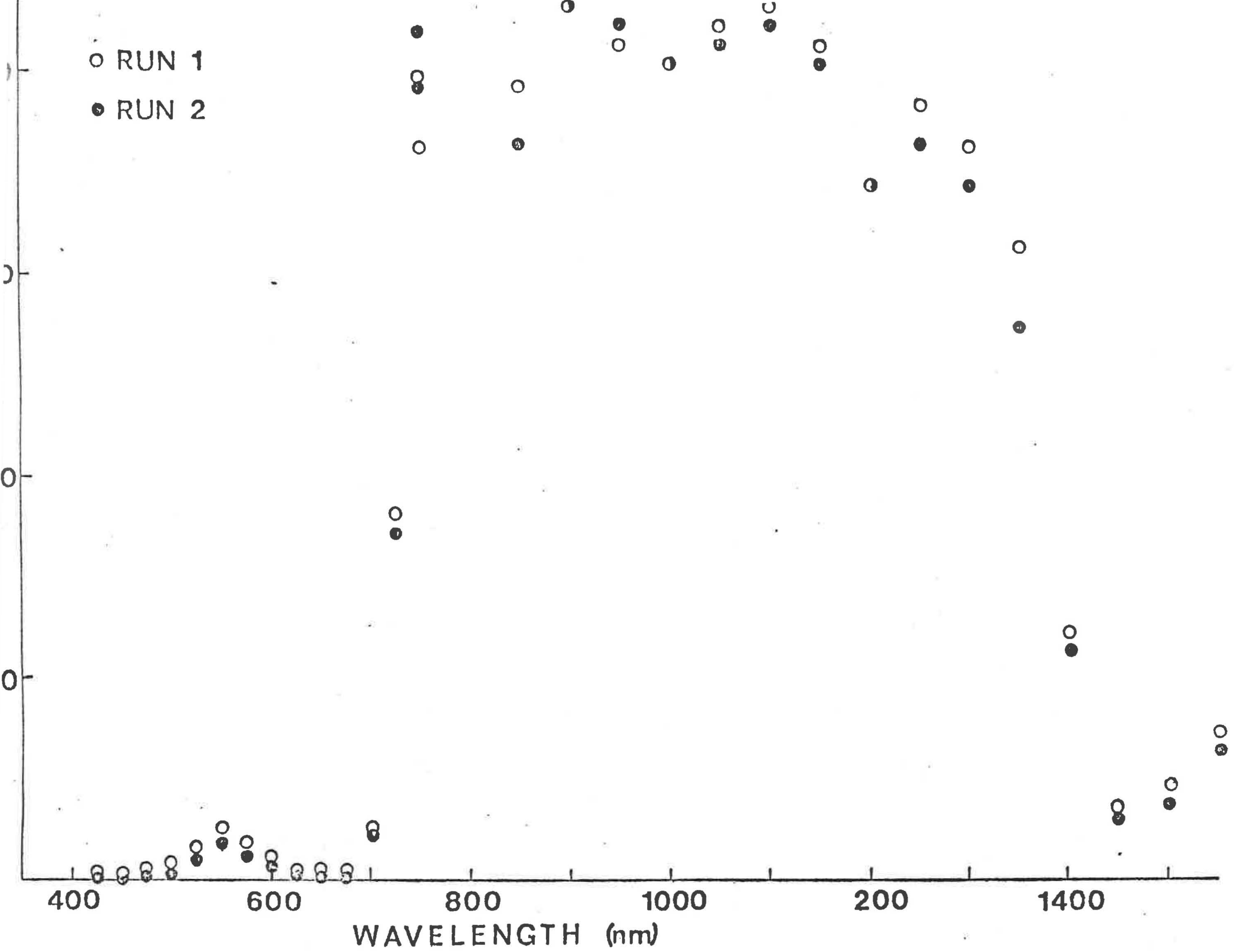


Fig. 6. Needle transmissivity of *Pinus banksiana* as a function of wavelength. Two runs with different needle batches are illustrated.

less than 0.01 of the radiation is transmitted, while transmissivity is as high as 0.4 in the infrared region. This is similar to the results obtained by other workers (e.g., Jarvis et al. 1976).

7.4.5 Canopy Effect upon Spectral Intensity

The results of the study of canopy effects upon light quality are shown in Fig. 7 and 8. Figure 7 shows the spectral intensity at 4 sites on the hill. The reduction in intensity is obvious. Figure 8 shows the spectral intensity at the top of the hill and at the midslope study site normalized against the intensity at 550 nm. There is obviously no effect of the canopy. Federer and Tanner (1966) reported a marked increase in the normalized values for wavelengths greater than 700 nm (ca. 1.8 at 740 nm). This indicates that the Jack pine canopy at Richardson Fire Tower is not sufficiently closed so as to influence the spectral quality of radiation and means the stand is not similar in this respect to the stand studied by Federer and Tanner (1966).

7.5 CONCLUSIONS

(a) The tree geometry study indicates that the trees can be expected to have very asymmetrical crowns. This may or may not be expected on different land forms but can be expected to influence canopy processes such as the transfer of heat and water (as well as CO_2 and SO_2) into and out of the stand.

(b) The observed randomness of tree spacing simplifies the modelling radiation penetration and interception.

(c) The needle transmissivity is much greater in the near infrared than in the visible. However, the spectral intensity of radiation is not altered probably because of the openness of the canopy. This may not be the case in other vegetation stands.

7.6 FUTURE STUDIES

(a) The tree geometry study will be simplified and extended to the stand. It will also be necessary to study the geometry of the vegetative canopy on the dike. This will be easier for shorter vegetation such as grasses, shrubs and forbs.

(b) The canopy spectral transmission was studied only once during the study period. It will be repeated to confirm the results at different times during the year.

(c) Parts have been ordered for a simple integrating sphere with which to measure the reflected spectrum from needles. This will complete the set of optical properties measurements.

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8. INVESTIGATIONS ON THE ROLE OF LICHENS IN THE JACK PINE-LICHEN FOREST ECOSYSTEM

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8.1 INTRODUCTION

In both mature and developmental plant communities on sand throughout North America, lichens frequently provide the major ground cover. In the Athabasca Oil Sands region, the extensive areas of sandy soils are covered with a Jack pine-lichen forest community. Any plant community allowed to develop naturally on the sands of the GCOS tailings dike may therefore be assumed to have a considerable lichen component during at least one phase. Previous work on lichens in communities developed on sandy soils has shown that they prevent the establishment of seedlings of trees and shrubs, and play an important role in water relations, acting as an effective barrier to water exchange between the underlying soil and the atmosphere (e.g., Rouse and Kershaw, 1971). Lichens may therefore be a major factor influencing the establishment and maintenance of stable plant communities on the sands of the tailings dike.

The major lichen component of the ground layer under Jack pine is *Cladina mitis*. Studies were thus begun on this species, both in the field at Richardson Fire Tower and in the laboratory at Edmonton, to determine its role in the water relations of the Jack pine-lichen forest. Other investigations involved studying the geometric structure of the lichen canopy and its physical properties, and the water relations of needle duff, which forms a considerable part of the ground layer under Jack pine on slopes as at Richardson Fire Tower.

The objective of these studies is to provide data to enable a mathematical model of the response of the ground layer in Jack pine forest to be constructed and tested against field data. This model will then be incorporated into the main model predicting plant responses to environmental variables for assessing potential management strategies.

8.2 METHODS

8.2.1 Water Relations

The first step in investigating the water relations of the ground layer was to determine the water potential (ψ) of the two major components involved, *Cladina mitis* and needle duff. This property determines the responses of the ground layer to changing microclimatic conditions. (For a definition of water potential refer to the section on Plant Physiology).

8.2.1.1 Determination of water potential

Saturated solutions of various solutes were made up in conical flasks, with excess solute added to the container, to provide known relative humidities (Winston and Bates 1961). Lichen thalli or dead needles were then suspended over the solutions on wire hooks inserted into the stoppers. The flasks were then submerged in a water bath in a controlled environment chamber maintained at 20°C and allowed to equilibrate. After equilibration, wet and oven-dry weights were obtained and percentage water contents calculated. Water content was then plotted against water potential.

how long?

The experiment was conducted with material saturated by soaking in distilled water for 24 hr and with material air dried in the laboratory for 3 days.

8.2.1.2 Evaporation from the ground layer

Studies were carried out in the field and the laboratory. Field studies consisted of integrated observations made during intensive runs involving collection of gravimetric samples at regular intervals for determination of water content and weighing small mesh pots (5 cm diameter) containing lichens at regular intervals to determine evaporation rates and secondarily, to check on water contents. These measurements were made at the intensive site at Richardson Fire Tower, where the following parameters of a lichen carpet were recorded: air temperature at 50 mm, at the lichen surface, and at depths of 7, 15, and 20 mm in the lichen carpet; soil temperature at the soil/lichen interface; and relative humidity at 50 mm above the lichen surface. Temperatures were measured by copper/Constantan thermocouples and relative humidity by Thunder Scientific humidity sensor. Si~~gnals~~ Sensors signals ~~arising~~ from these sensors were fed into the Fluke datalogger system.

During intensive runs, material for the mesh pots and gravimetric samples was obtained from the lichen carpet adjacent to the instrumented site, with the mesh pot being placed as close as possible to ensure that the instrumented carpet and the mesh pots experienced the same microclimate. Weighing of the mesh pots were weighed ~~was accomplishe~~d on a Torsion balance set up a short distance away.

Investigations in the laboratory involved the construction and use of a wind tunnel. This was 200 x 35 x 35 cm, fitted with a 40 x 30 cm observation window in the top, access hatch in the side and aperture for the lichen or needle duff core to rest on a Mettler top pan balance in the base. Wind speed through the tunnel was controlled by adjusting the voltage to the fan, and air flow was smoothed by use of tubular baffles 25 x 4 cm in the anterior section of the tunnel. Flow at all wind speeds was checked by suspending cotton thread at various heights in the tunnel and found to be laminar except directly above the lichen carpet where it would be expected to be turbulent. Wind speed was checked by inserting a Hastings hot-wire anemometer probe up through the lichen carpet via the aperture in the base of the wind tunnel. Radiation load could be varied by shielding the plexiglass window and by placing floodlights at various heights above it. The floor of the tunnel and the core (14.75 cm diameter) were covered with lichen carpet or needle duff collected from Richardson Fire Tower. The experimental apparatus is illustrated diagrammatically in Fig. 1.

The tunnel was instrumented for air and lichen temperatures and relative humidity, the former being recorded by copper/Constantan thermocouples leading to an ice bath and an Esterline Angus D2020 datalogger. Relative humidity was measured by a Thunder Scientific humidity sensor reading on a voltmeter.

At the start of a drying run, the plant material in the wind tunnel was saturated with excess distilled water and allowed to drain. The central core of plant material was weighed at chosen intervals after slowing down the fan. Drying runs were carried out at several wind speeds to determine the influence of wind on boundary layer resistance. Runs were also carried out in near darkness and with a radiation load of 3.2 watts m^2 ~~min^{-1}~~ to assess the influence of radiation on drying rates.

From the following formula, it is possible to calculate total resistance of the plant material to water loss:

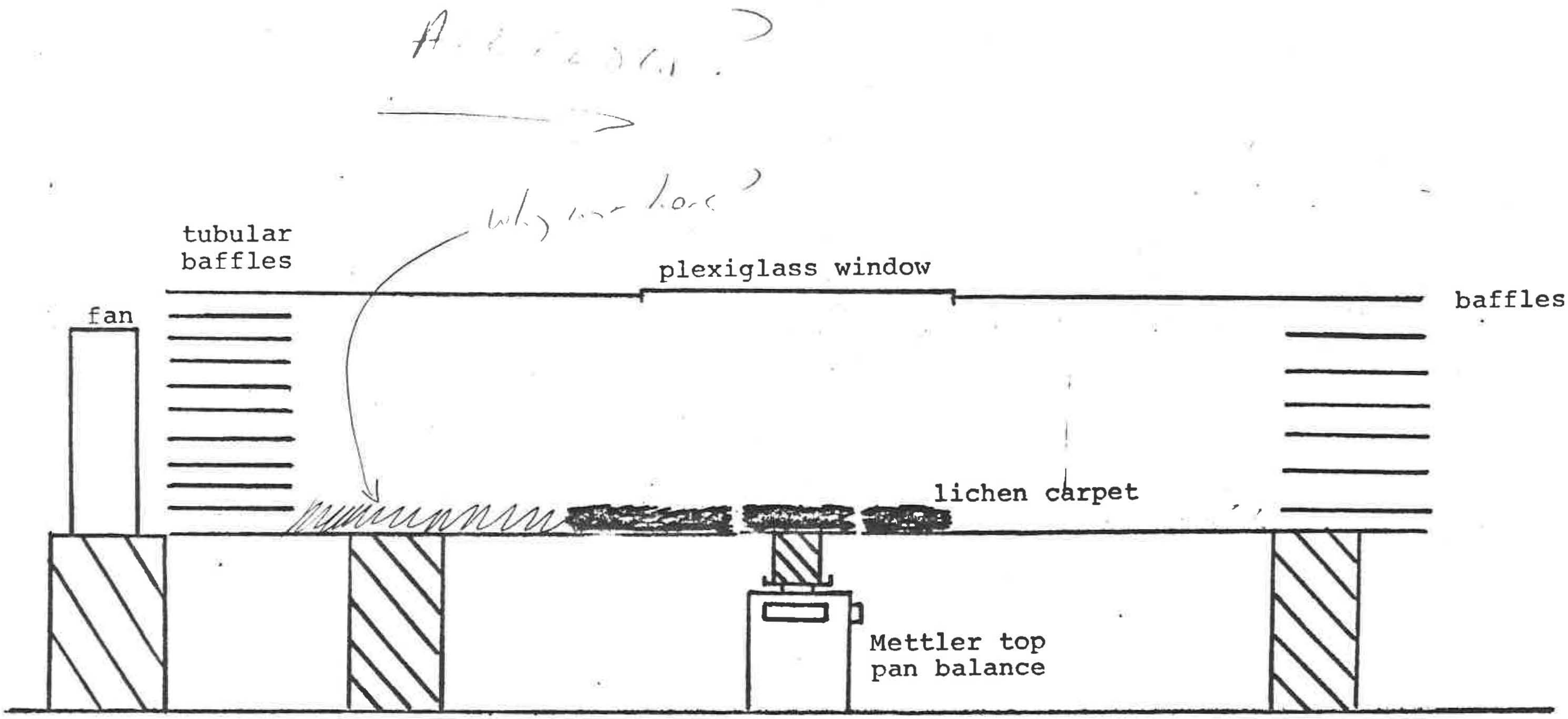

Figure 1. Diagram of wind tunnel aparatus used to determine resistance to water loss.

$$r_t + 1.138\, r_b = \frac{2\alpha(e_T - e_A)}{E\,(T_T^A + T_A^A)}$$

where r_t = thallus resistance min cm^{-1}

r_b = boundary layer resistance min cm^{-1}

α = $2.17 + 10^{-4}$

e_T = thallus vapour pressure

e_A = air vapour pressure

E = evaporation rate gm cm^2 min^{-1}

T_T^A = thallus temperature °A

T_A^A = air temperature °A

Thallus vapour pressure (e_T) is calculated from the formula

$$e_T = e_o\,(T_T)\ \mathrm{Exp}\left(\frac{\psi_T}{4.62\,T_T^A}\right)$$

where $e_o(T_T)$ = saturated vapour pressure at thallus temperature

ψ_T = thallus water potential

T_T^A = thallus temperature °A

[illegible]

8.3.1.3 Water uptake by the ground layer

As with evaporation, this feature of the ground layer was studied both in the field and laboratory. This section of the research consisted of two subtopics: uptake by the ground layer overnight as part of the diurnal drying/wetting cycle typical of lichens in such habitats and precipitation retention and infiltration.

Uptake of water in the field by lichens during the diurnal uptake/loss cycle was studied by weighing the mesh pots used in the intensive runs. Weighing these pots gave some indication of the amount of water absorbed from the air during the night and early morning by lichens.

The main part of the work connected with water uptake by the ground layer has been its role in precipitation retention and infiltration, i.e., how much rainfall is retained in the ground layer and how much penetrates through to the underlying soil. Examination of the literature on rainfall simulators showed that such apparatus has been designed primarily for field or large scale applications of rain and that no suitable apparatus had been designed for small-scale laboratory use. The apparatus used to simulate rainfall in laboratory experiments is shown diagramatically in Fig. 2. A watering can rose was used to produce raindrops of uniform size; the fall of these was randomized by use of an oscillator fan blowing at 2 m sec^{-1}. An aluminium tray with a fine mesh base was used to hold lichen carpet or needle duff with a plastic funnel 15 cm diameter placed centrally underneath. This funnel was supported on a sealed container. The rate of rainfall was obtained by running the apparatus without any plant material in the mesh tray. Two rates were used, 2.2 mm hr^{-1} and 20 mm hr^{-1}, to simulate light and moderately heavy showers. Plant material was air dried and weighed before each run, [illegible] weighed wet after each shower and the amount of infiltrate collected in the sealed container measured in a measuring cylinder. From the area of funnel and volume of infiltrate it is possible to calculate the amount of infiltrate in mm rainfall equivalent. [illegible] From the duration and rate of showers it is possible to calculate total rainfall; thus the amount of rainfall intercepted and retained by the ground layer can be obtained.

Raindrop size was checked by the flour pan method (Steinhardt and Hillel, 1966) and was found to be similar to natural raindrops, the majority being 2.5 mm diameter, with a range from 1.0-4.0 mm diameter. Terminal velocity was not determined, being considered relatively unimportant.

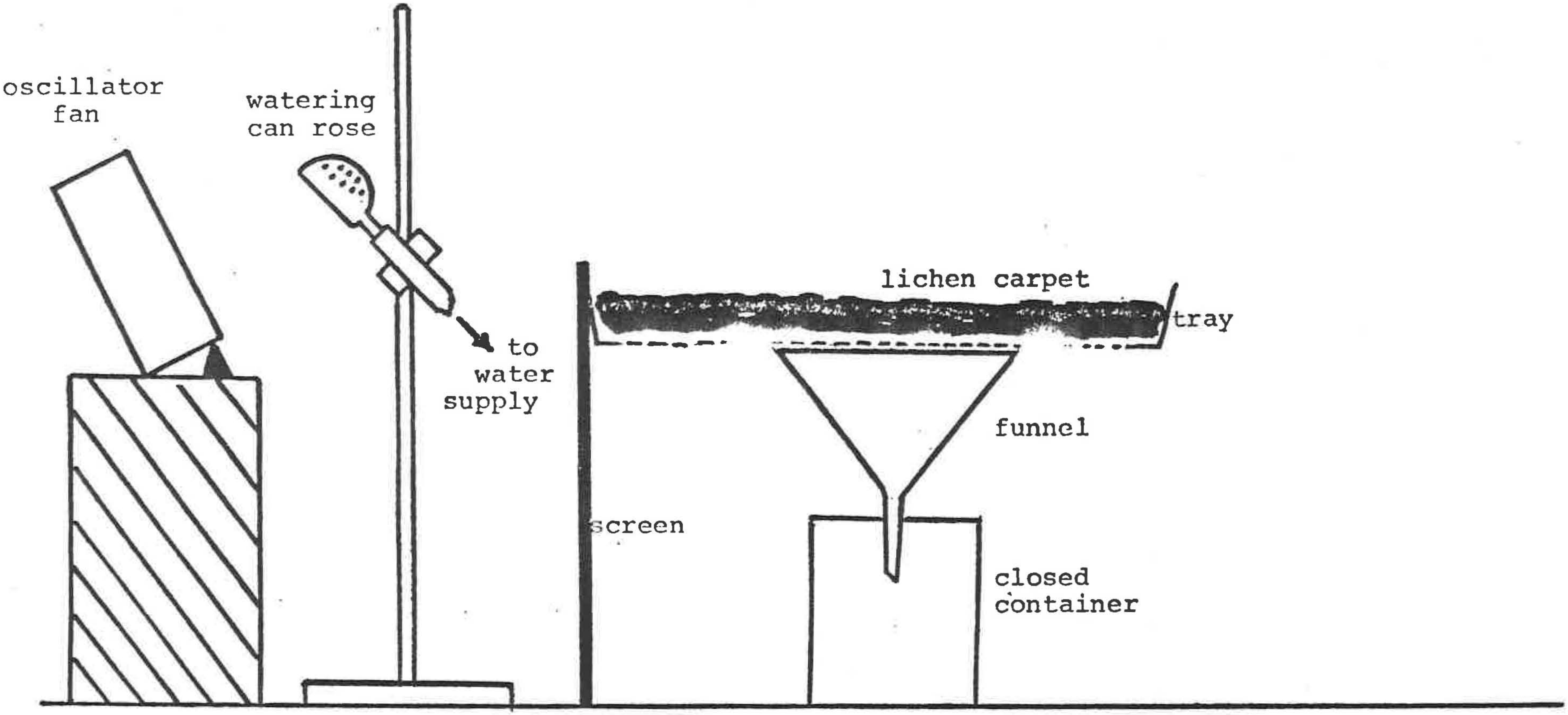

Figure 2. Rainfall interception apparatus.

Gravimetric samples of each type of ground layer were obtained, with soil samples from the underlying soil surface and soil at 10 cm depth, at Richardson Fire Tower, to show that the ground layer acts as a barrier to rainfall penetration through to the soil. Care was taken to ensure that all samples were collected from sites beneath the tree canopy.

English!

8.2.2 Structure of the Lichen Canopy and its Properties

From an understanding of aspects of the physiology of the lichen carpet it is essential to have data on its structure. Experiments were designed to elucidate the structure of *Cladina mitis*, especially the distribution of biomass, and certain properties, such as light penetration and emissivity.

what is "this"

8.2.2.1 Geometrical structure of the carpet

This was studied by selecting representative podetia and measuring the following parameters: total height; total dry weight; number of internodes; length, total surface area, diameter and dry weight of each internode. Measurements were made on wet thalli under a binocular microscope and weighings on oven-dried thalli.

un-required

8.2.2.2 Penetration of PAR

Experiments were carried out to determine whether light penetrates through the lichen carpet*. Small quantities of carpet 10 x 10 cm were

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* A technique has been described by Kershaw and Harris for measuring the light profile in a lichen canopy (1971) but this has a number of defects. The technique used here was somewhat more simplified. Several runs were carried out on different sections of lichen carpet, including those appearing to be very compact and those appearing to be very loose.

[illegible] ?

placed in a container also 10 x 10 cm with an 8 x 8 cm square cut out at the base. A Lambda quantum sensor was placed under this and PAR (photosynthetically active radiation) recorded at different depths by clipping away progressively a small tunnel upwards through the lichen carpet and measuring PAR at various depths by raising the sensor through this tunnel. This procedure was repeated with fresh lichen carpet under diffuse light and with light beams at 90°, 72°, 60° and 45° to the horizontal aimed at the sensor within the carpet. Percentage PAR received was plotted against depth within the lichen canopy.

8.2.3 Radiatvie Properties

8.2.3.1 Emissivity

This is the ratio of radiation emitted by a surface at a given temperature to the blackbody radiation at the same temperature. Integrating over all wavelengths it is defined as:

$$e = \frac{(T_r^4 - T_R^4)}{(T_s^4 - T_R^4)}$$

where

T_R = radiative T of sky (°A)

T_r = apparent surface T (°A)

T_s = true surface T (°A)

The apparatus used to determine the emissivity of a *Cladina mitis* carpet is shown diagramatically in Fig. 3. Material was placed in a container covered by a copper plate painted matt black on the lower surface and with copper heating coils soldered onto the other. A hole (5 mm diameter) was drilled through the center of the plate and a further hole 1 mm diameter drilled adjacent so that a thermocouple could be attached to the black surface. Several thermocouples were placed in

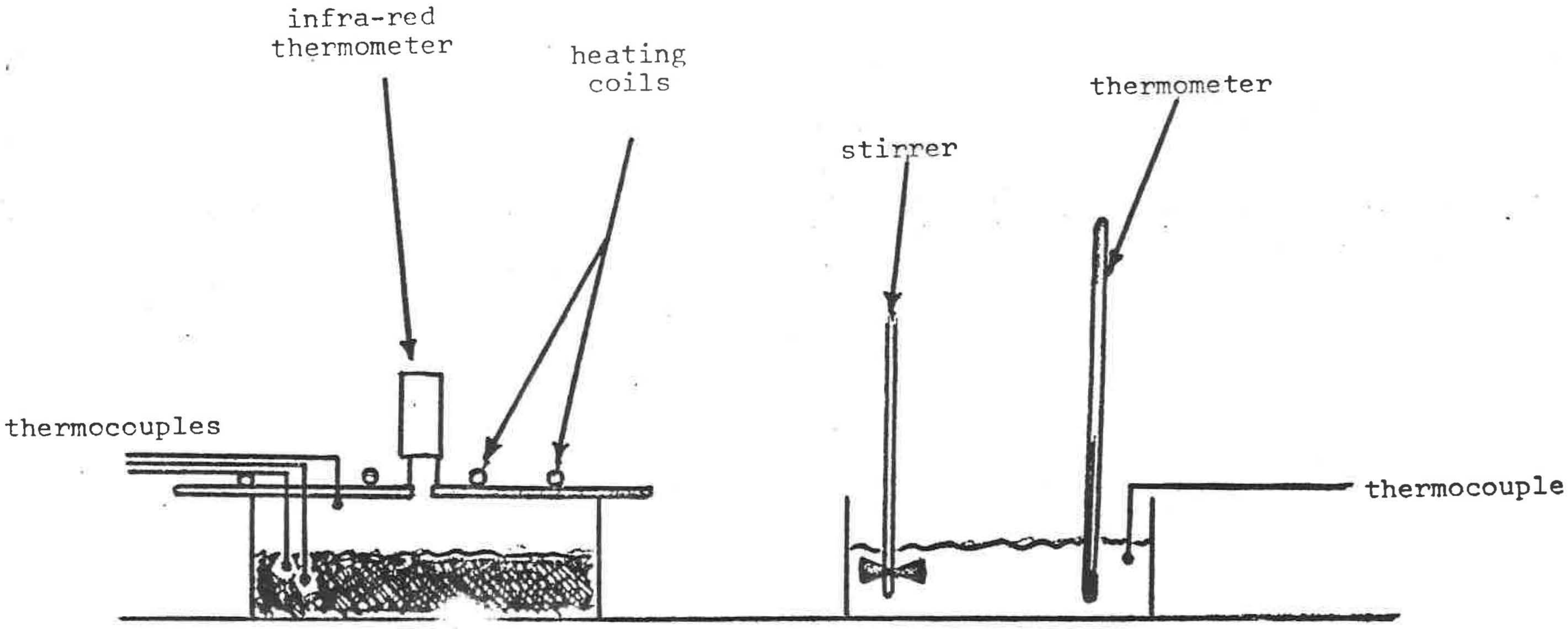

Figure 3. Diagram illustrating apparatus used to determine emissivity.

the lichen carpet. A water bath was placed adjacent to the lichen container, the water being continuously stirred and its temperature measured by both thermocouple and thermometer as a check. Hot water was run through the heating coils of the copper plate, raising its temperature to 45-50°C. Measurements of the apparent temperatures of the lichen carpet and water in the water bath were made by an infrared thermometer ~~as rapidly~~ in succession as possible.

on what? each other. the water temp?

8.2.3.2 Albedo

This is the ratio of reflected to incident global solar radiation. This was not studied since Petzold and Rencz (1975) have published data on lichen carpets and soil surfaces.

8.2.4 Long Term Studies

In May 1976 three 100 m^2 plots were scraped bare of shrub and ground layer vegetation at Richardson Fire Tower. Plots were lcoated near the top of the hill, middle of the hill and near its base. A buffer zone 2 m wide was delimited in each of these plots which were then divided into two equal halves, the uppermost 3-4 cm of soil being removed from one half to expose mineral soil. Each of these halves was further divided into 8 equal subplots 1.5 x 1.5 m square. Four were left undisturbed and the other four were seeded with a mixture of fragments of *Cladina mitis, Peltigera malacea* and *Stereocaulon tomentosum* at the rate of 10 gm m^2.

8.3 RESULTS

8.3.1 Water Relations

8.3.1.1 Water Potential (ψ)

The data obtained are plotted in Fig. 4, which shows a linear relationship on a log/log scale between water content of the lichen

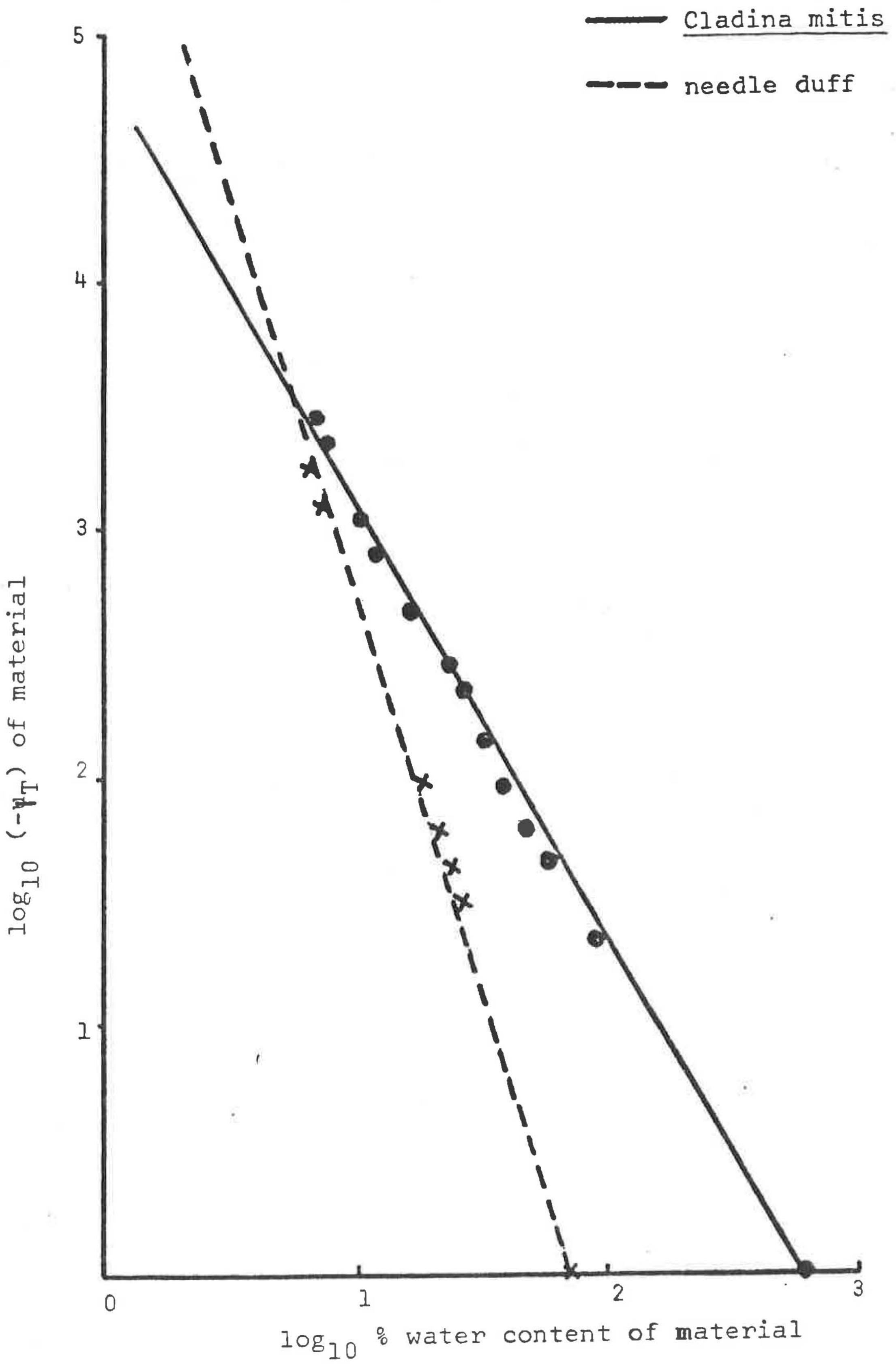

Figure 4. Graph showing relationship of water content and water potential in *Cladina mitis* and needle duff.

thallus and water potential. This relationship is expressed mathematically as:

$$\psi_T = -75900 \times w^{-1.806}$$

where w = % water content of the lichen thallus

The relationship between water potential and water content in needle duff is also linear on a log/log basis. The relationship is expressed:

$$\psi_P = -2511886 \times w^{-3.29}$$

where w = % water content of the needle duff

8.3.1.2 Evaporation from the ground layer

Data showing the diurnal cycle of drying/wetting of the lichen carpet at Richardson Fire Tower are shown in Figs. 8-10. Data obtained by weighing the mesh pots are considered more reliable than those from gravimetric samples, since the latter showed a wide scatter. The diurnal cycle typically consisted of uptake of water during the night and early morning with loss during the day, with maximum loss in mid-afternoon.

not a [illegible]

Data from wind tunnel drying experiments are shown graphically in Fig. 5 where total resistance to water loss, comprising its two components boundary layer resistance and thallus resistance, is plotted against water content of the lichen carpet. The data show that boundary layer resistance is related to the square root of wind speed. This relationship can be expressed:

$$r_b = 0.00585\ u^{-0.5}$$

where r_b = boundary layer resistance

u = wind speed m sec^{-1}

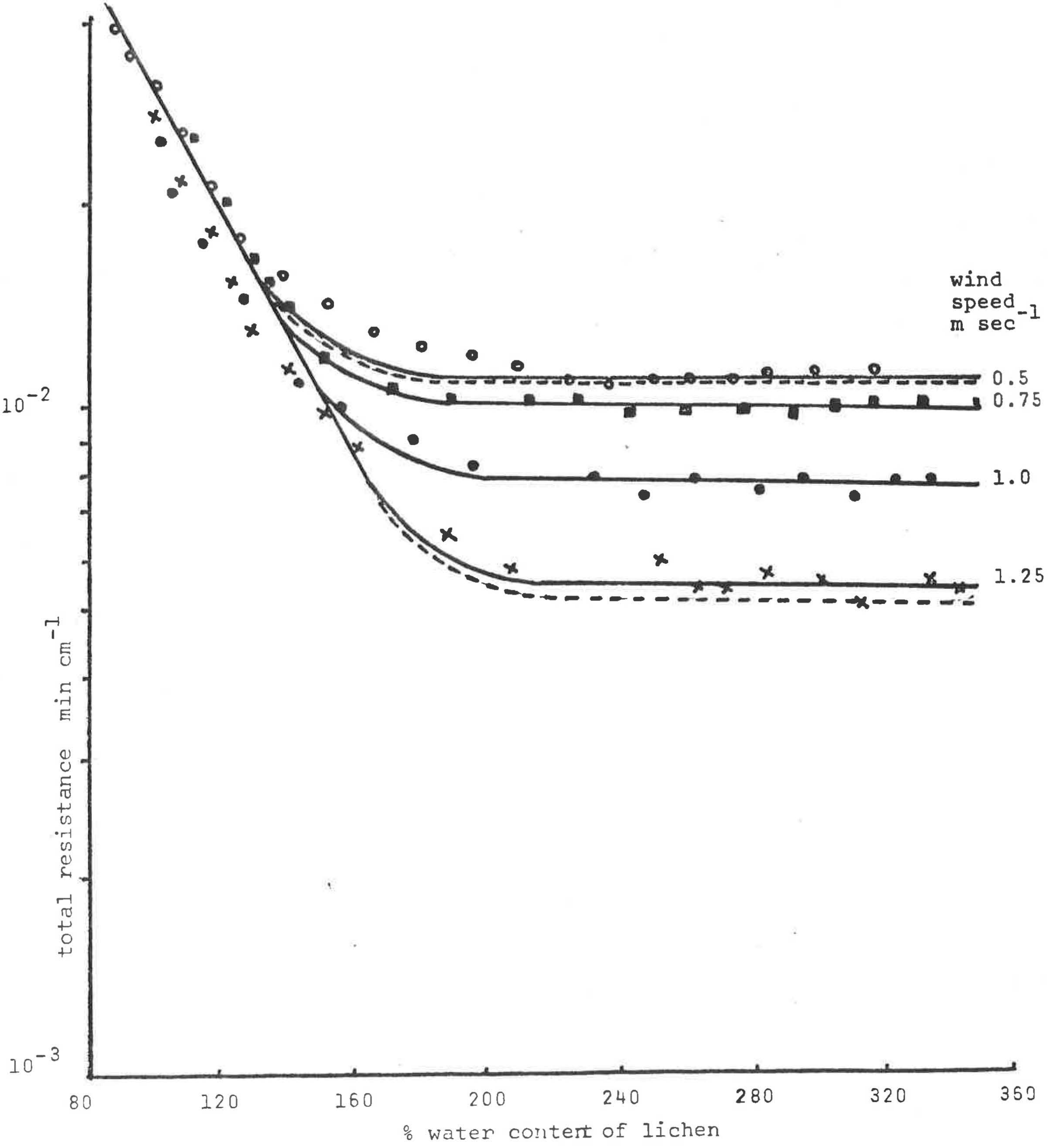

Figure 5. Total resistance to water loss of Cladina mitis at various wind speeds, water contents and radiation loads. Solid line = darkness, broken line = radiation load of 3.2 watts m^2.

Thallus resistance is related to water content and can be expressed:

$$r_t = 0.543 \exp^{-0.0308w}$$

where r_t = thallus resistance

w = water content

Radiation load was found to have little effect on boundary layer resistance. At high water contents, boundary layer resistance is the major factor controlling the rate of water loss, with thallus resistance becoming increasingly important as the lichen carpet dries out. Thus there is a gradual transference of emphasis on the controlling factor as the carpet dries, from external (wind speed) to internal (thallus resistance). During all the intensive runs carried out in 1976, water contents of the lichen carpet in the field rarely exceeded 80%. Thus wind speed would appear to have little influence on evaporation rates in the field.

Data concerning the behavior of needle duff in wind tunnel experiments are not yet complete, but indicate that total resistance to water loss is much lower than the lichen carpet.

8.3.1.3 Water uptake by the ground layer

The diurnal cycle of wetting/drying of the lichen carpet at Richardson Fire Tower is shown in Figs. 8-10. Typically the lichen carpet began taking up water after sunset, when ambient temperatures were dropping rapidly and relative humidity of the air was increasing. The diurnal cycle is well represented in Fig. 10, showing how water content of the lichen carpet varied during a 3-day period during September 1976. During the night the lichen carpet was able to take up enough water to replace that lost through evaporation during the day and this pattern occurred in nearly all the intensive runs. However when the lichen carpet was saturated by a rain shower, little uptake occurred during the night until the water content of the carpet had been reduced to 20-50%.

No data have been gathered on diurnal wetting/drying cycles in needle duff.

Rainfall interception and retention data were gathered both in the field and laboratory. Laboratory experiments showed that a lichen carpet would intercept and retain an average of 1.77 mm of precipitation before significant infiltration would occur. In comparable experiments, needle duff retained 1.36 mm of rainfall. Full data are presented in Table 1. There is some variability in the amounts of rainfall retained by the two types of ground layers, but this is to be expected since the lichen carpet and needle duff can vary in composition, density etc. The figure for % saturation is calculated assuming that the saturated water content of lichen thalli is that obtained in the water potential experiments, i.e., 460%. Percentage saturation figures show that the lichen carpet rarely approaches total saturation, a condition probably impossible to attain under field conditions, but indicate that the carpet has a "field saturation" around 255% (55.5% of total saturation) below which figure throughfall will not occur. Data are incomplete for the needle duff experiments, but indicate that field capacity is similar to total saturation.

Few runs were carried out with prolonged showers, but the data obtained indicate that the ground layer will retain most or nearly all precipitation until "field saturation" is attained. Once this has been reached, throughfall occurs but the ground layer continues to absorb water steadily, approaching total saturation.

Only a small number of gravimetric samples was obtained, since conditions required that they be collected after precipitation and after

Table 1. Rainfall Interception and Throughfall Data for Lichen Carpet and Needle Duff.

Rainfall rate	Rainfall mm	Throughfall mm	Retained mm	% Saturation	No. of runs
Lichen carpet, intact					
20 mm hr^{-1}	0.368	-	0.368	46.63	1
	0.817	-	0.817	58.25	1
	1.244	-	1.244	41.77	2
	3.667	2.119	1.548	58.67	3
	3.732	1.891	1.841	53.04	5
2.2 mm hr^{-1}	1.881	0.037	1.844	69.35	1
Lichen carpet, upper 2 cm					
2.2 mm hr^{-1}	1.129	0.112	1.017	52.89	1
Needle duff					
20 mm hr^{-1}	0.368	-	0.368	*	1
	0.733	-	0.733	*	1
	3.667	2.265	1.402	*	3
	3.732	2.301	1.431	*	3
	4.078	2.886	1.192	*	1
	4.746	3.827	0.919	*	1
2.2 mm hr^{-1}	1.881	0.612	1.269	*	1

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* figures not yet available

a long period of dry weather, circumstances that were not too frequent during the 1976 summer at Richardson Fire Tower. The data obtained are summarized in Table 2. Although relatively few samples were taken it is obvious that the ground layer has acted as a barrier to precipitation penetration, the soil surface being noticeably drier under the ground layer than at sites where there is no plant cover.

8.3.2 Structure of the Lichen Canopy

8.3.2.1 Geometrical structure

The main points of the data are summarized in Fig. 6. From 50 podetia collected at Richardson Fire Tower, it was found that mean height was 40.2 mm, with algal cells occurring to a depth of 75.9%. Assuming that one internode is produced each year, the mean age of the podetia was 12.7 years. The mean diameter of each internode increased with age, reaching a maximum of 1.2 mm at age 8 years, stabilizing at that diameter. Mean internode length continued to increase with age, reaching a maximum of 4.6 mm. Internode dry weight and surface area increased rapidly to a peak at age 3 years before declining and stabilizing at 6 years at about one half of the maximum values. (Fig 6) Similar studies were made on a depth basis, sampling each 5 mm layer of podetium. Again, internode length and diameter increased with depth, internode surface area and weight are greatest just below the surface, at 1.5-2.5 mm depth. Both with age and depth, the number of internodes decreases rapidly to only one at age 6-7 years.

8.3.2.2 Penetration of PAR

The results are presented in Fig. 7. Very little radiation penetrates through the lichen carpet, in no case was more than 3%

[illegible]

Table 2. Water Content (% by Weight) of Soil Following Precipitation at Richardson Fire Tower, October 1976 (Means from Six Sites).

Sample depth	Bare sand	Lichen carpet	Needle duff
ground layer	-	224.1	187.7
soil surface	14.9	9.8	10.3
soil 10 cm depth	6.9	6.9	5.5

Table 3. Literature Reports of Precipitation Retention by Species of *Cladina* Following Excess Rainfall

Species	Precipitation retained	Type of precipitation	Source
Cladina arbuscula	4.5 x dry weight	natural	Porter and Woollett (1929)
Cladina arbuscula	2.54 - 3.81 mm	natural	Jack (1935)
Cladina arbuscula	2.29 - 5.08 mm	artificial	Jack (1935)
Cladina arbuscula	5.59 mm	artificial	Moul and Buell (1955)
C. subtenuis	1.97 mm	artificial	Klepper (1968)

1.6

$1.6 - \frac{1.1}{2}$

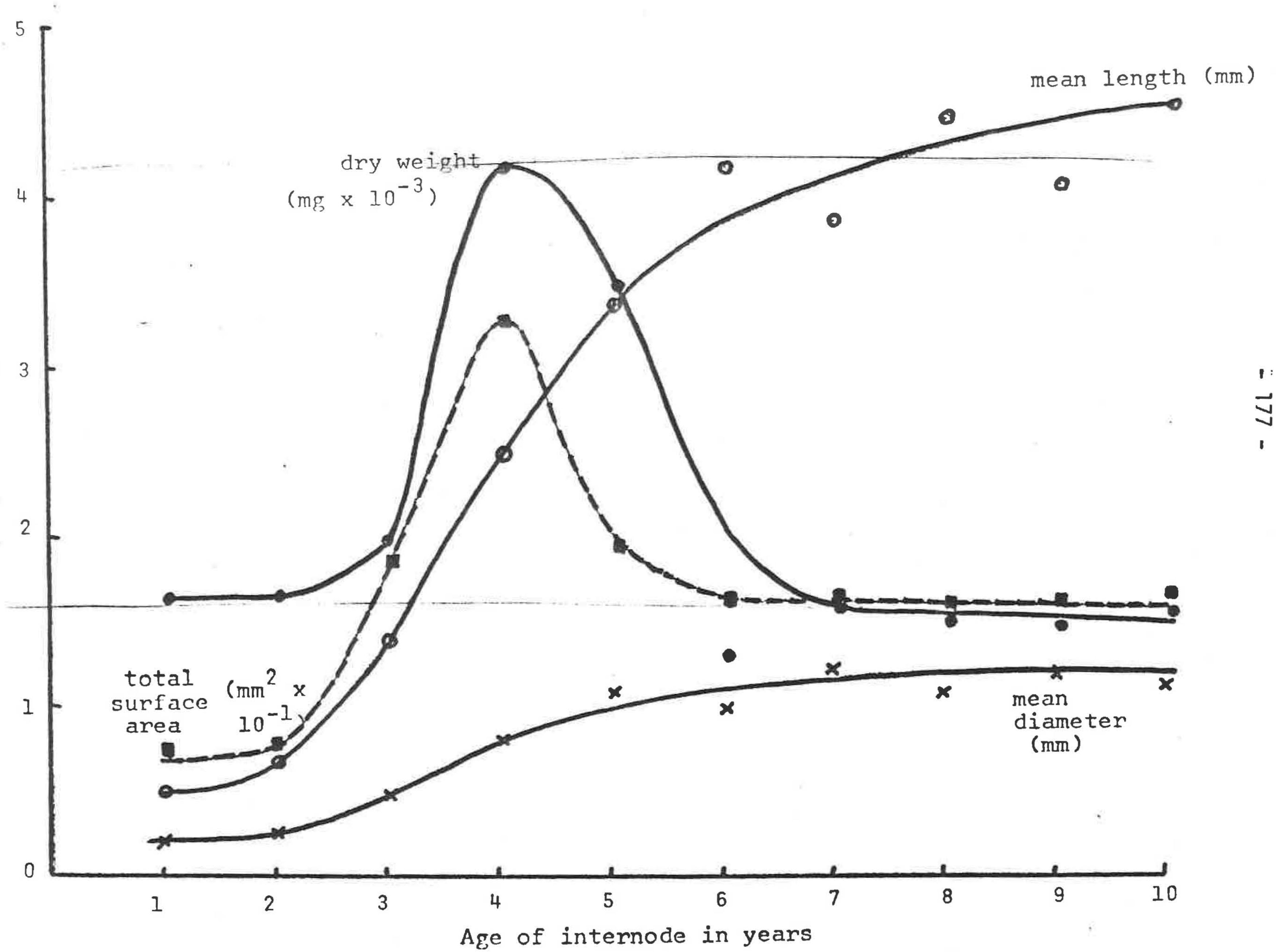

Figure 6. Surface area, dry weights, diameter and lengths of internode age groups.

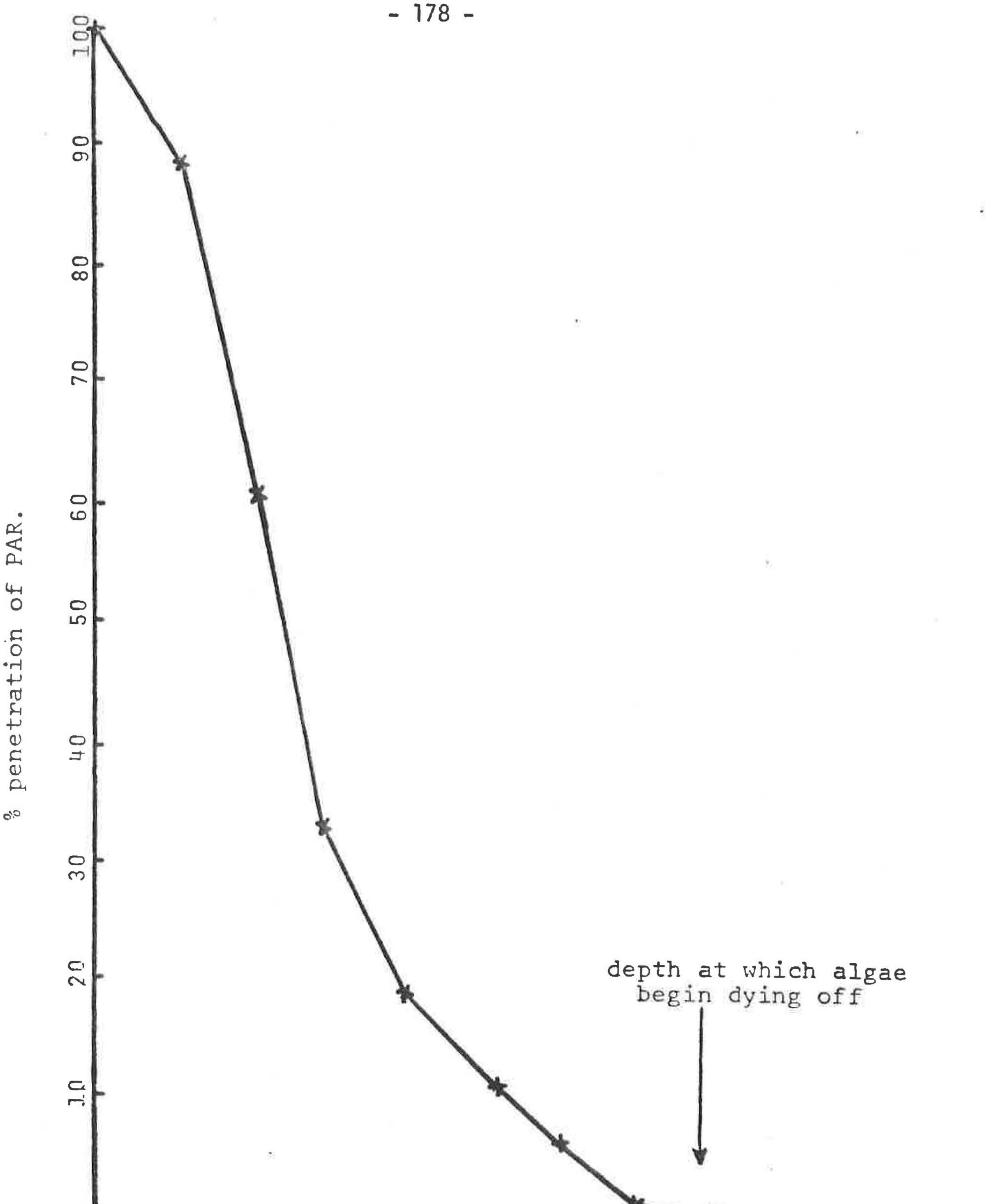

Figure 7. Penetration of PAR in *Cladina mitis* carpet.

penetration recorded. Only 50% of the radiation penetrated to a depth of 30% of the lichen carpet, being intercepted by the great number of internodes with large surface area near the surface. Similar results were obtained by Kershaw and Harris (1971). They found that algal cells began dying off at depths of 35% (10% full illumination) in *Cladina stellaris* (= *C. alpestris*), 40% (40% full illumination) in *C. rangiteria* and 40% (10% full illumination) in *C. arbuscula*. Algal cells began dying off at 85% depth (5% PAR) in *C. mitis* from Richardson Fire Tower, probably indicating the less compact nature of *C. mitis* carpets compared with those of the other species. Angle of illumination had no effect on the rate of attenuation of PAR.

8.3.2.3 Emissivity

Several runs established the emissivity of dry *Cladina mitis* carpets to be 0.96-0.98, similar to that of water. The experiment was checked by using oxidized aluminium foil in place of the lichen carpet. Its emissivity was found to be 0.21, in reasonable agreement with published values of 0.11-0.19.

8.3.3 Modelling Water Relations of the Ground Layer

Using the equations presented in the Methods and Results sections, it has been possible to develop a computer program designed to predict the behaviour of the lichen carpet when subjected to various environmental conditions. Input consists of water content of the carpet, air and lichen temperatures, wind speed and relative humidity. From these variables, water content, thallus and boundary layer resistances, evaporation rates and thallus vapour pressure can be calculated for specified time periods.

The model was checked by inputting data from wind tunnel experiments and agreement was very close between the laboratory data and the model predictions. Less satisfactory agreement occurred between field data and model predictions. why?

8.4 DISCUSSION

The main objective of this research has been to examine the water relations of the ground layer, especially *Cladina mitis*, in Jack pine forest to determine its significance within the ecosystem. Unlike vascular plants, lichens have no mechanisms to control water uptake or loss and thus respond passively to environmental influences (Blum 1974). Therefore the main pattern of water uptake and loss will be diurnal rather than seasonal. To ~~examine this~~ pattern experiments were carried out in the field, through intensive runs, and in the laboratory. Previous workers, e.g., Jack (1935), Moul and Buell (1955) and Rouse and Kershaw (1971) have shown that lichens can act as an efficient barrier to water exchange between the atmosphere and the soil and the objective of much of the research carried out has been to define as exactly as possible the physical parameters of the ground layer with respect to this function. Little work has been published on this aspect.

8.4.1 Evaporation from the Ground Layer

Very few studies have been published regarding lichens (e.g., Heatwole 1966, Rouse and Kershaw 1971) in the field and wind tunnel experiments to examine their behaviour have only recently been carried out (Larson and Kershaw 1976).

Field studies showed that evaporation and the diurnal dry/wetting cycle followed the same pattern found in previous studies (e.g., Heatwole 1966) i.e. maximum evaporation during the early afternoon with uptake occurring during the night. However none of the few previous studies have attempted to follow this diurnal cycle for more than one day or repeat the experiment throughout the season. Data obtained from the intensive runs carried out during the field season at Richardson Fire Tower show that the diurnal cycle is similar throughout, the lengths of each phase varying with season. These data agree essentially in all respects with those collected by Kershaw and Rouse (1971a) in their study of the water relations of *Cladina alpestris* (= *Cladina stellaris*) in northern Ontario. The lichen carpet can be considered stratified, with drying and wetting proceeding from the surface downward. Gravimetric samples collected throughout the season at Richardson Fire Tower indicated this, samples of the upper half of the carpet drying more rapidly during the day and absorbing more water at night than the lower half. Dew formation, an uncommon event in spruce-lichen woodland in northern Ontario during the summer (Kershaw and Rouse 1971a), apparently plays an insignificant role in the water relations of the ground layer.

The wind tunnel experiments have shown that at high water contents, evaporation from the ground layer is mainly controlled by wind speed with a transference of control from this external factor to the internal factor of thallus resistance at low water contents. Klepper (1968)

Cladonia

carried out experiments on the drying rate of *Cladina (= Cladina) subtenius*, deriving an equation relating evaporation rate to "resistance to vapour transfer", and found that resistance comprised two components, but was unable to present any data on the factors controlling total resistance. Larson and Kershaw (1976) have recently carried out wind tunnel experiments using several lichen species to examine influence of thallus morphology on evaporation rate. Their experimental design appears to have a few defects and although they claim that changes in morphology induced by the influence of wind tend to reduce evaporation rate, other studies (Kershaw and Rouse, 1971b) have shown that soil moisture content has a strong influence on thallus morphology. The present wind tunnel studies are considered to have a better design than those carried out by Larson and Kershaw (1976), who suspended individual thalli and aggregated podetia in an air current. The design presented in Fig. 1 is believed to produce results concerning intact carpet that can be compared with field data. Larson and Kershaw (1976) have calculated total resistances in the order of 1.0×10^{-3} to 2.8×10^{-3} min cm^{-1} for *Cladina stellaris* at a wind speed of 1.6 m sec^{-1}. These resistances are similar to those obtained for *Cladina mitis* with low water contents both in field and laboratory experiments. Kershaw and Rouse (1971a) and Rouse and Kershaw (1971) have shown that these values render the lichen layer in spruce-lichen forest an extremely effective barrier to water loss from the underlying soil.

No work appears to have been done on the water relations of needle duff.

8.4.2 Water Uptake by the Ground Layer

As with evaporation, little has been published on this aspect of ground layer. Heatwole (1966), Klepper (1968) and Kershaw and Rouse

(1971a) have provided data on various species of *Cladina*, but mainly incidental to their studies of evaporation. These authors showed that lichens could absorb water vapour from non-saturated atmospheres, typically those in which relative humidity was increasing due to lowering of temperatures. The diurnal cycle of drying and wetting has been well established (cf. Figs. 8-10) but the mechanisms underlying water uptake are not clear. Although several mechanisms have been postulated for water uptake (Blum, 1974), the theory that lichens behave as hydrophilic gels in this respect is widely held. nm [illegible]

More work has been done on the role of lichens in the interception and retention of precipitation, to determine how effective the lichen layer is in preventing the penetration of rainfall to the underlying soil. Previous work is summarized in Table 3. The amount retained by *Cladina mitis* was found to vary between 1.448 and 1.956 mm during short showers. These figures are lower than the published reports, but cannot be related to them in any way, since precipitation retention appears to be a function of thickness, and thus dry weight, of the lichen layer. Jack (1935) noted that *Cladina arbuscula* could absorb 4.5 times its dry weight of rainfall, similar to the maximum value obtained for *Cladina mitis*. However field values for saturation, at which point precipitation begins to penetrate the lichen carpet, are much lower, being around 255% water content for *Cladina mitis*. Jack (1935) and Moul and Buell (1955) noted that many of the showers recorded by them were not of sufficient duration or intensity to bring the lichen layer to field saturation necessary for penetration through to the soil. At Richardson Fire Tower, several showers were noted during intensive runs, and although they increased the water content of the upper layers of the lichen carpet, no penetration was noted, the soil remaining dry underneath. ?

[illegible] [illegible]?

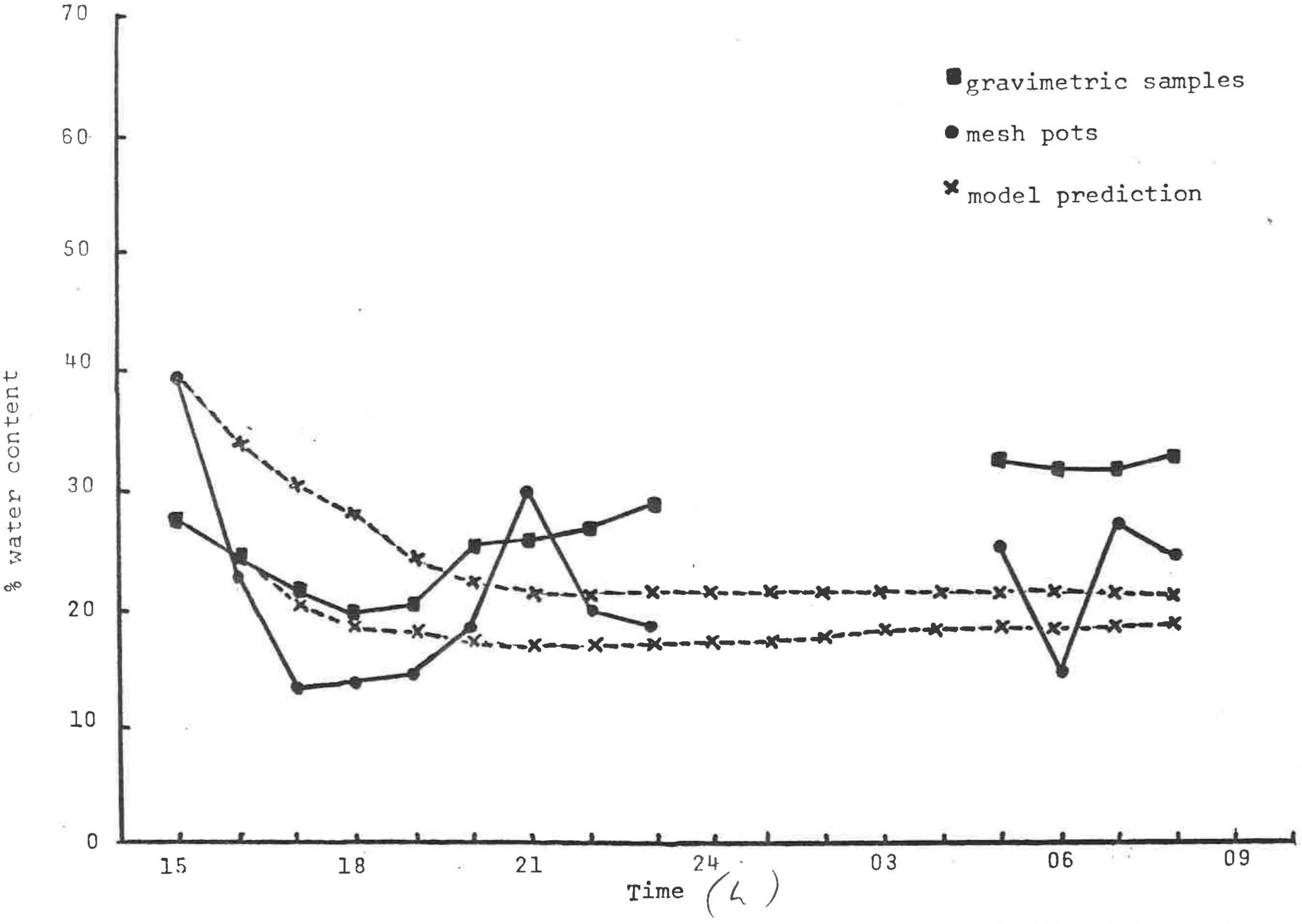

Figure 8. Water content of Cladina mitis carpet measured in the field compared with model prediction. 2-3 June 1976.

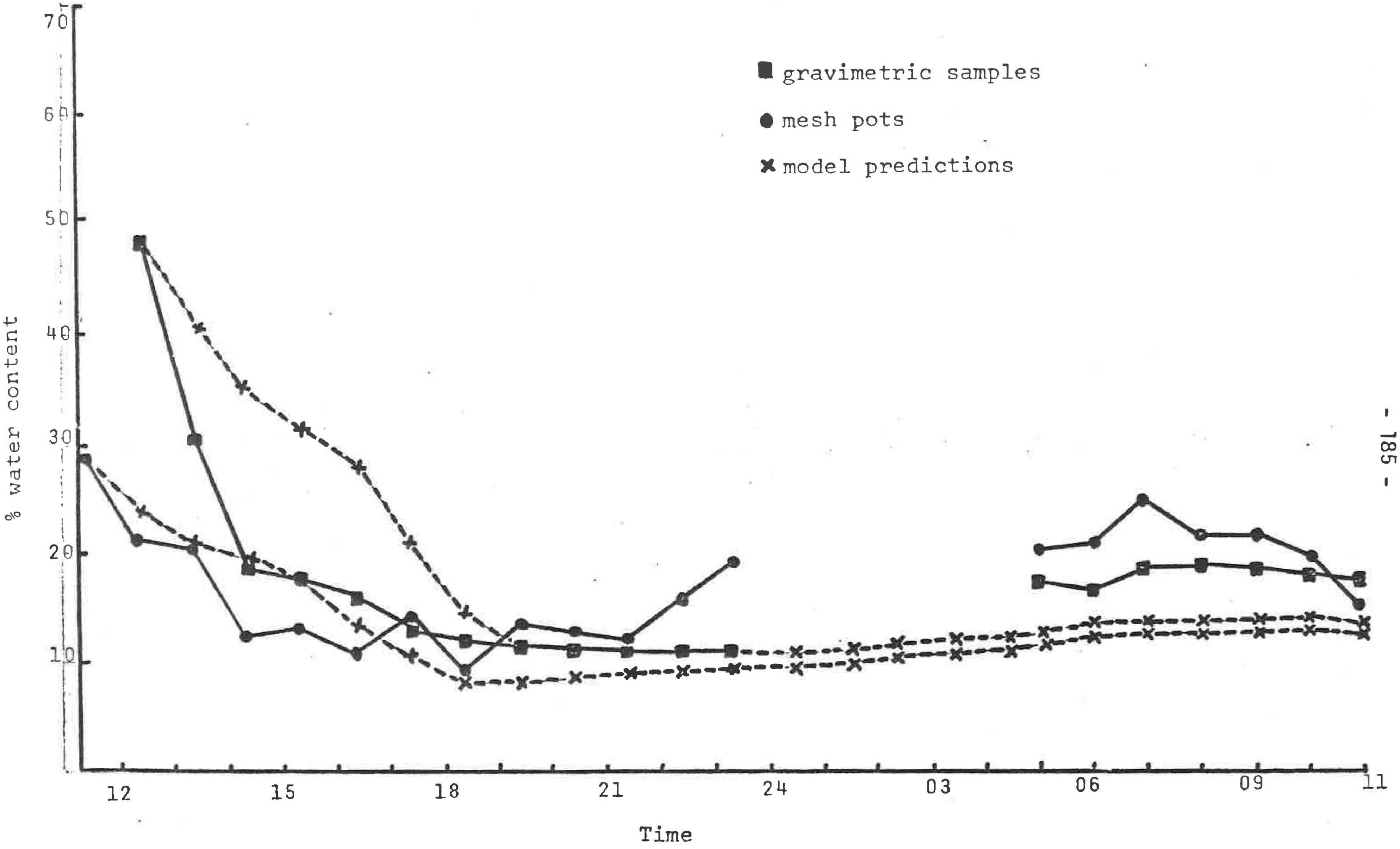

Figure 9. Water content of Cladina mitis carpet measured in the field compared with model prediction. 29-30 June 1976.

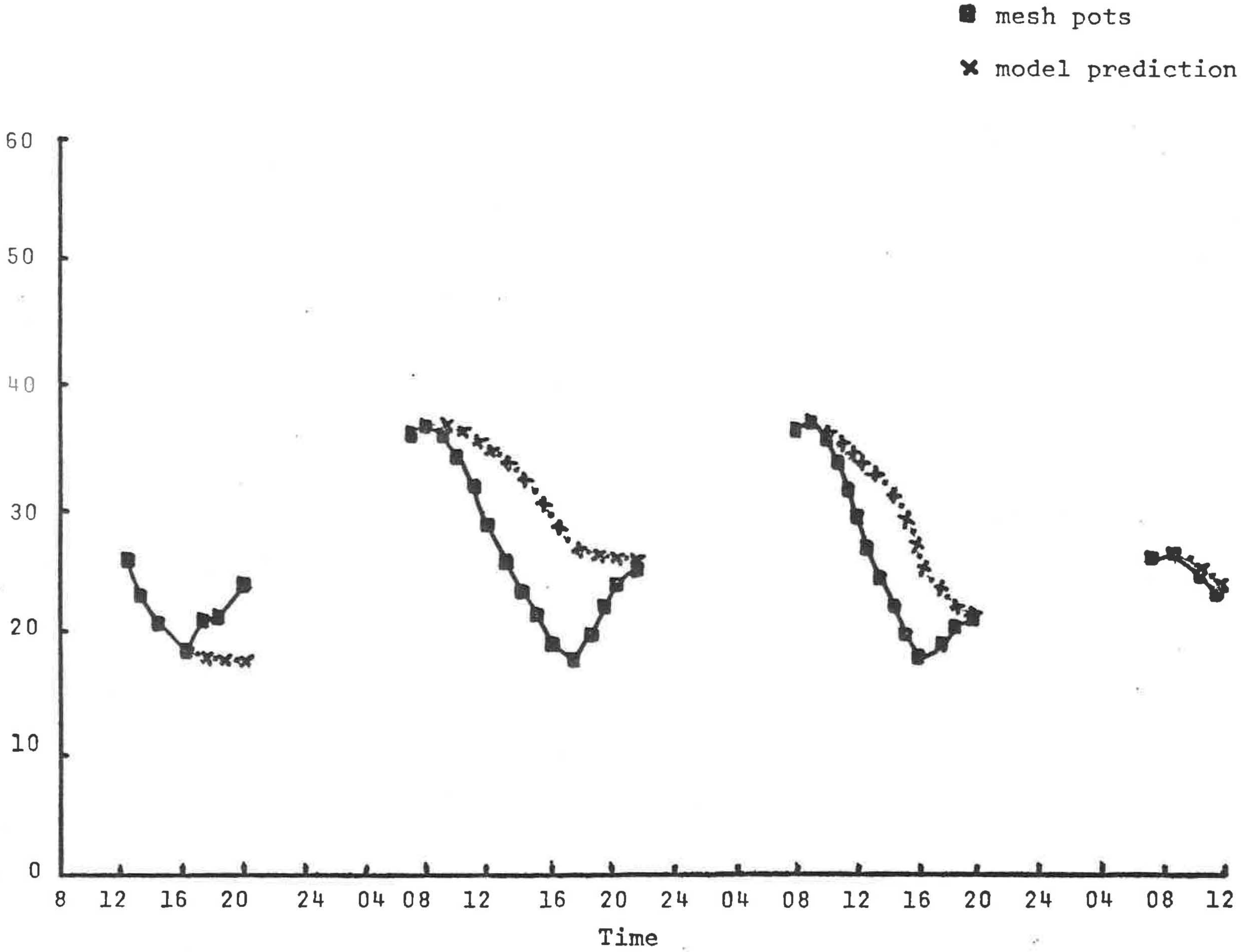

Figure 10. Water content of Cladina mitis carpet measured in the field compared with model prediction. 24-27 September 1976.

Preliminary gravimetric samples obtained after prolonged precipitation showed the reverse effect, that the lichen layer acted as an effective barrier to water loss from the soil. These results agree with those obtained by Porter and Woollett (1929) and Rouse and Kershaw (1971).

The literature has indicated that the lichen ground layer acts as a mechanical barrier to water exchange between the soil and the atmosphere, and the few published data have been augmented and extended so that this function is now fairly well documented. Few data however are available on the water relations of needle duff.

The model of lichen water relations was tested using laboratory and field data and while agreement between model predictions and laboratory data was very close, there was less satisfactory agreement between model predictions and field data. [illegible] ~~While~~ field data indicated that the lichen carpet dried out fairly rapidly under certain conditions, model predictions showed the lichen carpet drying out less rapidly. Considering all the factors operating in the laboratory experiments and intensive runs at Richardson Fire Tower, relative humidity is considered the one most likely to be in error. In the wind tunnel experiments, the air flowing over the lichen carpet is laminar except for a 2 cm thick layer immediately above the lichen. The relative humidity sensor was placed at a height 5 cm above the carpet, in the non-turbulent stratified layers of air. Stratification of RH had been shown in preliminary testing of the wind tunnel. In the field, the air immediately above the lichen is rarely stratified as in the wind tunnel, being more turbulent, so that RH measurements at a height of 5 cm above the carpet are probably more representative of the microclimate experienced by the lichen carpet than similar measurements made in the wind tunnel. However, as shown

Figs. 8-10, the error in the model predictions compared with field data is never very great.

8.5 FUTURE WORK

Studies will continue on the water relations of the lichen and needle duff components of the ground layer. Intensive runs to be carried out during the spring and early summer will provide more data, especially for the assessment of the role of the ground layer during snow melt. Gravimetric samples will be collected after precipitation and after drought to define more clearly the mechanical barrier to water imposed by the ground layer.

The long term revegetation plots will be examined for colonization and similar plots will be set up on the GCOS dike.

Laboratory work will finish studies on the water relations of needle duff and attempt to refine the model so that there is greater agreement between field data and predictions.

8.6 ACKNOWLEDGEMENTS

Many of the experiments carried out were suggested by Dr. D.W.A. Whitfield, who derived the mathematical formulae quoted in the text and constructed the lichen water relations model. George Davis assisted with the construction of the long-term revegetation plots.

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8.8 APPENDIX

List of Non-vascular Cryptograms Recorded from the Richardson Fire Tower Area.

No published records have been traced referring to cryptograms from this area, although Stringer (1976) listed 11 lichens and 4 bryophytes from Richardson Airstrip, approximately 3 miles to the west of Richardson Fire Tower. Bryophytes were identified by Dr. D.H. Vitt; specimens are being deposited in the herbarium of the University of Alberta (ALTA).

1) Lichens

Acarospora fuscata (Schrad.) Arn. R
Alectoria fremontii Tuck. P
Buellia punctata (Hoffm.) Nassal. P
Cetraria ericetorum Opiz L.
    halei Culb. et Culb. P
    nivalis (L.) Ach. G
    pinastri (Scop.) Gray L,P
Caloplaca cerina (Ehrh.) Th. Fr. A
    jungermanniae (Vahl.) Th. Fr. M
Candelariella aurella (Hoffm.) Zahlbr. R
Cladina arbuscula (Wallr.) Rabenh. F
    mitis (Sandst.) Hale et Culb. G
    stellaris (Opiz) Brodo (syn. *C. alpestris* (L.) Harm.) G
Cladonia amaurocraea (Flörke) Schaer. G
    bellidiflora (Ach.) Schaer. G
    botrytes (Hag.) Willd. L
    chlorophaea (Flörke ex Sommerf.) Spreng. G
    crispata (Ach.) Flot. G
    cristatella Tuck. G
    cornuta (L.) Hoffm. G
    deformis (L.) Hoffm. G
    gracilis (L.) Willd. G
    multiformis Merr. G
    phyllophora Hoffm. G

pleurota (Florke) Schaer. G
squamosa (Scop.) Hoffm. G, L
uncialis (L.) Wigg. G
verticillata (Hoffm.) Schaer. G
Cornicularia aculeata (Schreb.) Ach. G
Dimelaena oreina (Ach.) Norm. R
Evernia mesomorpha Nyl. P
Hypogymnia physodes (L.) Nyl. A, P
tubulosa (Schaer.) Hav. P
Icmadophila ericetorum (L.) Zahlbr. F
Lacanora allophana Ach. P
cadubriae (Massal.) Hedl. P
chrysoleuca (Sm.) Ach. R
polytropa (Ehrh.) Rabenh. R
Lecidea scalaris (Ach.) Ach. L
Parmelia exasperata De Not. A
olivacea (L.) Ach. A
sulcata Tayl. A, G, L, P
taractica Kremp. A, G, P
Parmeliopsis ambigua (Wulf.) Nyl. L,P
hyperopta (Ach.) Arnold L
Peltigera aphthosa (L.) Willd. G
canina (L.) Willd. G
lepidophora (Nyl.) Vain. G
leucophlebia (Nyl.) Gyeln. G
molacea (Ach.) Funck
rufescens (Weis) Humb. G
Physcia aipolia (Ehrh.) Hampe A
adscendens (Th.Fr.) Oliv. R
orbicularis (Neck.) Poetsch R
Rhizocarpon disporum (Naeg. ex Hepp) Müll. Arg. R
Stereocaulon tomentosum Fr. G
Umbilicaria muhlenbergii Ach. R
Usnea hirta (L.) Wigg P
Xanthoria elegans (Link) Th. Fr. R
fallax (Hepp) Arnold A

2) Bryophyta

a. Musci

Aulacomnium palustre (Hedw.) Schwaegr. F
Bryum pseudotriquetrum (Hedw.) Gaertn. B
Ceratodon purpureus (Hedw.) Brid. S
Dicranum polysetum Sw. G
undulatum Brid. G
Grimmia apocarpa Hedw. R
Hedwigia ciliata P. Beaux. R
Hylocomium splendens (Hedw.) B.S.G. G
Orthotrichum anomalum Hedw. R
Pleurozium schreberi (Brid.) Mitt. G
Polytrichum juniperinum Hedw. S
piliferum Hedw. S
Pyliasiella polyantha (Hedw.) Grout. P
Sphagnum angustifolium (Russ.) C. Jens. F
fuscum (Schimp.) Klinggr. F
warnstorffii Russ. F
Tomenthypnum falcifolium (Ren. ex Nich.) Podp. F
Tortella fragilis (Drumm.) Lemipr. R
Tortula muralis Hedw. R

b. Hepaticae

Marchantia polymorpha L. B
Ptilidium ciliare (L.) Hampe G

Habitat abbreviations:

A : on bark of aspen
B : bare ground at edge of fen
F : in black spruce/Sphagnum fen
G : on ground in Jack pine forest
L : on decaying logs
M : on decaying plant matter
P : on Jack pine branches and twigs, occasionally trunks
R : on pebbles and erratic boulders
S : on sand, especially at edges of tracks

9. MYCORRHIZAE IN JACK PINE STANDS AT THE RICHARDSON FIRE TOWER SITE

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9.1 INTRODUCTION

Mycorrhizae have repeatedly been shown to be necessary for normal growth of nearly all higher plants (Harley 1969) and the influence of mycorrhizae becomes increasingly important as environmental conditions become increasingly adverse (Schramm 1966, Voigt 1971). Schramm (1966) showed that ectomycorrhizae were necessary for successful survival of woody plants colonizing coal wastes that were characterized by hot, dry soil conditions. He found that few species of symbiotic fungi could tolerate these conditions and it is likely that the species present were adapted to the special conditions of the site. Marx (1975) has shown that the use of *Pisolothus tinctorius* as a symbiont can significantly increase survival and growth of pines on these adverse sites. The work of Marx (1975) and others (Mikalo 1973) have shown that the symbiotic efficiency of fungi varies with environmental conditions and that inoculation of planting stock with fungi adapted to specific conditions can have a profound influence on growth and survival of plants.

The mycorrhizal research at the Richardson Fire Tower site is aimed at defining the host - mycorrhizal relationships of *Pinus banksiana*, *Arctostaphylos uva-ursi* and *Hudsonia tomentosa* as they occur under natural conditions on sandy soils and applying this knowledge to revegetation problems on oil sands tailings. The fungi involved and their importance on the site has been studied by: 1) collecting and identifying fruiting bodies of mycorrhizal fungi; 2) direct isolation of symbionts from mycorrhizae; and 3) identification of mycorrhizae. Pure culture synthesis techniques are being used to confirm specific fungus - host associations and as an aid in mycorrhizal identification. From the data on occurrence and abundance, candidate fungal species will be selected for field trials to determine their relative efficiency on growth and survival of Jack pine seedlings.

In addition to the Richardson Fire Tower slope, the mycorrhizae occurring in an area burned by wildfire in 1970 and regenerating to Jack pine was studied. This provided a comparison of the mycorrhizae in mature pine stands with pine on a recently disturbed area. The burn area lacked the *Cladina* lichen carpet characteristic of mature pine stands in the area. Bearberry and *Hudsonia* as well as some grasses were common plants on the burn.

9.2 SPECIES OF MYCORRHIZAL FUNGI ASSOCIATED WITH JACK PINE WITH NOTES ON SELECTED SPECIES

Sporocarps of fungi fruiting on the slope and in other Jack pine stands were collected in 1975 and 1976. Hypogeous fungi were usually found by observing where rodents had been digging and then raking the area. In addition, fungi were collected in stands of lodgepole pine in the Calgary area as these stands were readily accessible and the mycorrhizal associates of the two pine species are similar. A brief foray was also made in a lodgepole pine - bearberry stand situated on sand dunes on the Oregon coast. Although the climate is quite different in coastal Oregon than at the Richardson site, the soils and vegetation are similar.

The ectomycorrhizal fungi that have been collected at the Richardson site are listed in Table 1. If more than one potential host was present, the host plant could not be determined. Many of the species remain to be identified but 55 species were collected that are potential symbionts of Jack pine. Many or most of these may also be associated with bearberry as typical mycorrhizal fungi of pine have been shown to form ectendomycorrhizae with bearberry (Zak 1976a). Four species of hydnums are included in this list although hydnums are not included in the list of mycorrhizal fungi by Trappe (1962). The circumstantial evidence that they may be mycorrhizal include the consistant association with certain forest types and the failure to grow in culture (Harrison 1971).

A species list of fungi associated with lodgepole pine in central Alberta has not been completed but to date only six of the 55 species found with Jack pine have been collected under lodgepole pine. These are *Gautieria monticola, Hygrophorus acuticonicus, H. chrysodon, Rhizopogon rubescens, Suillus tomentosus* and *Tricholoma flavovirens*. The flora associated with lodgepole pine on Oregon dunes was more similar to the Richardson site than central Alberta sites with different soil conditions. The species that occurred on both the Richardson and Oregon sites included: *Hygrophorus* sp. 2466, *Suillus tomentosus, Scleroderma meridionale, Tricholoma flavovirens, T. zelleri, Laccaria laccata, Hydnellum peckii* and *Elaphomyces granulatus*. The similarity of the plant and fungal flora on sandy soils under very different climatic conditions indicate that results obtained in this study would have application in other sandy pine areas.

Table 1. Mycorrhizal Fungi Collected at the Richardson Fire Tower Site.

Species	Possible Associates
Alpora diplophloeus f. *diplophloeus* (Zeller & Dodge) Trappe & A.H. Smith	Green alder
Amanita muscaria (L. ex Fr.) Hooker	Jack pine
Armillaria ponderosa (Pk.) Sacc.	Jack pine
Astraeus hygrometricus (Pers.) Morgan	Jack pine
Bankera fuligineo-alba (Schmidt ex Fr.) Pauzar	Jack pine
Cantharellus cibarius Fr.	Jack pine
Cenococcum graniforme (Sow.) Ferd. & Winge	Jack pine, bearberry
Chroogomphus rutilus (Schaeff. ex Fr.) O.K. Miller	Jack pine
Cortinarius armillatus (Fr.) Fr.	Paper birch
C. ?semisanguinensis Fr.	Jack pine
C. sp. 1719 and others	Jack pine
C. sp. 1734	Jack pine
C. sp. 1712	Jack pine
C. sp. 1722	Jack pine
C. sp. 1819	Jack pine
Elaphomyces granulatus Fr.	Jack pine
E. muricatus Fr.	Jack pine
Gautieria ?monticola	Jack pine
Hydnellum peckii Banker	Jack pine
Hydnum imbricatum L. ex Fr.	Jack pine
Hygrophorus acuticonicus (Clements) Sm.	Jack pine
H. chysodon (Fr.) Fr.	Jack pine
H. ?niveus Fr.	Jack pine or alder
H. sp. 1718	Jack pine
H. sp. 2478 and others	Jack pine
Inocybe sp.	Jack pine
Laccaria laccata (Scop. ex Fr.) Cke.	Jack pine, bearberry
Lactarius rufus (Scop. ex Fr.) Fr.	Jack pine
L. sp. 2191 and others	Jack pine
L. sp. 2194 and others	Jack pine
L. sp. 2205	Jack pine, aspen or white birch
L. sp. 2474	Jack pine, spruce or alder
L. sp. 2475	Jack pine, spruce, alder or birch
Leccinum sp. 1737	Jack pine
L. sp. 2187	Jack pine
Phellodon melaleucus (Fr.) Karst.	Jack pine or alder
Rhizogogon rubescens Tul.	Jack pine
R. sp. 1986	Jack pine
Russula sp. 1706	Jack pine
R. sp. 1710	Jack pine
R. sp. 1720	Jack pine
R. sp. 2422	Jack pine
R. sp. 2176	Jack pine or aspen
R. sp. 2198	Jack pine or alder

Table 1. (continued)

Species	Possible Associates
Scleroderma meridionale Demoulin & Malencon	Jack pine
Suillus tomentosus (Kauff.) Sing., Snell & Dick	Jack pine
S. sp. 2440	Jack pine
Thelephora terrestris Ehrhart ex Fr.	Jack pine
Tricholoma flavovirens (Pers. ex Fr.) Lundell	Jack pine
T. zelleri (Stuntz & Smith) Ovrebo & Tylutki	Jack pine
T. sp. 2421, 2488	Jack pine
T. sp. 2444	Jack pine
T. sp. 2476	Jack pine
T. sp. 2469	Jack pine
T. sp. 1730	Jack pine
T. sp. 2453	Jack pine
T. sp. 2455 and others	Jack pine

The most common sporocarps observed on the site were those of *Suillus tomentosus* and *Russula* spp. The abundance of fruiting bodies is usually not considered an indicator of the importance of a particular species as a symbiont (Riffle, 1973). However Laiho (1970) found a significant positive correlation between the number of sporophores of *Paxillus involutus* and the number of mycorrhizae formed by *P. involutus* in mixed forest stands.

In order to determine if the fungi associated with Jack pine were similar under different environmental conditions, observations and collections were made on four areas. These were the Richardson Fire Tower slope forested in mature Jack pine, other Jack pine stands in the vicinity, roadsides in the area with bare sand and on the area burned in 1970 and regenerating to pine.

Fruiting was rare in the burn area thus limiting the possible comparisons with the other sites but sporocarps were common on the more protected roadsides. Observations on the sporocarps on the disturbed and natural areas suggests that different fungi form mycorrhizae with pine on natural and disturbed soils (Table 2). Caution is in order however when interpreting observations on sporocarps as their absence may be due to unfavorable conditions for fruiting and the fungi may be present and active in a vegetative state. The genus *Russula* is not included as species could not be determined in the field. Distinct preferences for fruiting in natural stands were noted for *Elaphomyces* spp., hydnums, *Suillus* spp. and several agarics. *Elaphomyces granulatus* was found in the driest Jack pine stands with a *Cladina* lichen carpet, where as *E. muricatus* was always found in mixed stands of pine, often with a deep cover of feather mosses, in association with hardwood species (e.g. green alder, paper birch, aspen).

Table 2. Distribution of Sporocarps of the Most Common Mycorrhizal Fungi.

	Area Where Found			
Species	Richardson Slope	Other Mature Pine Stands	Bare Sand By Roadsides	1970 Burn
Elaphomyces granulatus	+*	+	-	-
E. muricatus	-	+	-	-
Hydnellum peckii	+	+	-	-
Hydnum imbricatum	+	+	-	-
Bankera fuligineo-alba	+	-	-	-
Phellodon melaleucus	-	+	-	-
Cantharellus cibarius	-	+	-	-
Suillus tomentosus	+	+	(+)	-
S. sp. 2	+	+	-	-
Armillaria ponderosa	+	-	-	-
Chroogomphus rutilis	+	+	-	-
Cortinarius ?semisanguinensis	+	-	-	-
C. sp. 1719	+	-	-	-
Astraeus hygrometricus	-	(+)	+	+
Scleroderma meridionale	-	-	+	+
Thelephora terrestris	-	-	+	-
Rhizopogon rubescens	(+)	-	+	+
Lactarius sp. 2191	(+)	-	+	+
Laccaria laccata	-	-	+	+
Tricholoma flavovirens	(+)	(+)	+	+
Hygrophorus sp. 2478	-	+	+	-

*+ = present, - = absent, (+) = present but rare in comparison with the other areas where found.

In 1975 *Laccaria laccata* was very abundant along roads and among bearberry in the airstrip. In 1976 conditions were less favorable for fruiting and it was rarely encountered. Considering the reputation of this species as a "weed" and its very wide distribution (Miller 1972), it may be significant that it was not found in mature stands. Laiho (1970) found that *L. laccata* and *Thelephora terrestris* increased in abundance in cutover areas as compared to closed stands. Although these two species are adapted to disturbed soils in the Richardson area they may not be desirable mycorrhizal associates. Both are common in forest nurseries (Hacskaylo 1965, Stack et al. 1975) but they may be relatively ineffective symbionts (Mikalo 1970). Inoculation of planting stock with more effective fungi may be desirable on nutrient poor, excessively drained soils.

Astraeus hygrometricus and *Scleroderma meridionale* were conspicuous components of the fungal flora in disturbed soils in exposed locations. There importance is likely to be overestimated in that the tough gastrocarps persist on the soil and can overwinter in place. In contrast, the agaric species are rapidly riddled by insects and short lived.

The spores of *Scleroderma* and *Astraeus* could possibly be used to inoculate seedlings as the gastrocarps are easily recognized and collected. Spore viability cannot be evaluated directly as they do not germinate on agar media, thus the gastrocarps are easily recognized and collected. Spore viability cannot be evaluated directly as they do not germinate on agar media, thus the gastrocarps should be collected in the fresh state. Both of these species were observed to develop in the late summer and fall. *Astraeus* resembles an earthstar but matures underground (hypogeous). When the mass of spores are mature the thick outer layer of the peridium splits in a stellate manner and during periods of high soil moisture the rays reflex and push the fruit bodies toward the soil surface. When the soil dries the peridial rays close over the spore sac. If this sequence is repeated several times, the fruit body will emerge and the spores can be disseminated by the wind. The literature on the time of emergence, i.e., when the spores are most likely to be viable, is somewhat confusing. Smith (1951) states that the fruit bodies mature in the fall but later Smith (1975) says that maturation occurs in the spring. To determine the timing of development in the Richardson area, areas with old fruit bodies on soil surface were excavated in April, June, August and September. In April fruit bodies were found 2-3 cm deep and breaking through the soil surface. A few fruit bodies were found as deep as 15 cm but in all cases the spore case had collapsed and the peridium was in such a condition that it appeared that the rays would be unable to flex sufficiently to lift them to the surface. No immature gastrocarps were observed at this time or in June. In the second week of August and last week of September immature gastrocarps, i.e., those in which the peridium had not begun to split, were found at depths of 3-4 cm. No sound gastrocarps were found at any greater depths other than an occasional aborted one. Schramm (1966) reported *A. hygrometricus* at a depth of 15 cm in coal spoils. From the observations at Richardson it appears that fruit bodies may develop at depths greater than 3 or 4 cm but they are unable to successfully emerge. No very young specimens were found but the absence of fresh gastrocarps in June indicates that development takes place in the summer months and emergence occurs in the fall if rainfall patterns are favorable or they may overwinter hypogeously and emerge in the spring. These observations indicate that the best time to collect *Astraeus* gastrocarps for spore inoculum is in the fall. Spores collected from fruit bodies of another gastromycete, *Pisolithus tinctorius,* have been used successfully to inoculate loblolly pine in the southeastern U.S. (Marx 1976). The fruit bodies of *Astraeus* are much smaller than *P. tinctorius* and a very large number would be required for inoculating large numbers of trees.

Rhizopogon rubescens was the most common hypogeous fungus at Richardson and was always found along roadsides except for one find at the border of the plots. A few immature specimens were found on 20 June, a few mature specimens in mid-August, and abundant mature basidiocarps in late September. It was also associated with lodgepole pine in central Alberta in August. The preference for fruiting on bare or disturbed soils is not a characteristic of the species but it is a complex and widespread species with many varients (Smith & Smith 1973). Species of *Rhizopogon* have frequently been used in synthesis studies with pine (Trappe 1962).

9.3 DIRECT ISOLATION OF SYMBIONTS FROM MYCORRHIZAE

Populations of ectomycorrhizal fungi on the Richardson slope and the 1970 burn were compared by examining fungi cultured from surface sterilized mycorrhizae. It is inherent in the method that only a portion of the mycorrhizal fungi will be detected as many will not grow in culture. However the importance of those fungi that do grow in culture can be more accurately assayed than by observations on fruit body abundance.

9.3.1 Methods

On the slope two 50 m transects were made, one through the lower plots and one through the upper plots. Soil cores, 5.3 cm diameter and 10 cm deep, were taken every meter for a total of 50 cores for each transect. In the burn a single 50 m transect was made along a slightly sloping south-facing ridge. The soils on both areas were very similar, consisting of fine grained sands. In that roots were much less frequent in the burn cores than on the slope and many were dry and probably non-viable, 25 pine root samples were taken. These were obtained by digging up entire Jack pine seedlings, 0.5-1 m tall, shaking much of the sand off the roots and cutting off three lateral roots. The 15 cm sections of roots were placed in plastic bags with some moist sand to prevent drying. The core samples were placed in plastic bags with moist paper towels.

[illegible]

The samples were stored at 7-10°C for 5 to 6 days until they could be transported to the laboratory where they were stored at 2°C until they could be processed.

Each of the soil cores and root samples were washed free of soil and the roots stored in water at 2°C until they were plated. From each core sample three roots were randomly selected and five mycorrhizae from the end of each root were surface sterilized and plated. With the seedling roots, five mycorrhizae from each end of three roots were selected. Thus a total of 1500 mycorrhizae from each site were plated out.

Nearly all of the mycorrhizae selected appeared to be on pine roots although some bearberry roots, which may be indistinguishable from pine, may have been included. A few *Hudsonia* mycorrhizae were randomly included in the burn transect samples.

The mycorrhizae were surface sterilized by dipping in 95% ethanol, soaking in 30% H_2O_2 for 15 sec and washing in an excess of sterile distilled water. The individual mycorrhizae were then placed on plates of MMN agar (Marx 1969) modified by the substitution of dextrose for sucrose and the addition of 100 ppm of Streptomycin, 50 ppm of Aureomycin and 5 ppm benomyl. In preliminary tests the addition of benomyl to the medium greatly enhanced the chance of recovering possible symbionts. Its selective effects for basidiomycetes have been previously shown by Edgington et al. (1971) and Taylor (1971). The chance of benomyl eliminating mycorrhizal ascomycetes was probably nil as they rarely grow in culture (Trappe 1971) and *Cenococcum* was excluded from the otherwise random selection of mycorrhizal root tips. The plates were incubated at room temperature and examined after 1 and 2 months. All fungi that grew from the tips were considered possible mycorrhizal associates except phycomycetes. No hyphomycetes grew from the 3000 tips.

Representative isolates were subcultured and arranged in "species" groups. The range of cultural variation that was permitted within each group varied and was based where possible (e.g. *Suillus* and *Rhizopogon*) on the variation observed on a range of isolates obtained from basidocarps. General colony morphology and the types, but not necessarily the amounts, of pigments appeared to the most reliable characters for separating different species. Macrochemical tests (according to Singer 1975) on the colonies including 10% KOH, Phenol-aniline, H_2SO_4 and NH_4OH were also useful with some groups. No positive results were found with phenol, $FeCl_3$, guaiac or formalin. Chlorovanillin was useful in referring one set of cultures to *Lactarius* as specialized hyphal elements stained dark blue exactly like laciciferous and oleiferous hyphae in the Russulaceae (Singer 1975).

9.3.2 Results

The rate of recovery of possible symbionts indicate that the surface sterilization - medium combination was a successful method for isolating ectomycorrhizal fungi. The addition of benomyl to the MMN medium increased the rate of recovery from 9.5 to 32.2% on a separate isolation experiment with 1300 root tips. The recovery of possible symbionts from the slope and burn was 36 and 20% respectively. The difference in recovery rate from the two areas was largely due to the presence of very slow growing hyaline species on the slope which were largely absent on the burn.

The fungi isolated from the mycorrhizae were placed in 82 species groups (Table 3). Of these 82 groups, 49 were found in only one sample on either the slope, the burn or both. Sixteen percent of the 82 species

Table 3. Species of Mycorrhizal Fungi Isolated from Two or More Samples at Either Site by Surface Sterilization of Mycorrhizal Root Tips.

	Slope		Burn	
Species or Group	Percent of Samples	Number of Tips	Percent of Samples	Number of Tips
Astraeus hygrometricus	0	0	8	16
Lactarius sp. 1	4	6	21	76
Lactarius sp. 2	3	13	3	5
Rhizopogon rubescens	3	4	4	5
Suillus tomentosus	4	8	0	0
Suillus sp. 2	4	9	15	29
Tricholoma sp. 2488	5	19	0	0
Tricholoma sp. 2	12	41	0	0
Tricholoma sp. 3	2	3	7	12
Tricholoma sp. 4	8	12	0	0
Tricholoma sp. 5	3	6	0	0
Species number 11	45	130	3	2
Species number 22	15	42	0	0
Species number 38	7	11	1	1
Species number 13	4	8	0	0
Species number 58	4	4	0	0
Species number 47	3	7	0	0
Species number 16	3	6	3	8
Species number 91	3	5	0	0
Species number 82	2	5	0	0
Species number 40	2	4	0	0
Species number 12	2	3	0	0
Species number 45	2	3	0	0
Species number 48	2	3	0	0
Species number 51	2	3	0	0
Species number 39	2	2	0	0
Species number 85	2	2	0	0
Species number 14	0	0	12	28
Species number 17	1	2	5	6
Species number 19	0	0	4	13
Species number 32	0	0	4	11
Species number 27	0	0	3	3
Species number 80	1	1	3	3

were found on both areas, 23% exclusively on the burn and 61% only on the slope. The species diversity was almost twice as much on the slope as on the burn, 62 vs. 32 species. The total number of species is very large, especially considering that only one-fifth to one-third of the mycorrhizae yielded viable cultures.

Forty-five percent of the species had clamp connections on the hyphae. This figure is close to that for the Basidiomycetes in general. Lamb and Richards (1970) isolated 40 species of mycorrhizal fungi from the roots of *Pinus radiata* and *P. elliottii* but they included only a few isolates that had simple septa. Zak and Marx (1964) isolated 22 species from mycorrhizae of *P. elliottii* by including primarily clamp-bearing isolates. They also tested isolates lacking clamps and found that 14 of 18 isolates formed mycorrhizae in pure culture. Thus the actual number of species isolated in our study and in the Lamb and Richards study is very close if only the clamped species are included as possible associates. Pure culture synthesis experiments are currently being conducted to determine how many of the 82 isolates can form mycorrhizae with pine.

Only a small percentage of the isolates could be matched up with isolates from fruit bodies or placed in generic groups. The 11 taxa that were recognized accounted for 32% of the isolates but only 9% of the total root tips plated.

Astaeus hygrometricus was isolated exclusively from the burn and *Lactarius* sp. 1 and *Suillus* sp. 2 were more abundant in the burn than on the slope. *Tricholoma* species were more common on the slope and *Suillus tomentosus* (based on only 8 isolates) was confined to the slope. The two most common species isolated from the slope could not be identified (numbers 11 and 22). Of the species that were commonly isolated, it appeared that they occurred at a low frequency over the entire area sampled. Species Number 11 was found in 45 samples on both slope transects with no obvious clustering. Of the possible 15 tips per sample, it occurred on one tip 23 times, two 24 times, three 12 times and four to six 5 times, showing a general rather than clustered occurrence. Data for the other species, where sufficient, indicates similar distribution patterns.

9.4 IDENTIFICATION AND ABUNDANCE OF SPECIFIC MYCORRHIZAL TYPES

In order to determine the importance of specific fungi as mycorrhizae formers, the ideal method would be a direct examination of the root tips. However, few mycorrhizae are distinctive enough to permit identification (fungus species + host; Zak 1973) or if they are distinctive, the fungal associate is usually unknown. Repeated attempts were made during the study to classify the mycorrhizae on the basis of morphology and colour. However, the majority of the mycorrhizae were a nondescript dull reddish brown to blackish and either monopodial or irregularily branched once or twice. This broadly defined type is thought to be formed by a large number of fungi based on our isolation studies. A similar type of mycorrhizae formed the surface crust of *Elaphomyces muricatus* and *E. granulatus*.

Visual estimates of the occurrence and abundance of several distinctive types of mycorrhizae were made on the soil core and seedling samples from the slope and burn. These included mycorrhizae formed by *Cenococcum graniforme* and *Suillus tomentosus* and vinaceous and green types. The *S. tomentosus* type was a dense cluster of dicotomously branched tips enclosed in a felt-like outer mantle of pale brown or vinaceous tinted mycelium. Cultures obtained from this subtuberculate type matched cultures from *S. tomentosus* basidiocarps. The green type may be formed by a species of *Lactarius* as cultures of *Lactarius* sp. 1 developed erect hyphal aggregations of green hyphae. Synthesis studies are being conducted with *Lactarius* sp. 1. Green rhizomorphs were attached to the green mycorrhizae and were often fused to suberized roots. The green pigmentation was erratic and abruptly disappeared giving rhizomorphs that were either hyaline or green.

Two of the seven specific mycorrhizae types which yielded cultures of *Lactarius* sp. 1 were green. The inconsistant occurrence of green pigmentation would result in an underestimate of the abundance of this type. The vinaceous type was distinctive due to the colour and the abundance of radiating vinaceous mycelial strands. This type could not be cultured by direct isolation techniques.

The occurrence of the mycorrhizae types showed distinct site preferences (Table 4). *Cenococcum* was common in both the slope and burn, while the *Suillus* and vinaceous types were largely restricted to the mature pine stand. Green mycorrhizae were infrequently observed and green rhizomorphs were most common on the burn. These results are in agreement with the distribution of basidiocarps of *Suillus tomentosus* and *Lactarius* sp.1 (Table 2) and the direct isolation data (Table 3).

Cenococcum was widely distributed but it was usually present as only a small fraction of the total mycorrhizae (Table 5). The *Suillus* type rarely constituted more than 5% of the total. As *Suillus tomentosus* was the most common mycorrhizal fungus fruiting in mature pine stands, these data show the lack of a quantitative correlation between sporocarps and mycorrhizae abundance.

Direct isolations were attempted from distincitve types of mycorrhizae in October 1975 and April and June 1976 in order to try to link specific

Table 4. Occurrence of Specific Mycorrhizal Types in Core and Seedling Samples in June 1976.

		Number of Samples Each Type Occurred In				
Area	Total Number of Samples	*Cenococcum*	*Suillus*	Vinaceous	Green	Green Rhizomorphs
Slope transects	100	96	45	21	2	2
Burn - transect	50	41	0	0	4	17
Burn - seedlings	25	23	1	0	3	-

Table 5. Visual Estimates of *Cenococcum graniforme* and *Suillus tomentosus* Mycorrhizae in Core and Seedling Samples as a Percentage of the Total Mycorrhizae.

		Percent Abundance Classes				
		0	<1	1-5	5-30	30
Site	Total Samples	*Cenococcum* - Number of Samples in Each Abundance Class				
Slope transects	100	6	56	27	8	2
Burn - transect	50	9	23	9	8	0
Burn - seedlings	25	2	17	5	1	0
		Suillus - Number of Samples in Each Abundance Class				
Slope transects	100	55	26	13	5	0
Burn - transect	50	50	0	0	0	0
Burn - seedlings	25	24	1	0	0	0

fungi with mycorrhizae types. Isolates derived from the mycorrhizae were compared with isolates from basidiocarps. Basidiomycetes and a few hypogeous ascomycetes were collected from the Richardson site and lodgepole pine stands in central Alberta. The fungi were isolated by breaking the fruit bodies and plating small pieces of the context or peridium and hymenial tissues on MMN and MMN + benomyl media. Of the 38 taxa in which isolations were attempted from Richardson site, 19 grew in culture (Table 6). Notable among those that did not grow were the hydnums, *Cantharellus cibarius, Chroogomphus rutilis, Hygrophorus* sp. and several species of *Russula*. With the exception of the hydnums, all of these species are generally assumed to be mycorrhizal associates (Trappe 1962). The observation that less than half of the presumed mycorrhizal associates would grow in culture compares fairly well with the maximum 36% recovery from root tips.

9.5 PURE CULTURE SYNTHESIS OF JACK PINE MYCORRHIZAE

Pure culture techniques were used to establish if specific fungi could form mycorrhizae with Jack pine. A variety of containers and substrates were tried in attempt to find a method which would make the most efficient use of growth chamber space and to provide different growth conditions for the roots and shoots. The standard synthesis method in which the entire plant is enclosed in Erlenmeyer flasks places the tops in an unnaturally high humidity environment. The development of a technique with the tops exposed such as used by Trappe (1967) would provide a means to experimentally approach the effects of mycorrhizae on the water relations of seedlings.

9.5.1 Methods Used In All Experiments

Jack pine seeds (DA 93-10-4-74) were subjected to a variety of

Table 6. Isolation of Mycorrhizal Fungi from Sporocarps.

Species	Probable Associate	Growth in Culture
Alpova diplophloeus	Green alder	+
Amanita muscaria	Jack pine	+
Armillaria ponderosa	Jack pine	+
Astraeus hygrometricus	Jack pine	+
Bankeri fuligineo-alba	Jack pine	-
Boletus sp. (2487)	Jack pine or alder	+
Cantharellus cibarius	Jack pine	-
Chroogomphus rutilis	Jack pine	-
Coltrichia perennis (Fr.) Murrill	Saprophyte?	+
Cortinarius ?semisanguinensis	Jack pine	-
Elaphomyces granulatus	Jack pine	-
E. muricatus	Jack pine	-
Gautieria ?monticola	Jack pine	-
Geopora cooperi	White spruce	-
Hysterangium separabile	Lodgepole pine	-
Hydnellum peckii	Jack pine	-
Hydnum imbricatum	Jack pine	-
Hygrophorus sp. (2478)	Jack pine	-
Laccaria laccata	Jack pine and bearberry	+
Lactarius rufus	Jack pine	+
L. sp. (2454 and others)	Jack pine	+
L. sp. (2474)	Jack pine or others	-
Leccinum sp.	Jack pine	+
Rhizopogon rubescens	Jack pine	+
R. subsalmonius	Lodgepole pine	+
R. sp. 2065	Lodgepole pine or spruce	+
R. sp. 2069	Lodgepole pine	+
Russula brevipes	Lodgepole pine	-
R. spp. (6 species)	Jack pine	-
Suillus tomentosus	Jack pine and bearberry	+
S. sp. 2467	Jack pine	+
S. sp. 1940	Lodgepole pine or others	+
Thelephora terrestris	Jack pine	-
Tricholoma flavovirens	Jack pine	+
T. zelleri	Jack pine	+
T. sp. 2488	Jack pine	+
T. sp. 1730	Jack pine	+
T. sp. 2444	Jack pine	+
T. sp. 2453	Jack pine	-
T. sp. 2469	Jack pine	+
T. sp. 2476	Jack pine	+

treatments to sterilize the seed coats and initiate germination (Table 7). The most successful method was to soak the seeds in cold running water for 24 hr followed by 30 min exposure to 30% H_2O_2. Soaking in cold water or long exposure to H_2O_2 resulted in lower rates of germination. Contamination was low with all treatments. The sterilized seeds were rinsed with sterile water and placed on 0.7% water agar plates. The plates were taped shut and placed on edge in a light cabinet (16 hr day, 8 hr night) at room temperature. Placing the plates on edge resulted in straight radicles ~~which~~ that were easy to plant. Seedlings were planted when the radicles were 1 to 3 cm long.

The growth chambers were set for an 18 hr day, 6 hr night cycle with 2000 ft-C at the seedling level. The temperature in the substrates was a constant 18°C. The nutrient medium used in all experiments was MMN solution (Marx 1969). The criteria for confirming mycorrhizal formation were the presence of a mantle and Hartig net as determined with hand cut sections and recovery of the symbiont on MMN agar.

9.5.2 Preliminary Synthesis Studies With Test Tubes And Exposed Tops

Glass test tubes 150 x 25 mm with a drain hole approximately 4 mm diameter were used in the first series of experiments. These tubes were not sealed and were periodically watered with water or MN mineral salts (Marx 1969) by inserting a hypodermic needle beneath the substrate surface and thus reducing the chance of washing in airborne spores. The substrate was either pure fine grained sand or a mixture of sand and peat moss (4:1, V:V). The tubes with sand and MMN solution were autoclaved for 15 min and one seedling planted in each tube. The initial moisture content was about 21% in the sand tubes and 29% in the sand - peat tubes.

A set of 120 tubes was inoculated with isolates of mycorrhizae

Table 7. Germination of Jack Pine Seeds Subjected to Water and H_2O_2 Treatments.

Water Treatment	Min. in H_2O_2	Number of Seeds	Germination, % 7 da	21 da	Contamination %
None	30	30	0	0	0
Running, 10°C, 48 hr	30	20	30	40	0
Running, 10°C, 48 hr	60	23	35	43	0
Running, 10°C, 48 hr	120	30	23	23	7
Soak, 3°C, 48 hr	30	20	25	30	0
Soak, 3°C, 48 hr	60	25	20	24	0
Soak, 3°C, 48 hr	120	30	13	13	0
Running, 5-10°C, 24 hr	30	355	41	43	-
Running, 5-10°C, 24 hr	30	1028	34	45	1

Table 8. Pure Culture Synthesis of Jack Pine Mycorrhizae in Sand and Vermiculite - Peat Tubes.

Isolate	Substrate	Number of Tubes	Average Shoot	Length Root	pH[2]	Percent[3] Infection
Suillus tomentosus #3[1]	Sand	3	5.3	9.3	6.1	0-10
Suillus tomentosus #3[1]	Vermiculite	4	6.4	26.5	4.7	60-90
Suillus tomentosus #24[1]	Sand	4	6.5	9.1	6.1	1-10
Suillus tomentosus #24[1]	Vermiculite	4	7.7	23.3	4.7	50-90
Suillus tomentosus #1711	Sand	4	6.1	9.9	6.1	0-10
Suillus tomentosus #1711	Vermiculite	1	7.0	13.0	4.8	90
Suillus tomentosus #1715	Sand	2	6.0	13.5	-	0
Suillus tomentosus #1715	Vermiculite	3	7.7	27.7	-	30-60
Scleroderma meridionale	Sand	5	6.2	11.5	6.1	0
Scleroderma meridionale	Vermiculite	4	7.7	31.8	4.5	50-80

[1] Isolated from mycorrhizal roots.

[2] Determined in 1:2 dilution in water.

[3] Visual estimate.

fungi using agar plugs. The mortality rate was unacceptably high in these tubes and root growth was generally poor in the sand tubes. Roots in the sand - peat tubes were much healthier. The pressure of the sand strongly compressed the roots and the sand was nearly impossible to remove. Mycorrhizae formation did not take place in these tubes.

In a second series of experiments using tubes without drain holes, materials were tested for toxicity and effectiveness in sealing the area between the stem and the tube cover. The tubes were filled with sand and MMN solution and the tops sealed with aluminum foil covers that were taped down or rubber serum caps with a hole punched in the center. The foil and serum caps were covered with another layer of aluminum foil until the trees were planted. After the tubes were autoclaved for 15 min and cooled, the protective layer of foil was removed and a hole was aseptically punched through the foil cover near the wall of the tube. The radicle of a germinating seedling was inserted through the hole and the hole sealed with one of the test materials. An 18G hypodermic needle plugged with cotton was inserted in the other side of the tube to provide aeration. It was sealed in with Dow Corning Silicone sealant (Silastic 732) which is toxic if applied directly to the seedlings. After planting, the tubes were wrapped in aluminum foil and placed in the growth chamber. The materials tested were sterile stopcock grease, high vacuum grease, Slipicone, Vaseline and rubber cement. The rubber cement was allowed to thicken by evaporation previous to application so it would not run down the radicle. The procedure with rubber serum caps was similar but the hole for the seedling had been cut out with a cork borer prior to autoclaving.

Of the 47 trees treated with the three silicone materials, 44 were dead within 3 weeks. The trees died slowly with the tops gradually drying out. The roots appeared healthy indicating that the silicone materials interferred with water movement to the tops. The Vaseline was nontoxic but it did not make a firm seal around the stem. After 3 weeks, 5 of the 40 seedlings treated with rubber cement had died. In all five cases, the radicle had failed to penetrate into the sand. In that the radicle could be seen along the wall of the tube when a foil cover was used, the combination of foil and rubber cement was used in all future experiments. Rubber cement has previously been used by Trappe (1967) in synthesis studies and showed no toxic effects with prolonged seedling growth.

Tubes containing healthy seedlings sealed with rubber cement were inoculated with cultures derived from pine mycorrhizae or sporocarps. Inoculum was prepared according to Zak (1976b) and 1 ml of the mycelial suspension was injected directly onto the roots in each tube. The hole made by the hypodermic needle was sealed with Dow Corning Silicone sealant. A spore inocula of *Astraeus hygrometricus* and *Scleroderma meridionale* were prepared by cutting open gastrocarps collected in April, removing some spores and dispersing the spores by shaking them in a sterile solution of 0.2% Tween 20 in bottles containing pieces of broken glass. One milliliter of the spore suspensions (*Astraeus* = 10^6 spores/ml, *Scleroderma* = 4×10^5 spores/ml) were injected onto the roots in the same manner as the mycelium. The tubes were placed in the growth chamber and periodically sterile water and MN salts were aseptically added.

The use of sand as a substratum was generally unsatisfactory as the tubes required frequent additions of water which resulted in a high rate of contamination. In addition mortality was high probably due to either poor water relations or poor aeration. In addition, the roots were difficult to clean. Regardless mycorrhizae formed in some tubes which met the criteria of sterility and symbiont recovery. Mycorrhizae were formed by *Suillus tomentosus, Scleroderma meridionale* and *Rhizopogon rubescens* from mycelial suspensions and *Astraeus hygrometricus* from spore inoculum. No mycorrhizae were formed in uninoculated tubes. In all cases the tops of seedlings showed nutrient deficiencies while the root systems appeared healthy.

9.5.3 Synthesis In Vermiculite - Peat Substrate

A mixture of peat moss and vermiculite has been the traditional substrate for mycorrhizae synthesis studies (Marx & Zak 1965). Due to the poor results obtained with sand the major synthesis efforts were made using a vermiculite - peat mixture in both the 150 x 25 cm sealed tubes with tops exposed and confined seedlings in 1 L Erlenmeyer flasks. The proportions of substrate were those used by Zak (1976b) with 420 ml of sieved vermiculite, 30 ml peat moss and 275 ml MMN solution per flask. The flasks were autoclaved for 30 min and the final pH of the medium was 5.2. A series of tubes filled with the same substrate was set up with aluminum foil tops and rubber cement sealant. For comparative purposes a series of tubes using sand was also tested. One seedling was placed in each flask and in each tube. If the shoot had not appeared after two weeks in the flasks they were replanted. Five replicates were used for each treatment. Inoculum was in the form of mycelial suspensions (Zak 1976b) and 10 ml was added to each flask and 1 ml to each tube at the time of planting.

Due to an apparent malfunction of the growth chamber after 4 months growth, many of the seedlings suddenly died and others had a portion of the needles turn reddish brown. At this time all of the trees in tubes were harvested and a portion of the trees in flasks. All contaminated flasks or tubes were discarded.

The superiority of the vermiculite substrate as compared to sand was readily evident (Table 8). The degree of infection of four strains of *Suillus tomentosus* never exceeded 10% in sand and ranged from 30-90% in vermiculite. *Scleroderma* infected a majority of the root tips in the vermiculite substrate but all the feeder roots were mycorrhizal-free in sand.

The only trees in flasks that were harvested after 4 months growth were those that did not survive the growth chamber malfunction or that were contaminated. Mycorrhizae were formed by *S. tomentosus* (1715), *Scleroderma* (1814) and an unknown root isolate. *Rhizopogon rubescens* also formed mycorrhizae in a single, nonreplicated flask with Jack pine roots. A series of flasks were inoculated with parts of the ascocarps of *Elaphomyces granulatus*, a fungus that cannot be cultured. No mycorrhizae were formed after 3 months. Exposure of the intact ascocarp to 95% ethanol for 30 min failed to surface sterilize it and contaminants were introduced with the inoculum.

9.6 OBSERVATIONS ON *HUDSONIA TOMENTOSA* MYCORRHIZAE

Eight entire *Hudsonia* plants were collected 27 April and transported to the laboratory in order to evaluate the mycorrhizal status of the roots. Four were collected on the slope and four from the burn area. The roots were washed free of soil and separated from the roots of other plants. The roots of *Hudsonia* are very fine and fiberous, unlike pine and bearberry, and infection is difficult to determine by direct observation. Thus the roots were cleared and stained following the procedure of Phillips and Hayman (1970). A single root from each plant was randomly selected and the number of mycorrhizal and nonmycorrhizal root tips counted with the aid of a dissecting microscope.

The only mycorrhizal type that could be identified was formed by *Cenococcum graniforme* and it was the most common fungus on the roots (Table 9). It infected 15.6 and 14.0% of the root tips from the slope and burn, respectively. The dominance of *Cenococcum* on this pioneer species may be related to its drought tolerance. *Cenococcum* mycorrhizae have been reported to be dominant on trees in droughty soils (Trappe 1962). *Cenococcum* has not previously been reported to be associated with *Hudsonia* (Trappe 1964).

Mycorrhizae formed by other fungi composed only 3.5% of the root tips on the slope and 6.4% of the roots on the burn. The counts made on the April samples did not indicate any differences between the two areas. It is interesting that 80% of the root tips were not infected. A majority of the Jack pine roots collected at the same time were dark and wrinkled and appeared old and inactive. Many of the *Hudsonia* root tips rated as noninfected were lightly covered with *Cenococcum* hyphae and the degree of infection may have increased with time. Plants were sampled later in the season but the roots have not been examined.

9.7 BEARBERRY MYCORRHIZAE

Collections of bearberry roots made in the fall of 1975 showed that this species was both ectomycorrhal and ectendomycorrhal. In order to examine the frequency of the two anatomical types 20 bearberry plants in the burn and 20 on the slope were sampled in June and September, 1976. The June samples were preserved in FAA and have not been examined. The September samples were cleaned and hand sections cut of 150 mycorrhizae.

All 150 mycorrhizae selected were still attached to the plant.

Table 9. Mycorrhizae Occurring on Roots of *Hudsonia tomentosa* in April 1976.

		Percent		
Sample	Number of Root Tips	*Cenococcum*	Other Mycorrhizae	Noninfected
Slope 1	297	9.8	0.7	89.6
Slope 2	244	3.3	2.5	94.3
Slope 3	517	29.0	6.2	64.8
Slope 4	147	20.4	4.8	74.8
Burn 5	485	15.5	6.2	78.3
Burn 6	305	25.6	0.7	73.8
Burn 7	446	11.2	4.0	84.8
Burn 8	640	3.9	14.8	81.3

In contrast to 1975, the ectomycorrhizal type was rare as only 6 of the 150 mycorrhizae were of this type. The remaining samples must be sectioned to determine if there is a seasonal effect.

In order to determine the associates of bearberry it is necessary to perform synthesis experiments as is being done with Jack pine. However we have been unable to germinate the seeds under aseptic conditions. Several techniques have been used including the procedure outlined by Zak (1976a) but all have failed up to this time. Modifications of Zak's technique are now being tried.

9.8 CONCLUSIONS

It is apparent that a large number of mycorrhizal fungi are associated with Jack pine at the Richardson site. No single species or group of species could be shown to be dominant by observations on sporocarps, mycorrhizae or by direct isolation techniques. However the three methods of studying mycorrhizal fungi did compliment each other in demonstrating the distribution of these fungi on disturbed and nondisturbed areas. Fungi typical of disturbed soils were *Astraeus hygrometricus, Scleroderma meridionale, Rhizopogon rubescens, Laccaria laccata* and a species of *Lactarius*. Fungi typical of mature Jack pine - lichen forests were *Elaphomyces granulatus, E. muricatus,* hydnums, two species of *Suillus, Chroogomphus rutilis* and *Cantharellus cibarius*. Additional observations are required to confirm these distribution patterns and isolations from more sporocarps may permit the identification of species now known only in culture and thus not identifiable.

Previous to this study no mycorrhizal associations of Jack pine had been confirmed by aseptic synthesis techniques (Trappe 1962). Although these studies are still in progress and this report is preliminary, the following species have been confirmed in at least one test: *A. hygrometricus, S. meridionale, Suillus tomentosus* and *R. rubescens*. The first two species have never been subjected to synthesis experiments previously.

From the experiments and observations made in 1975 and 1976, candidate species for inoculation and field performance tests have been made. Most of these are species characteristic of the dry, disturbed areas and from which mycelial inoculum can be prepared. The species selected are *Cenococcum graniforme, A. hygrometricus, S. meridionale, S. tomentosus, Lactarius* sp. and *Tricholoma* sp. In addition *Pisolithus tinctorius,* the fungus used so successfully by Marx (e.g. 1975) will be included.

9.9 FUTURE RESEARCH

(a) Contination of pure culture synthesis experiments on Jack pine.

(b) Inoculation of Jack pine seedling with the candidate species for efficiency tests. The seedlings will be planted in either oil sands tailing transported to Calgary or in the GCOS dike.

(c) Development of a system in which the roots are in a sterile environment and the tops exposed. This system will be used to determine the effects of mycorrhizae on the moisture relations of Jack pine seedlings.

(d) Attempts to synthesize mycorrhizae with fungi that cannot be cultured, e.g., hydnums and hypogeous ascomycetes. The species used will depend on which species fruit at the Richardson site.

(e) A brief study of the types of mycorrhizae on Jack pine growing on sand dunes to determine if certain fungi are adapted to pioneer situations. These mycorrhizae will be compared to those found in mature pine stands.

(f) Further attempts to grow bearberry and *Hudsonia* under aseptic conditions and to synthesize mycorrhizae with them.

9.10 ACKNOWLEDGEMENTS

We wish to express our appreciation to J.M. Trappe for identifying *Elaphomyces granulatus* and *Gautieria ?monticola* and confirming identifications of *E. muricatus* and *Geopora cooperi*, to K.A. Harrison for identifying *Hydnellum peckii* and *Phellodon melaleucus* and to D.R. Hosford for confirming the identification of *Rhizopogon rubescens*. A very special thanks is due to Nancy Whittaker for so ably and patiently performing much of the laboratory work.

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10. ENERGY AND WATER BALANCE MODEL

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10.1 INTRODUCTION

The purpose of the model is to predict the water status of the plants and soil, given a minimal input of environmental measurements. Since these predictions are desired over a wide range of conditions, it is necessary to use a mechanistic rather than an empirical model. Thus, the model must consist of mathematical equations pertaining to the mechanisms of atmospherical, biological, and physical interactions. The equations that we use are either obtained from literature, or derived using our own theoretical developments, or derived using data gathered by reseachers in this project, or derived using data in the literature. The practical situation which we are modelling (nonhomogeneous vegetation on a slope) is very different from the ideal (homogeneous vegetation on level terrain) on which most theoretical and experimental work has been concentrated. In fact, the only work done that is similar to our situation is that of Bergen (1969, 1971), and he considered only one special situation.

However, we are obtaining good results with the model which we have developed, and we have many ideas for its improvement.

10.2 RELATED WORK

Most aspects which are unaffected by the slope can be modelled in ways similar to those reported in the literature. For example, the equations for the energy balance of needle clumps and the diffusion of water through the soil are commonly used (Murphy and Knoerr 1975; Goudriian and Waggoner 1972). However, the momentum and temperature of the air cannot be treated in any standard manner, since existing theory applies only to level surfaces. As previously mentioned, Bergen has made the only attempt to study temperature and wind speed on forested slopes. Modelling the water movement into and through plants, although unaffected by the slope, has not been solved satisfactorily (Gardner et al. 1975). However, in developing our model we have followed Jarvis' (1975) suggestion that the storage of water in sapwood is significant.

10.3 MODEL

10.3.1 General Description

Since the conditions in the atmosphere, plants, and soil vary with height, we must consider interactions at different levels. The microclimatic factors of radiation, temperature, humidity and wind are determined at different levels in the canopy. Then it is possible to calculate the temperature of sunlit and shaded leaves at different heights on the trees. This leads to transpiration at different heights, and integration over height yields total transpiration. This results in a change in average needle water potential and a flow from sapwood to needles. This in turn results in a change in the sapwood water potential and a proportionate flow from the soil into the sapwood. Now the roots are distributed in a certain vertical pattern in the soil so extraction of water from the soil is not uniform over depth. Therefore, we keep track of the soil water potential at different depths. Thus, the equations for radiation, wind speed, air and needle temperature, and soil water potential are solved at several levels, whereas the equations for the water potential of the sapwood and needles are solved once for an average value for the tree. A simplified flow chart of the model is given in Fig. 1. The equations are given in Appendix 1 and symbols used there and in this discussion are defined in Appendix 2.

10.3.2 Canopy Geometry

The pattern of distribution and the amount of needle area in the canopy is based on preliminary measurements of the physiologists (Section 7). View factors of one level of the canopy for another are calculated with a negative exponential function of needle area and a suitable effective area fraction. This results from treating the needle area as randomly distributed which allows treating penetration through the canopy as a Poisson process. However, since the needle area is not random but is clumped to some degree, actual penetration will be greater than expected. Thus, we insert a clumping factor into the negative exponential function to allow for increased penetration. View factors are calculated for diffuse radiation and are used for diffuse shortwave penetration from the sky into the canopy, for shortwave scatter within the canopy, and for longwave radiation transfer.

10.3.3 Shortwave Radiation

Atmospheric radiation is partitioned into shortwave and longwave radiation.

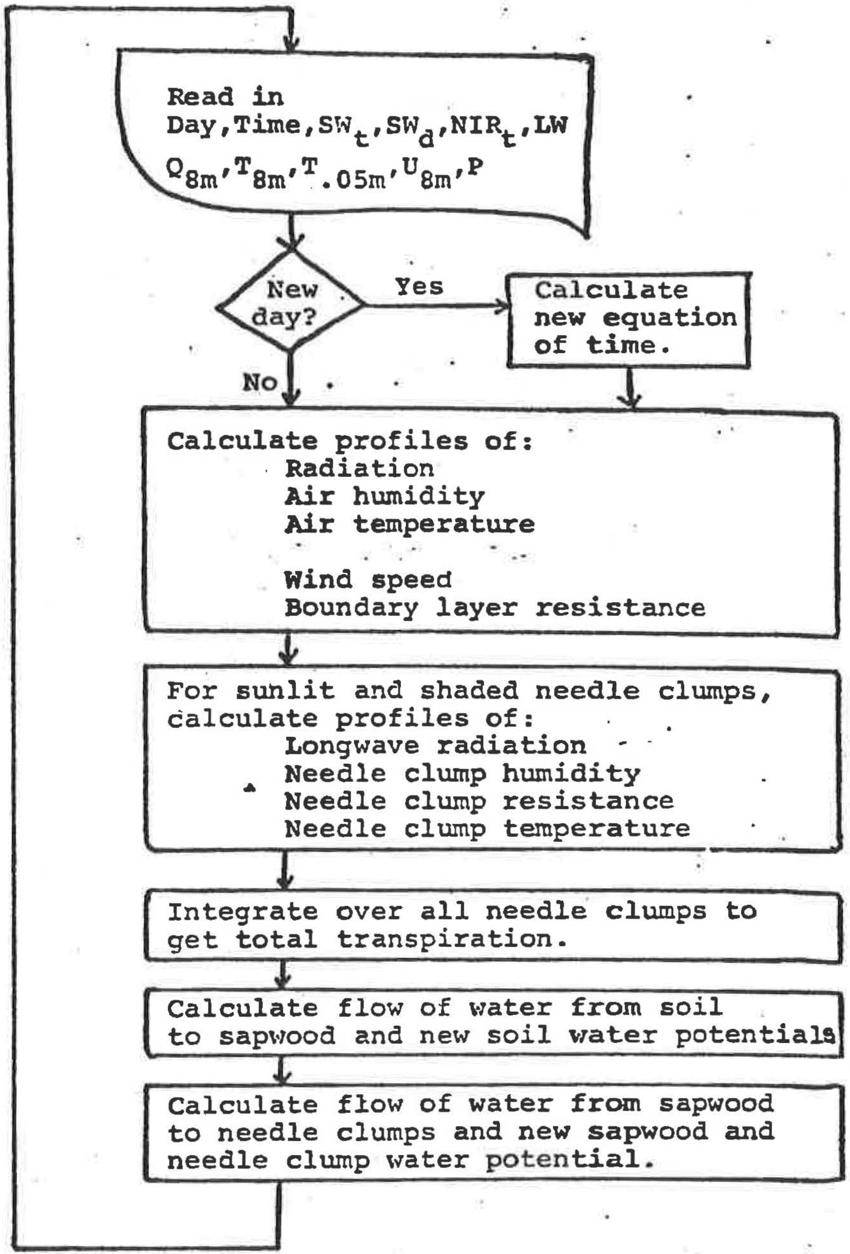

Figure 1. A simplified flow diagram of the model.

Shortwave radiation is divided further into direct and diffuse PAR and direct and diffuse NIR. From three measurements at the top of the hill, the four types of shortwave radiation are calculated using formulae derived from data of Sceicz (1974). The actual amount of diffuse radiation intercepted by the slope comes from the sky and from reflection off the forest on the plain below. The angle of incidence and the azimuth of direct radiation intercepted by the slope is a complex function of the latitude and longitude of the site, the slope and aspect of the hillside and the year, day, and time. Equations are derived using data from the American Ephemeris for 1974 and using equations ~~for~~ from Gloyne (1965).

The amount of direct radiation penetrating to any level in the canopy is the intensity of radiation from the sun times the view factor for direct radiation at the angle of incidence. The amount of diffuse radiation impinging on the hillside times the view factor, plus the sum of the reflected direct radiation from other levels in the canopy. no verb

Finally, we can calculate the shortwave radiation absorbed per m^2 needle surface area for needle clumps in direct sunlight and needle clumps in the shade. It is important to note that all of the view factors and penetration probabilities can be calculated independently of the rest of the model and the results stored in an array which can be quickly referenced by the model.

10.3.4 Air in the Canopy

The air temperature at any level in the canopy is approximated by the average of the temperature at canopy height and the value resulting from a line drawn from the temperature at canopy height to the temperature at 5 cm above the lichen carpet. We have resorted to this empirical approximation because there is no theory for heat transfer in a non-homogeneous plant canopy on a slope. Indeed, the equations using eddy diffusivity which have been applied to homogeneous canopies on level ground do not produce entirely satisfactory temperature profiles (Mehlenbacher and Whitfield 1977). However, the crude approximations used here do provide us with fairly good temperature profiles as seen in Fig. 2.

The air specific humidity profiles are surprisingly constant and so the specific humidity at any level can be approximated by the specific humidity at canopy height (Fig. 3).

Wind speed is exponentially attenuated into the canopy.

10.3.5 Energy Balance

The temperatures of the sunlit and shaded leaves at each level are found as solutions of energy balance equations of the form

$$ASW + ALW = \rho_a \, Cp \, \frac{(T_n - T)}{r_b} + \rho_a \, Lt \, \frac{(Q_n - Q)}{r_b + r_n}$$

We have already discussed the determination of ASW, T, and Q. So now we shall discuss in turn the air density (ρ_a), heat capacity (Cp) latent heat of vaporization (Lt), needle clump boundary layer resistance (r_b), needle clump transpiration resistance (r_n), and net absorbed long-wave radiation (ALW).

Air density is a function of air temperature derived from measurements in List (1966), and heat capacity is considered constant. The latent heat of vaporization for water in a needle clump is a function of needle clump temperature adapted from Murphy and Knoerr (1972). Needle clump boundary layer resistance has been determined as a function of wind speed for ponderosa pine needle clumps by Gates et al. (1965) (Fig. 4).

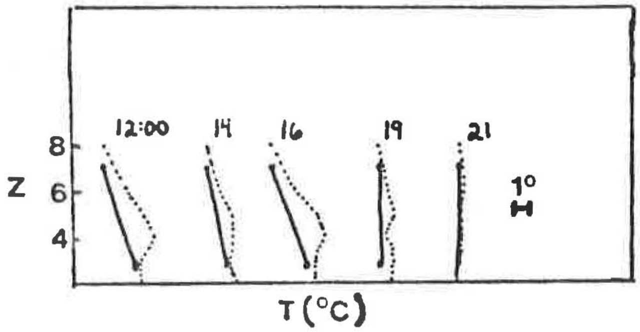

Figure 2. Modelled (solid line) and measured (dotted line) air temperature (T) variation with height (Z).

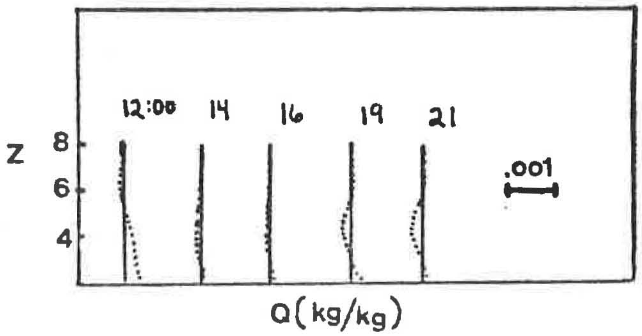

Figure 3. Modelled (solid line) and measured (dotted line) air specific humidity (Q) variation with height (Z).

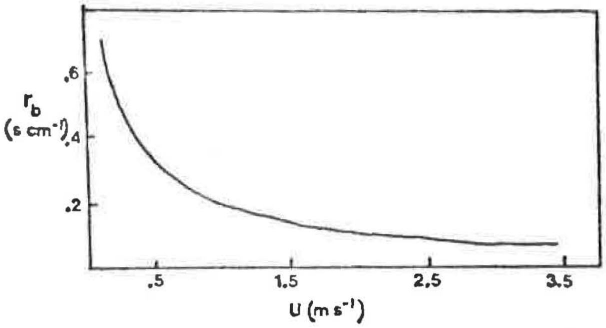

Figure 4. Needle clump boundary layer resistance (r_b) as a function of wind speed (U).

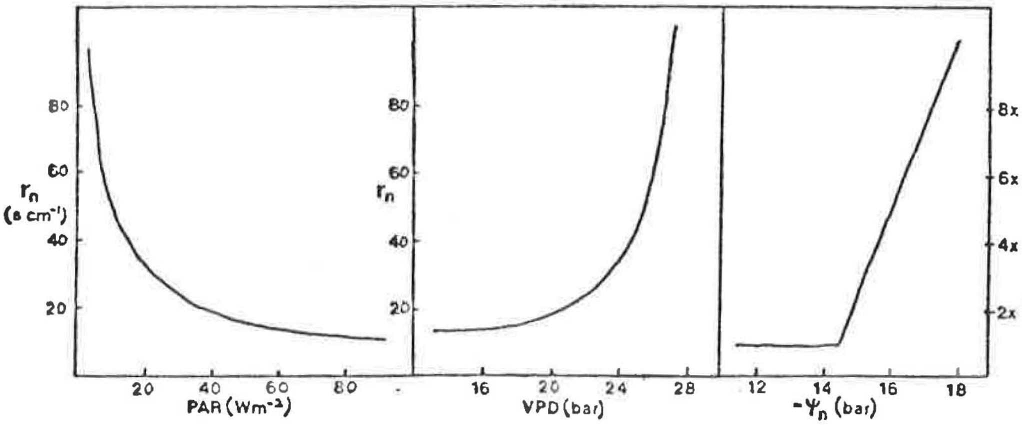

Figure 5. Needle clump transpiration resistance (r_n) as a function of visible radiation (PAR), vapor pressure deficit (VPD), and needle clump water potential (ψ_n).

Transpiration resistance has been studied quite intensively by the physiologists. It is a function of intensity of PAR, vapour pressure deficit, and water potential of the needles. Therefore, resistance is calculated separately for sunlit and shaded needle clumps. Figure 5 shows that transpiration resistance increases with decreasing PAR, with increasing VPD, and with increasing ψn.

The net longwave radiation at any level is a function of the longwave radiation lost by emission proportional to the needle clump temperature at that level. Therefore, it is also calculated separately for sunlit and shaded leaves. It is also a function of the longwave radiation emitted by the sky, the needle clumps at other levels, and the lichen mat, and the view factor of these sources for the level being considered.

The needle clump temperatures are obtained by an accelerated iterative solution of the energy balance equations. Then the specific humidity is obtained using an equation from Murray (1967).

10.3.6 Plant Water

The plant water environment has been partitioned into two compartments - sapwood and needle clump. The flow of water from the soil into the sapwood is the sum of the flows from the soil layers, which are functions of the sapwood water potential, the water potential and root area of the soil layers, and the root resistance. The flow of water from the sapwood into the needles is a function of the sapwood-needle water potential gradient and the sapwood resistance. Total loss of water from the needles to the air is the sum of transpiration from sunlit needles and shaded needles. Each of these is the sum over all layers in the canopy of a function of air and water density, needle clump-air specific humidity gradient, boundary layer and stomatal resistance, and needle area in the layer.

The dry weight of sapwood per m^2 area was obtained from estimates of sapwood radius (from R. Swanson), estimates of total tree volume, and the approximate density of Jack pine sapwood. The soil water potential is considered in the next section, and the distribution of root area is a reasonable estimate. Reasonable values of r_r and r_t can be obtained since assigning a steady state, we have

$$E = \Delta t \frac{(\psi t - \psi n)}{r_t} = \Delta t \sum_i \frac{(\psi s,i - \psi t)}{r_r} A_{r,i}$$

Using model simulations to obtain value of E and measurements of our plant physiologist and soil physicist we find that r_t and r_r are on the order of 10^{13} $Psm^{-3}kg$. The boundary layer and stomatal resistance have been discussed in the energy balance section.

As a result of the flow of water along potential gradients, the water content of each compartment changes during each time interval. The change in water content of the sapwood is the difference between the flow in from the soil and the flow out to the needle clumps. The change in water content of the needle clumps is the difference between the flow in from the sapwood and the flow out to the atmosphere. These changes in water content are added to the old water contents and updated water potentials are determined using a linear empirical formula based on measurements of the physiologists.

10.3.7 Soil Water

At the start of the simulation we are provided with the profile of soil water potentials, and then at half hr intervals we calculate the change in $\psi s,i$ resulting from uptake by the plants and from diffusion

Daily precipitation which penetrates through the Jack pine and lichen canopy is added into the soil water budget at midnight. Not all of the precipitation enters the soil system. Much of it is intercepted by and subsequently evaporated directly from the needle and lichen surfaces. The amount of precipitation intercepted by the needles is a function of interception of precipitation impinging directly on the needles and overflow from needles above. An empirical function of interception by the trees in terms of rainfall intensity has been derived using data of the meteorologists (Section 3). The lichenologist has provided a good average for interception by the lichen mat and needle duff. The water reaching the soil is distributed over the soil layers, assuming the top layer is filled to field capacity, then the next layer down, and so on. Water retention curves for 0 - .075m, .075m - .15m, .15m - .35m, and .35m + are stored in a table, and at each time interval the current $\theta_{s,i}$ is found by interpolation from the table using the current $\psi_{s,i}$. Now we are ready to consider the change in volumetric soil water content due to root extraction and diffusion. The change due to root extraction is a function of the sapwood-soil water potential difference, the root surface area, and the root resistance to water uptake. The change due to diffusion is a function of changing water potential with depth and hydraulic conductivity. The diffusion equation is a partial differential equation solved by finite differencing, while the hydraulic conductivity is a function of the water content. Finally, the new water potential is obtained by looking up the soil water potential in the tables corresponding to the water content $\theta_{s,i} + \Delta\theta_{s,i}$.

10.4 RESULTS

The model has been tested extensively using data from 7 May to 31 August, 1976. The predictions have been compared with measurements taken during intensive runs.

10.4.1 Diurnal Behavior

The most significant prediction made by the model is the water potential of the needle clumps since this is an indication of the stress.

Figure 6 shows diurnally predicted needle clump water potential and measured xylem tension for several of the intensive runs. The predicted plant water potential depends strongly on the predicted transpiration rate which is in turn a function of the calculated needle clump temperatures.

Figure 7 shows several measured and predicted profiles of needle clump temperature.

10.4.2 Seasonal Behaviour

Figure 8 shows the predicted pattern of transpiration through the summer. The cumulative loss of water from the system due to transpiration is compared with measured total loss in Fig. 9. Figure 10 shows the seasonal pattern of water content in the top meter (root zone) of the soil. Figure 11 shows the predicted pattern of daily maximum and minimum needle clump water potentials. Several measurements of water potential were taken throughout the summer. A comparison of the model predictions and the measurements is shown in Fig. 12. What would be perfect agreement is indicated by the dashed line.

10.4 DISCUSSION

The present version of the model produces good predictions of

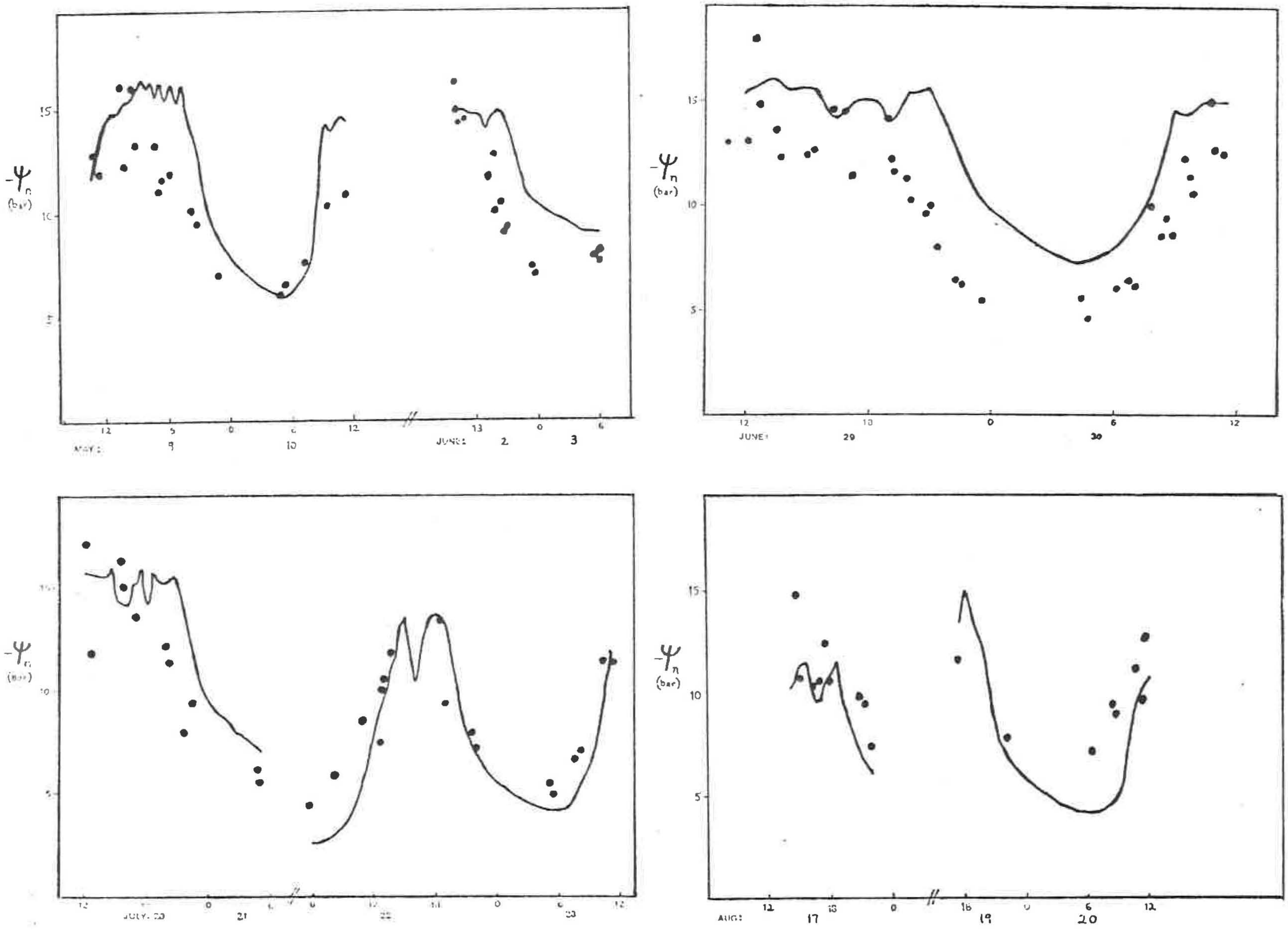

Figure 6. Diurnal trends of needle clump water potential at several times through the summer. Model - solid line; Measurements - dots.

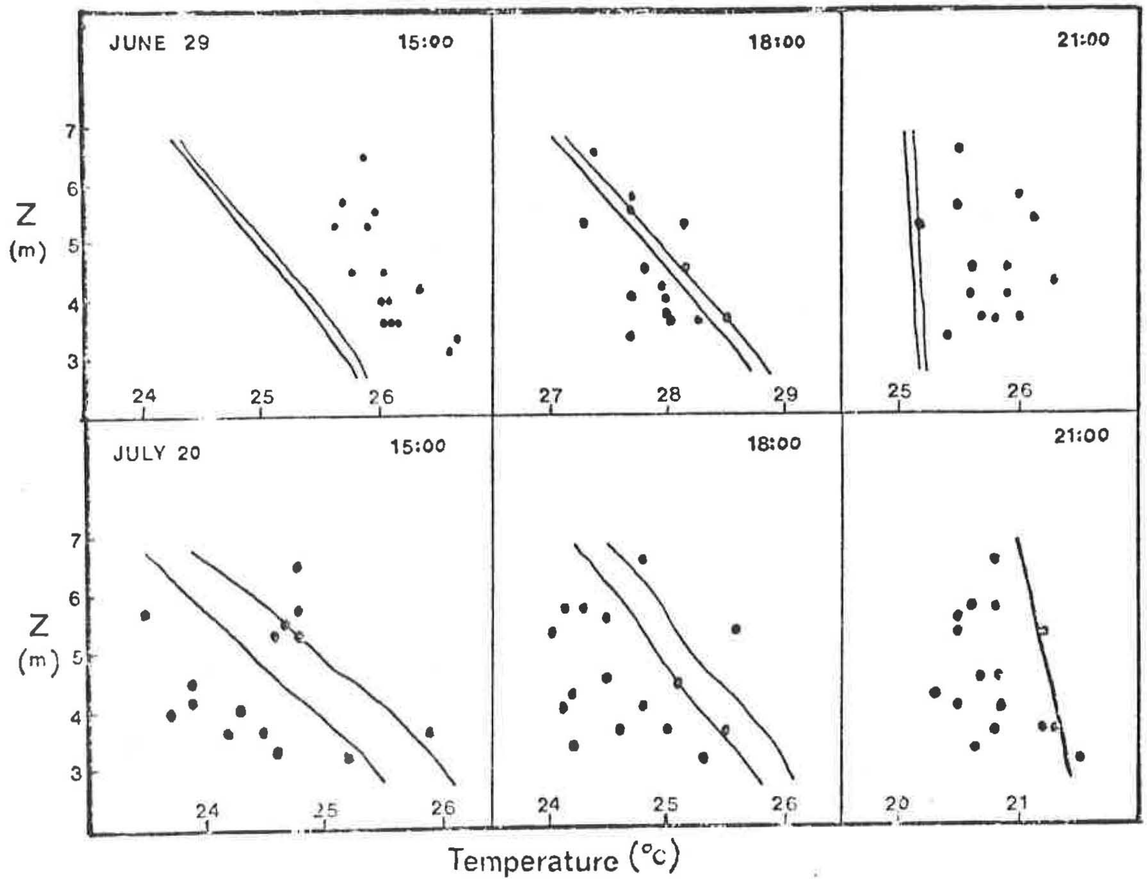

Figure 7. Temperature profiles of sunlit and shaded needle clumps at several times through the summer. Model - solid line; Measurements - dots.

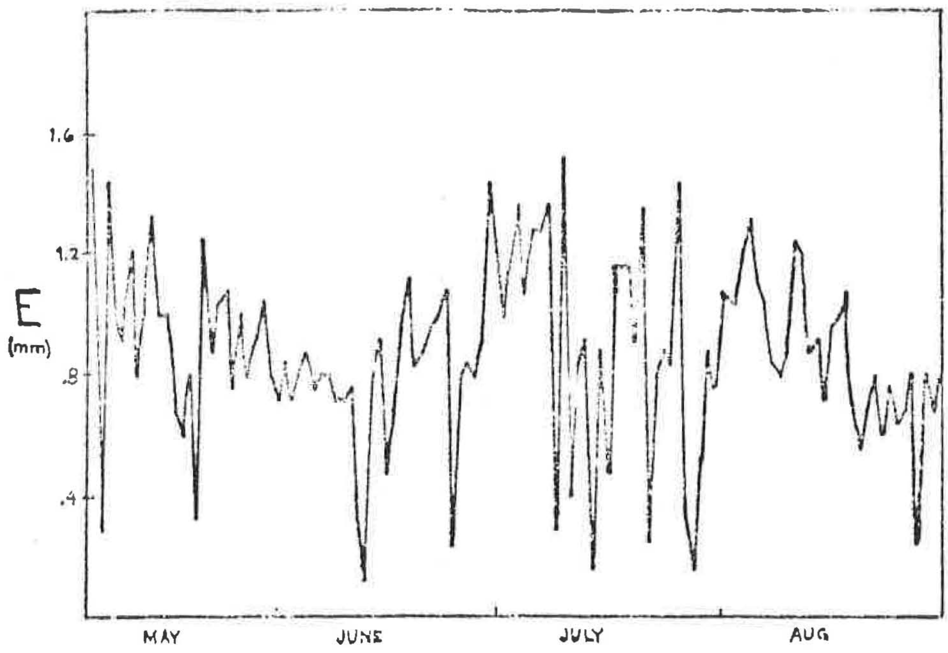

Figure 8. Seasonal pattern of total transpiration (E) predicted by the model.

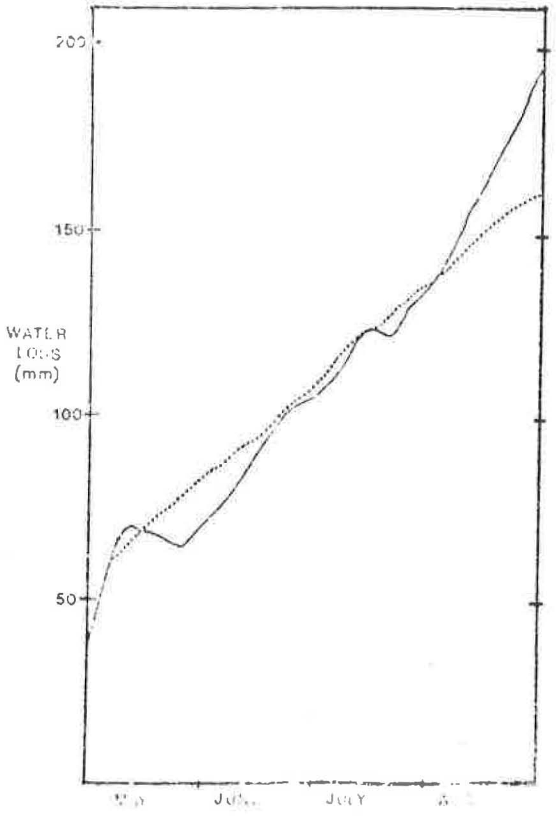

Figure 9. Cumulative loss of water from the system by transpiration (dotted line) compared with cumulative loss of water from the soil (solid line).

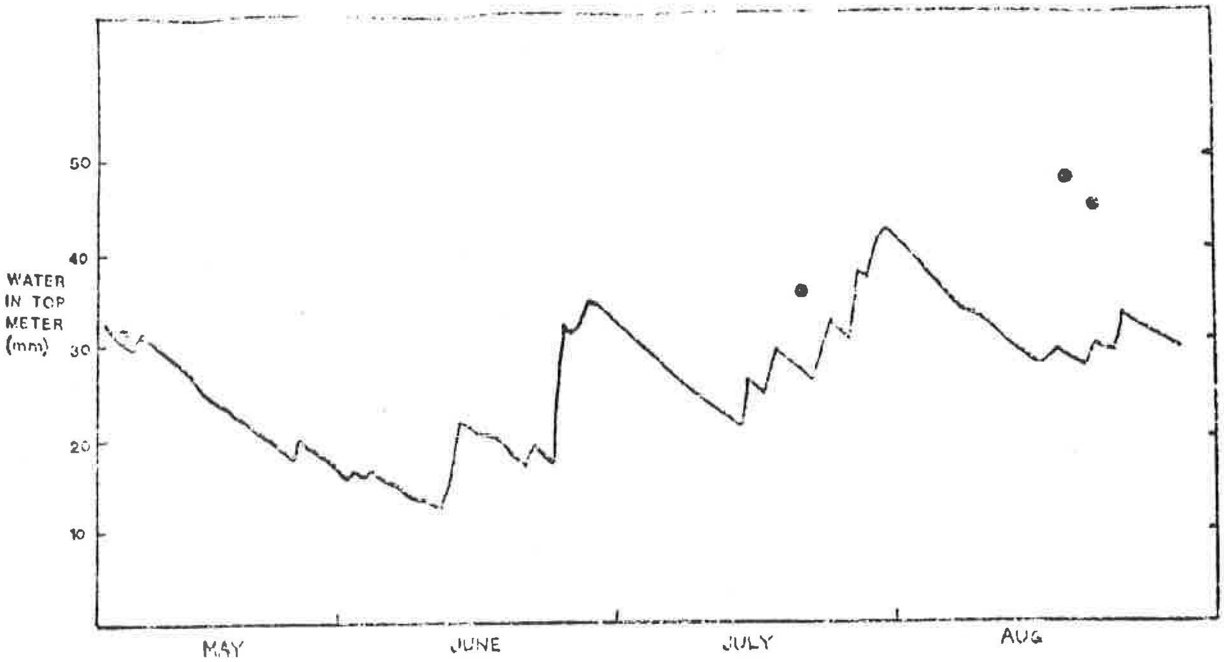

Figure 10. Seasonal pattern of water content in the top meter of soil. Model - solid line; Measurements - dots.

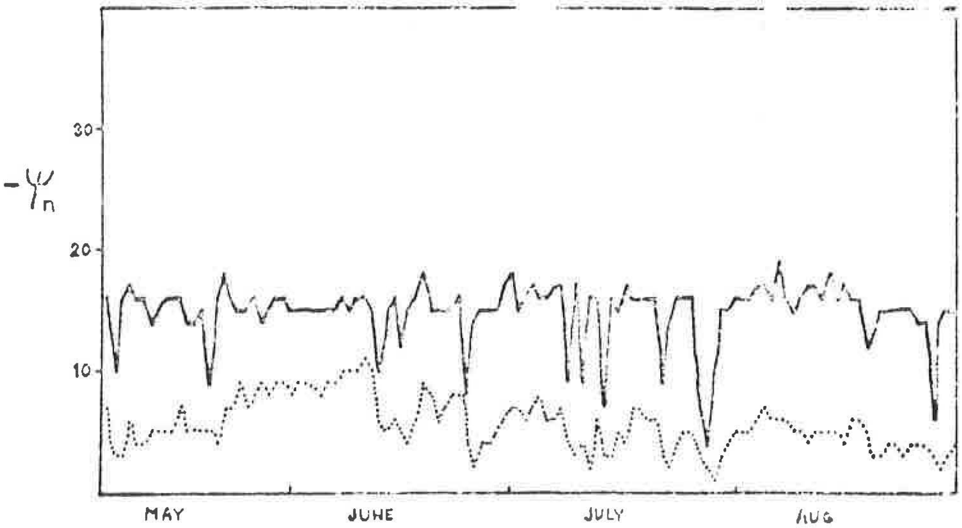

Figure 11. Seasonal pattern of needle clump daily maximum and minimum water potentials predicted by the model.

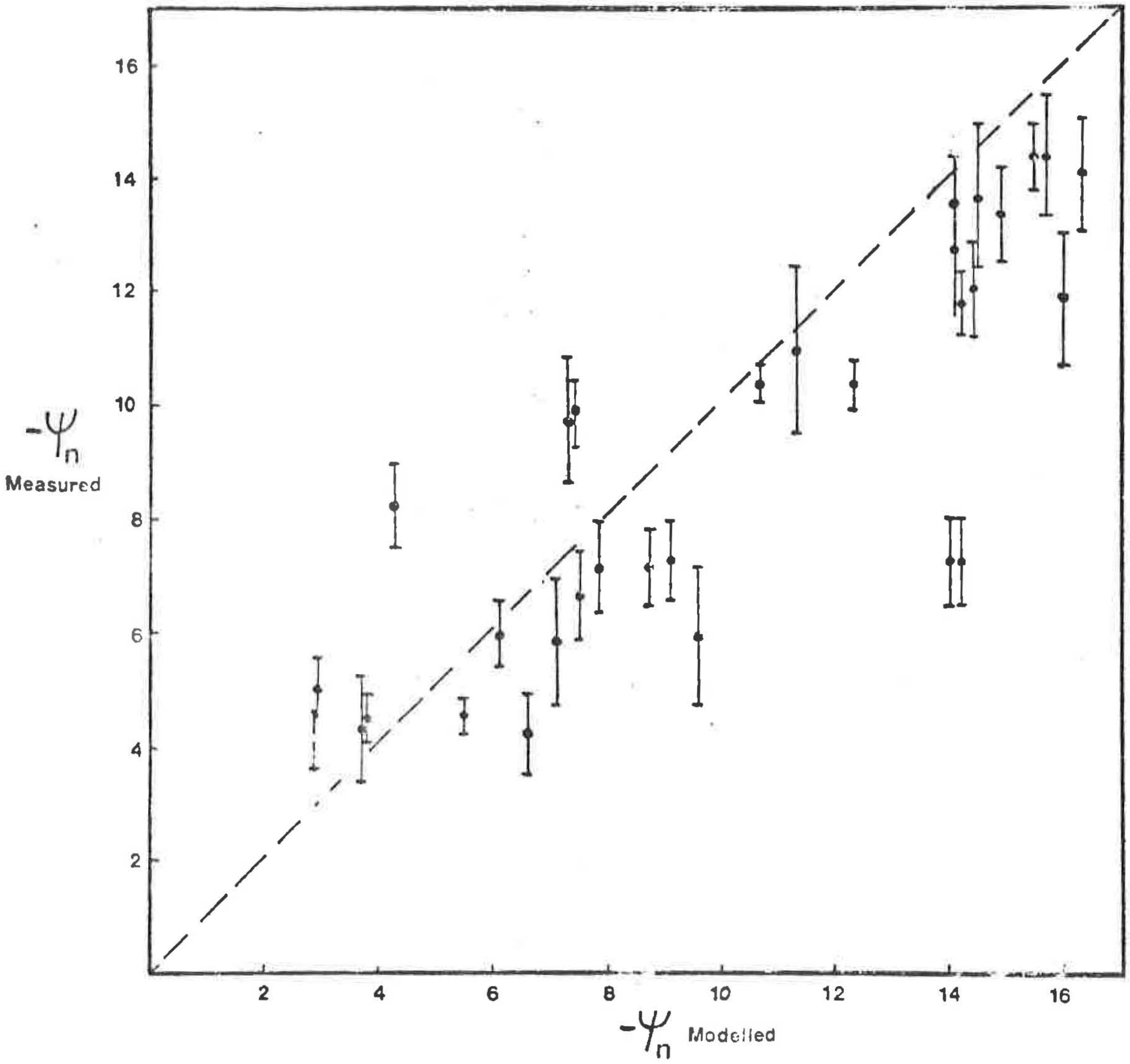

Figure 12. Comparison between model predictions and field measurements of needle clump water potential. Flags denote confidence intervals.

the heat and water status of the Jack pine forest system.

The predicted needle clump temperature profiles pass through or near the data points (Fig. 7). The cause of too high or too low average needle clump temperature is probably the simple model of air temperature. The differences between sunlit and shaded needle clump temperatures are probably not large enough. This may be due to the too simple radiation model.

The predicted diurnal trends of needle clump water potential are similar to the diurnal trends of the measurements (Fig. 6), although in general the modelled needle clumps tend to start to recover about two hours later than the real needle clumps. This is probably due to a lack of detailed information on trunk resistance (r_t) and root resistance (r_r). This is probably also the cause of the differences between measured and modelled potentials in Fig. 12. The modelled potentials are predicted by conceptually sound mechanistic equations, but these equations contain the resistances r_t and r_r. Probably these resistances are complex functions of several environmental and biological factors, but we know little about such functions. Therefore, we chose reasonable but arbitrary values which were kept constant for the entire group of points which lie slightly below the line in Fig. 12 would have been shifted upwards to lie along the line. There would then be 3 points lying well above the line and 2 points lying well below the line. The 3 points above the line are all from late in the summer (17-20 Aug.), while the 2 points below the line are from early in the summer. In other words, the model predicts too much stress early in the summer and too little stress late in the summer. This is what we might expect from using a constant root resistance if in fact the root resistance declines over the season.

As shown in Fig. 10, measured late season soil water content is considerably higher than predicted. This reinforces the idea that actual root resistance increases in late season causing stomatal closure and reduced transpiration.

We conclude that most discrepancies between measurements and the model output are the consequences of poor estimates of root and trunk resistances, and perhaps of a bad guess concerning the effect of xylem tension on leaf resistance. These indicate directions for future research on plant physiology.

10.6 FUTURE WORK

10.6.1 Canopy Geometry and Radiation

The completion of the work on canopy geometry (Section 7) will provide the necessary information for the completion of the shortwave radiation model (Section 11) The model will then be compared with radiation measurements (Section 3). Also work on the spectral properties of the needles will continue (Section 7).

10.6.2 Air in the Canopy

We will continue to experiment with new formulations for air temperature in the canopy. One possibility that looks promising is to let air temperature respond to local heating by the trees according to an empirically derived formula. This will be more certain when the new radiation model is in operation.

10.6.3 Energy Balance

The longwave radiation profile will be improved as a result view factors produced by the new radiation model.

10.6.4 Plant Water

Most of this part of the model is empirical, so improvement will result directly from the experiments of the physiologist (Section 5) and from student thesis work.

10.6.5 Soil

A soil heat model has already been prepared and programmed and will be included in future models. Heat capacity and thermal conductivities are calculated using de Vries (1966).

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10.8 APPENDIX

Appendix I. Equations

Canopy geometry

$$A_i = (-.2215 + 1.20933 \frac{Z_i}{Z_{CH}} - .998 (\frac{Z_i}{Z_{CH}})^2)$$

$$Ca_i = Ca_i + \frac{\Delta Z}{2} (A_{i+1} + A_i)$$

$$V_{sk,i} = \exp (- Df\ Cm\ Ca_i)$$

$$V_{n,i,j} = \exp (- Df\ Cm\ (Ca_i - Ca_j))$$

Shortwave radiation

$$D^h_{PAR} = D^{sk}_{PAR} [(1 - \frac{\beta}{\pi}) + \frac{\beta^2}{2\pi} .1] + I^{sk}_{PAR} \frac{\beta^2}{2\pi} .1$$

$$D^h_{NIR} = D^{sk}_{NIR} [(1 - \frac{\beta}{\pi}) + \frac{\beta^2}{2\pi} .4] + I^{sk}_{NIR} \frac{\beta^2}{2\pi} .4$$

$$D_{PAR,i} = D^h_{PAR} V_{sk,i} + \sum_{j=1}^{n} .2\ V_{n,i,j}\ I_{PAR,j}\ DrCm/\cos \eta$$

$$D_{NIR,i} = D^h_{NIR} V_{sk,i} + \sum_{j=1}^{n} .4\ V_{n,i,j}\ I_{NIR,j}\ DrCm/\cos \eta$$

$$I_{PAR,i} = I^{sk}_{PAR} \exp (- Dr\ Cm\ Ca_i/\cos \eta)$$

$$I_{NIR,i} = I^{sk}_{NIR} \exp (- Dr\ Cm\ Ca_i/\cos \eta)$$

$$ASW_{sh,i} = .8 \text{ Df } CmD_{PAR,i} + .2 \text{ Df Cm } D_{NIR,i}$$

$$ASW_{sl,\ i} = .8 \text{ Dr Cm}/\cos\eta\ I_{PAR,i} + .2 \text{ Dr Cm}/\cos\eta\ I_{NIR,i} + ASW_{sh,i}$$

Air in Canopy

$$T_i = T_{CH} + \frac{1}{2}\frac{(Z_i - Z_{CH})}{(.05 - Z_{CH})}(T_{5Cm} - T_{CH})$$

$$Q_i = Q_{CH}$$

$$U_i = U_{CH} \exp\left(3.0 \quad \left(\frac{Z_i}{Z_{CH}} - 1\right)\right)$$

Energy balance

$$\rho_{a,i} = .34838 \quad 1013.25\ /\ (T_i + 273.16)$$

$$Lt_n = (595 - .567\ T_n)\ 4187.0$$

$$r_{b,i} = \frac{100. \quad 60. \quad 2.91 \quad 10^{-4}}{(17. + .71 \quad 100. \quad U_i) \quad 10^{-3}}$$

$$r_n = \min\left\{\begin{array}{ll} 1500.0 & r_n^{min} \\ F_\psi & \max\left\{\begin{array}{l} r_n^{min} - X + \dfrac{Y}{(.2PAR + 1.0)} \\ 100/(.18511 - .00652 \times VPD) \end{array}\right. \end{array}\right.$$

where $F_\psi = \max\ (1.0,\ 2.5\ (\Psi_n - 14.0))$,

$$X = \frac{15000. - r_n^{min}}{20.} ,$$

$$Y = 21.\ X ,$$

and $$\mathrm{VPD} = \frac{\mathrm{Patm}}{62.2}(Q_n - Q_a)$$

$$\mathrm{ALW}_{n,i} = \mathrm{Df\ Cm}\ V_{sk,i}\ [\mathrm{LW}_{sk} - \sigma(T_{n,i} + 273.16)^4]$$

$$+ \sigma \mathrm{Df}^2\ \mathrm{Cm}^2 \sum_{j=1}^{n} V_{n,i,j}\ [(T_{sl,j} + 273.16)^4\ P_j$$

$$+ (T_{sh,j} + 273.16)^4\ (1. - P_j) - (T_{n,i} + 273.16)^4]$$

$$Q_{n,i} = \frac{62.2}{\mathrm{Patm}}\ 6.1078\ \exp\left(\frac{17.2693882\ T_{n,i}}{T_{n,i} + 237.3}\right)$$

<u>Plant water</u>

$$E_{sl} = \Delta t \sum_{i=1}^{n} \frac{\rho_a}{\rho_w} \frac{Q_{sl,i} - Q_{a,i}}{r_{b,i} + r_{n,sl,i}}\ A_{n,i} \Delta Z\ P_i$$

$$E_{sh} = \Delta T \sum_{i=1}^{n} \frac{\rho_a}{\rho_w} \frac{Q_{sh,i} - Q_{a,i}}{r_{b,i} + r_{n,sh,i}}\ A_{n,i} \Delta Z\ (1. - P_i)$$

$$\Delta W_n = \Delta t \frac{\psi_t - \psi_n}{r_t} - (E_{sl} + E_{sh})$$

$$\Delta W_t = \Delta t \sum_{i=1}^{ns} \left(\frac{\psi_{s,i} - \psi_t}{r_r}\ A_{r,i}\right) - \Delta t \frac{\psi_n - \psi_n}{r_t}$$

$$\theta_n = \frac{W_n + \Delta W_n}{W_n + \Delta W_n + DW_n}$$

$$\theta_t = \frac{W_t + \Delta W_t}{W_t + \Delta W_t + DW_t}$$

$$\psi_t = 400\ \theta_t - 202.$$

$$\psi_n = 400\ \theta_n - 202.$$

Soil water

$$P_{soil} = \max \begin{cases} 0., \\ P_{pt.}\ [1. - \max \begin{cases} .09, \\ 0.2948 + \dfrac{.64853}{P_{pt} 10^3} \end{cases}] - .00154 \end{cases}$$

$$K_i = 2.8\ 10^{-6}.\ 10^{5.76606\ -\ .21755/\theta_{s,i}\ -\ 4.0}$$

$$S_i = \max \begin{cases} 0., \\ \min \begin{cases} FC_i\ \Delta Z_i - \theta_{s,i}\ \Delta Z_i \\ P_{soil} - \sum\limits_{j=1}^{i-1} S_j \end{cases} \end{cases}$$

$$\left(\frac{\partial\theta_s}{\partial t}\right)_i = \frac{\partial}{\partial Z}\left(K \frac{\partial}{\partial Z}\left(10^{-4}\psi_s - Z\right)\right)_i + \frac{S_i}{\Delta Z_i\ \Delta_t} - \frac{A_{r,i}}{\Delta Z_i}\ \frac{\psi_{s,i} - \psi_t}{r_r}$$

$$\frac{\Delta\theta_{s,i}}{\Delta_t} \simeq 10^{-4}\left[\frac{K_{i+1} + K_i}{2}\ \frac{\psi_{s,i+1} - \psi_{s,i}}{\left(\dfrac{\Delta Z_{i+1} + \Delta Z_i}{2}\right)^2} - \frac{K_i + K_{i-1}}{2}\ \frac{\psi_{si,} - \psi_{s,i-1}}{\left(\dfrac{\Delta Z_i + \Delta Z_{i-1}}{2}\right)^2}\right]$$

$$- \frac{K_{i+1} - K_{i-1}}{\left(\dfrac{\Delta Z_{i+1} + 2\Delta Z_i + \Delta Z_{i-1}}{2}\right)}$$

$$+ \frac{S_i}{\Delta Z_i\ \Delta_t} - \frac{A_{r,i}}{\Delta Z_i}\ \frac{\psi_{s,i} - \psi_t}{r_r}$$

Appendix II. Symbols, Subscripts, Superscripts

Symbols

A	Area
ASW	Absorbed shortwave radiation
ALW	Net absorbed longwave radiation
Ca	Cumulative leaf area index
Cm	Fraction <1, representing degree of clumping
D	Diffuse radiation
Df	Effective surface area fraction for diffuse radiation
Dr	Effective surface area fraction for direct radiation
DW	Dry weight
E	Transpiration
I	Direct radiation
K	Hydraulic conductivity
Lt	Latent heat of vaporization
LW	Longwave
P	Penetration probability for direct radiation; fraction of sunlit needle clumps
Patm	Atmospheric pressure
Ppt	Precipitation
Psoil	Precipitation reaching soil
Q	Specific humidity
r	Resistance
S	Infiltration of water into soil
t	time
T	Temperature

U	Wind speed
V	View factors
VPD	Vapour pressure deficit
W	Total water content in cubic meters
Z	Height or depth
β	Slope angle from horizontal
η	Angle from normal to slope
ρ	Density
σ	Stefan's constant
ψ	Water potential (xylem tension)
θ	Water content (volumetric for soil, fresh weight for plants)

Subscripts, Superscripts

a	Air
b	Boundary layer
CH	Canopy height
h	Hillside
i	Level in canopy or soil
min	Minimum
n	Needle clumps (sunlit or shaded)
NIR	Near infrared radiation
PAR	Photosynthetically active radiation
s	Soil
sh	Shaded
sk	Sky
sl	Sunlit
t	Sapwood

11. RADIATION MODEL

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11.1 INTRODUCTION

A considerable amount of effort has been spent on developing a radiation model which fits our situation of nonhomogeneous vegetation on a slope. The problem cannot be solved directly by a geometrical analysis since there is no symmetry; that is, the canopy looks different from every angle. Thus, a Monte Carlo procedure was decided upon. We numerically construct a complex geometric model of the canopy and then calculate the penetration of several beams for each particular pair of zenith (η) and azimuth (ϕ) angles, and the average of all beams will yield the penetration probability for those angles.

Using these probabilities we calculate interception by needles, stems and trunk, including scattered radiation to any order. The results are stored in tables, indexed by ϕ and η, so that the soil-plant-atmosphere model only needs to take the day and time, calculate η and ϕ, and look up interception and penetration values in the tables. This model has been completely programmed and is awaiting the data on tree geometry.

11.2 PREVIOUS WORK

Anderson (1966) and others have assumed that light is exponentially attenuated in an environment of randomly distributed foliage, say $S(z) = S_o \exp(-K \quad Cl_{ai}(z))$, where K is a function of sun angle and leaf angle. Nilson (1971) pointed out that this formula is the zero term in the Poisson distribution. He extended the scope of radiation models to include positive and negative binomial distributions, assuming regular or clumped arrangement of foliage. These binomial distributions are empirical, i.e., they contain an arbitrary parameter which one adjusts to make the distribution fit the data.

Norman and Jarvis (1975) considered the clumping of needles into shoots, and shoots into whorls, using the Poisson distribution.

Brown and Pandolfo (1969) simulated interception by identical cylindrical shapes that are regularly arranged on a flat surface.

Our problem is more complex than those so far considered. We have needles clumped into needle clumps, so we can follow Norman and Jarvis (1975) at this point. But rather than being clumped into randomly arranged whorls, we have needle clumps clumped into discrete, three-dimensional tree shapes. Now, Brown and Pandolfo (1969) would help if our trees were cylindrical, regularly arranged, and on level terrain. However, our trees are shaped like cones on a cylinder, are more randomly than regularly arranged, and are on a steep slope.

We are also concerned with multiple scattering of radiation in the canopy. This has been done by Isobe (1969) and Norman and Jarvis (1975) in ways peculiar to their treatments of penetration; our treatment of scattering is similar to theirs.

11.3 MODEL STRUCTURE

11.3.1 Path Lengths Through Trees

We know the height distribution of trees on plot 47. (Section 2) Thus, assuming the height distributions on other plots are similar, using the known tree frequency and its variance, and assuming a uniformly random arrangement, we numerically construct a group of eight forest plots yielding a coordinate position and height for each tree. Using this data we can express the outer intercepting surface of each tree as equations for a cone and a cylinder (Fig. 1).

$$\text{cone:}\quad (x''')^2 + (y''')^2 = \left(\frac{R\cot\alpha - z'''}{\cot^2\alpha}\right)^2$$

$$\text{cylinder:}\quad (x''')^2 + (y''')^2 = R^2$$

This triple-primed coordinate system is unique for each tree, and is derived by translation and rotation from the origin at a corner of the plot (Fig. 2).

The path of a beam of radiation at angles η, ϕ is described in three dimensions by the equations:

$$x = (z_B - z)\tan\eta\cos\phi + x_B$$

$$y = (z_B - z)\tan\eta\sin\phi + y_B$$

where (x_B, y_B, z_B) is the point in the x,y,z system where the beam hits the plane $z=z_B$, where z_B is above the canopy height, say 8.5 meters.

For each beam the table of coordinates is searched and trees that are close to the beam path are set aside. Then for each of those trees, simultaneous solutions of the equations for the beam path and the surface yield the path length of the beam through the tree to any level in the canopy. These are summed to yield a total path length through trees for each beam. To account for variation of the needle area with height a suitable combination of cones and cylinders can be used inside

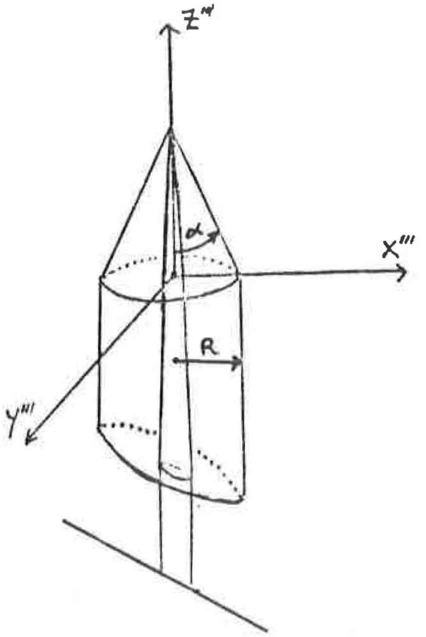

Figure 1. Coordinate system and geometric model for a Jack pine.

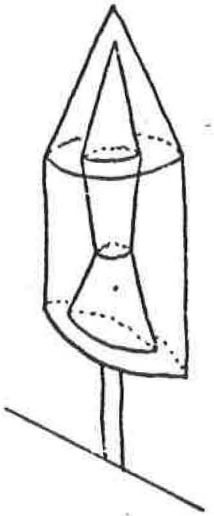

Figure 3. Possible configuration of outer and inner cone/cylinder models.

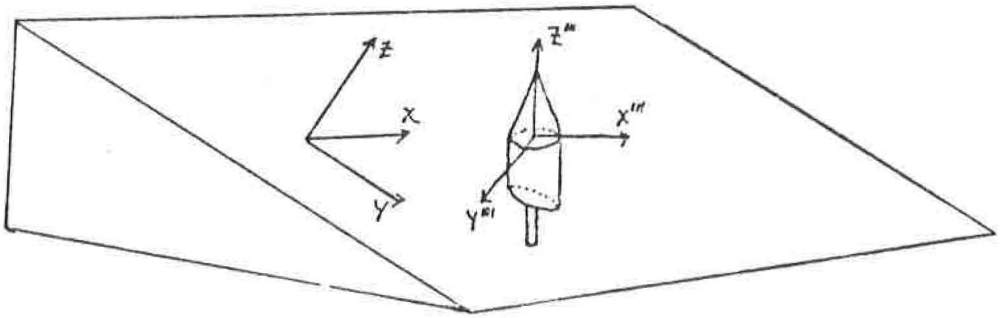

Figure 2. Coordinate system of a tree in relation to fixed coordinate system of slope.

the ones modelling the tree surface (Fig. 3). Also, another inner cone/cylinder may be used to similate interception by the trunk. Both of these possibilities are included in our model.

Figure 4 shows that the average path length converges after about 125 trials. However, rather than deal with an average, we keep track of the histogram of path lengths (Fig. 5).

11.3.2 Penetration Through Plant Elements

Now that we know the possible path lengths through trees we can calculate the probability that beams are intercepted. First, the projected areas of needle clumps and stems are calculated assuming that the needle clumps and stems can be modelled as cylinders and that they have been classified into N_R size classes with radii R_k, $N_\emptyset$ azimuth classes with angles $\emptyset_j$, and N_β elevation angle classes with angles β_i. These can be averaged over height to produce an average projected area:

$$A_{\substack{n\\ \text{or}\\ s}} (\eta,\emptyset) = \sum_{i=1}^{N_\beta} \sum_{j=1}^{N_\emptyset} \sum_{k=1}^{N_R} \{ f_{\beta_i} \; f_{\emptyset_j} \; f_{R_k} \; 2 \, R_k H \; \sin\gamma \; + \pi R_k^2 \; \cos\gamma \; \}$$

$$, \text{ where } \; \gamma = \cos^{-1} [\, \cos\beta_i \; \sin\eta \; \cos(\emptyset - \emptyset_j) + \sin\beta_i \; \cos\eta \,].$$

Then the probability of penetrating through needle clumps is given by:

$$P_n \, (z,\eta,\emptyset) = \sum_{i=1}^{N_L} f_{L_i} (z,\eta,\emptyset) \; \{ \sum_{k=1}^{5} \; Pin^{k-1} \; \exp\,(-\,\lambda_i) \, \frac{\lambda_i^{k-1}}{K!} \, \}$$

$$, \text{ where } \quad \lambda_i = L_i \quad A_n \, (\eta,\emptyset) \; \rho_n,$$

where the frequency of path length L_i for $(z,\eta,\emptyset)$ is f_{L_i} $(z,\eta,\emptyset)$, where there are ρ_n needle clumps per meter of tree height and where Pin is the

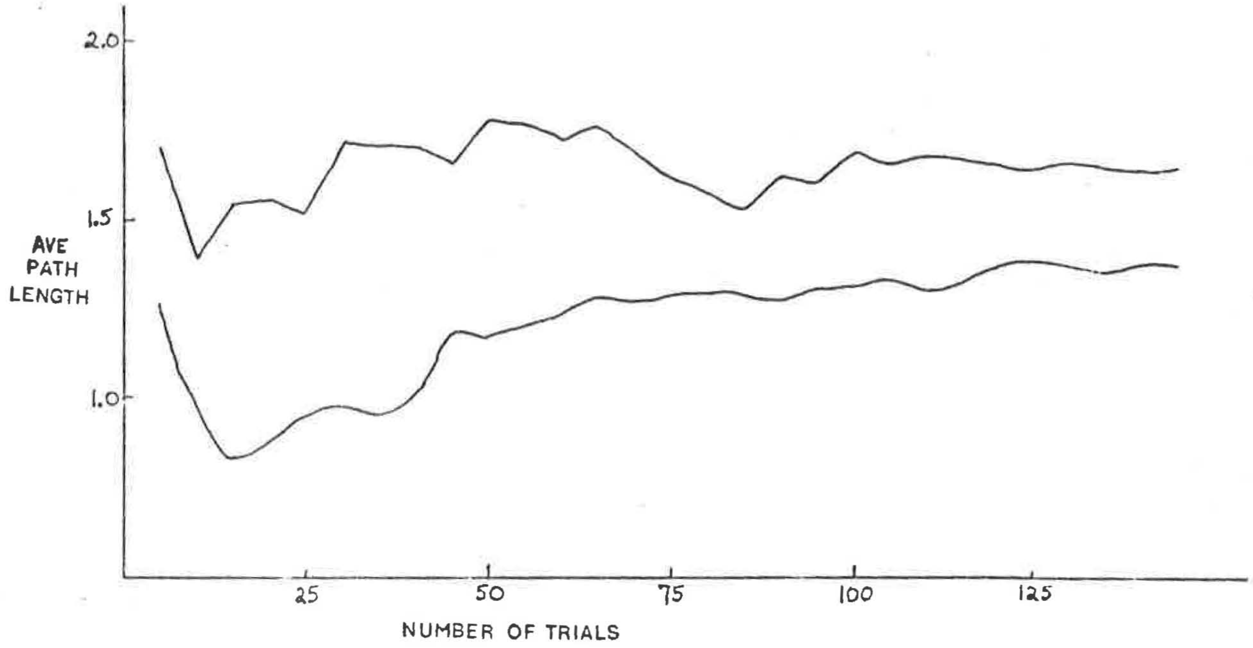

Figure 4. Convergence of average path length for penetration to five meters. $\eta = .9$, $\phi = .45$ (top line) and $\phi = 0.0$ (bottom line).

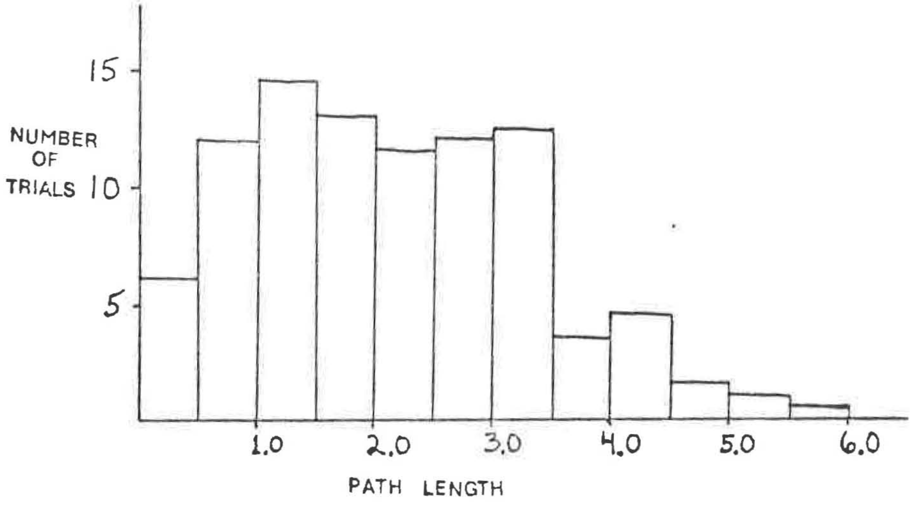

Figure 5. Histogram of pathlengths. $\eta = 1.05$, $\phi = 0$.

probability of penetrating through the needles of a needle clump. Pin has been determined by analysing needle clumps with a densitometer (Section 7). Figure 6 shows the variation with angle of interception of direct radiation by 7 needle clumps. The average is .55 for interception, so Pin is about .45.

Similarly the probability of penetrating among the stems is

$$P_s\ (z,\eta,\emptyset) \ = \ \sum_{i=1}^{N_i} f_{L_i}(z,\eta,\emptyset)\ \exp\ (-L_i A_s(n,\emptyset)\ \rho_s).$$

To determine the probability of penetration among the trunks to level z we have kept a record of the fraction (x_t) of beams hitting the trunks assuming no interception by stems or needles. Also a separate record of path lengths for beams hitting the trunks is ft_{L_i}. Now the probability of hitting a trunk accounting for interception by needles and stems is:

$$I_t(z,\eta,\emptyset) = \left[\sum_{i=1}^{N_i} ft_{L_i}(z,\eta,\emptyset)\ \left\{ \sum_{k=1}^{5} \text{Pin}^{k-1}\ \exp\ (-\lambda_i)\ \frac{\lambda_i^{k-1}}{k!} \right\}\right] \cdot \left[\sum_{i=1}^{N_i} ft_{L_i}\ (z,\eta,\emptyset)\ \exp\ (-L_i A_s\ (n,\emptyset)\ \rho_s\ )\right] \cdot X_t.$$

So now we have for penetration through the trunks:

$$P_t\ (z,\eta,\emptyset) = 1 - I_k\ (z,\eta,\emptyset).$$

The penetration of direct radiation through all elements to level z is

$$\hat{P}\ (z,\eta,\emptyset) = P_n\ (z,\eta,\emptyset)\ P_s\ (z,\eta,\emptyset)\ .\ P_t\ (z,\eta,\emptyset).$$

11.3.3 Interception by the Elements

11.3.3.1 Direct radiation

Overall interception of direct radiation is

$$\hat{I}\ (z,\eta,\emptyset) = \frac{\partial \hat{P}(z,\eta,\emptyset)}{\partial z}$$

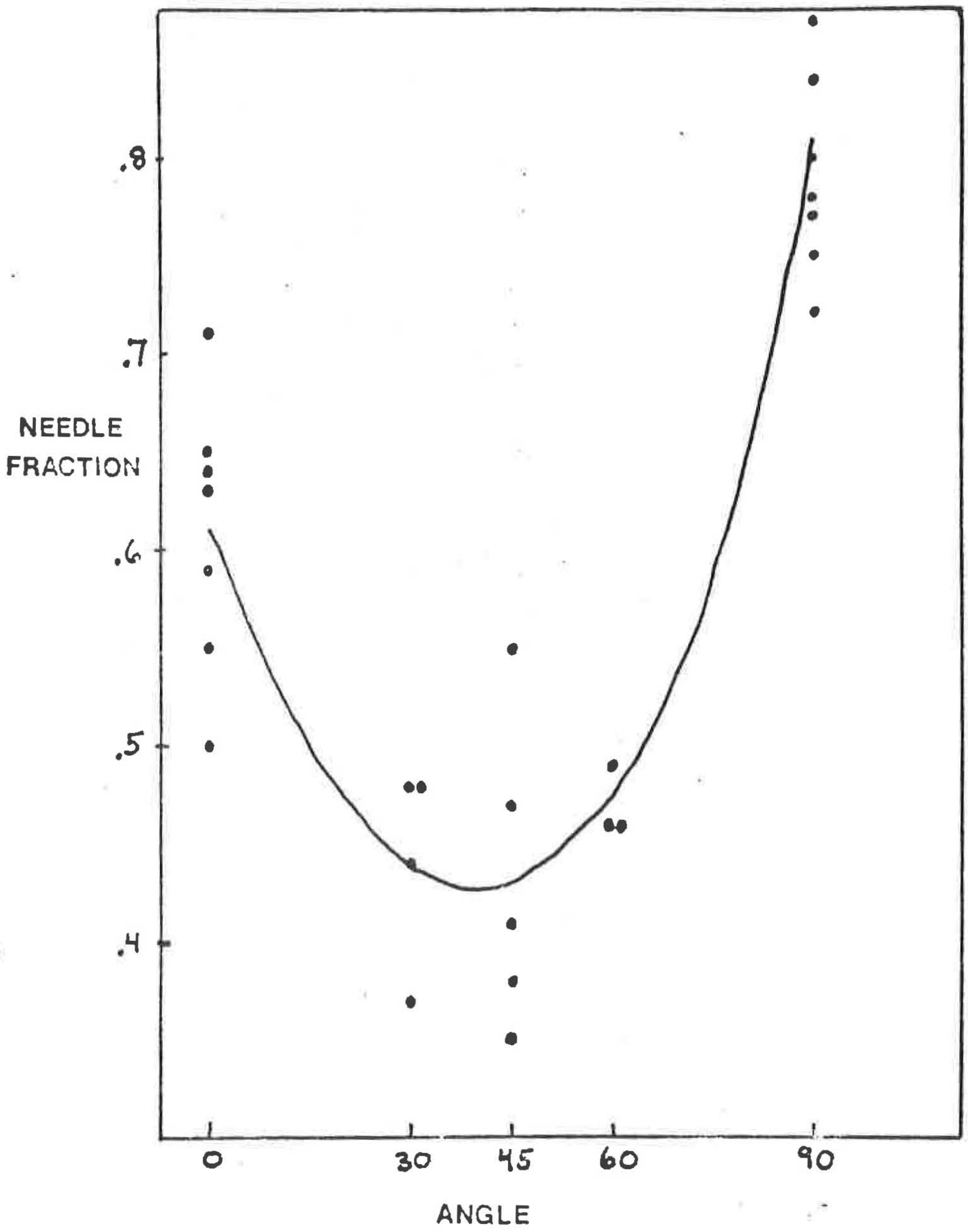

Figure 6. Fraction of projected area of needle clump cylinder that is occupied by needles, as a function of angle from radius.

Relative interceptions by trunk, stems, and needles is

$$\hat{I}_t(z,\eta,\phi) = (1 - \hat{P}_t\ (z,\eta,\phi))/\mathrm{Tot}$$

$$\hat{I}_s(z,\eta,\phi) = (1 - \hat{P}_s\ (z,\eta,\phi))/\mathrm{Tot}$$

$$\hat{I}_n(z,\eta,\phi) = (1 - \hat{P}_n\ (z,\eta,\phi))/\mathrm{Tot}$$

, where $\mathrm{Tot} = 3 - (\hat{P}_t\ (z,\eta,\phi) + \hat{P}_s(z,\eta,\phi) + \hat{P}_n(z,\eta,\phi))$.

Now the fractions of penetrating radiation that are intercepted by the elements are

$$\hat{F}_t(z,\eta,\phi) = \hat{I}(z,\eta,\phi)\ \hat{I}_t\ (z,\eta,\phi)/\hat{P}(z,\eta,\phi)$$

$$\hat{F}_s(z,\eta,\phi) = \hat{I}(z,\eta,\phi)\ \hat{I}_s\ (z,\eta,\phi)/\hat{P}(z,\eta,\phi)$$

$$\hat{F}_n(z,\eta,\phi) = \hat{I}(z,\eta,\phi)\ \hat{I}_n(z,\eta,\phi)/\hat{P}(z,\eta,\phi).$$

Let $D_n(z,\eta,\phi) = \hat{I}(z,\eta,\phi)\ \hat{I}_n(z,\eta,\phi)$.

For the ground surface,

$$\hat{F}_n(0,\eta,\phi) = 1.0 \quad \text{and}$$

$$\hat{D}_n(0,\eta,\phi) = \hat{P}(0,\eta,\phi).$$

11.3.3.2 Diffuse radiation

For diffuse radiation we have

$$\bar{P}(z) = \frac{\int_0^{\Pi} \int_0^{\frac{\Pi}{2}} \hat{P}(z,\eta,\phi)\ \sin\eta\ \cos\eta\ d\eta\ d\ \phi}{\int_0^{\Pi} \int_0^{\frac{\Pi}{2}}\ \sin\eta\ \cos\eta\ d\eta\ d\ \phi}$$

and view $(y,z) = \frac{\bar{P}(y)}{\bar{P}(z)}$

For needles:

$$\bar{I}_n(z) = \frac{\int_0^{\pi}\int_0^{\frac{\pi}{2}} \hat{I}\,(z,\eta,\emptyset)\,\sin\eta\,\cos\eta\,d\eta\,d\,\emptyset}{\int_0^{\pi}\int_0^{\frac{\pi}{2}} \sin\eta\,\cos\eta\,d\eta\,d\,\emptyset}$$

and $\bar{F}_n(z) = \bar{I}(z)\,\bar{I}_n(z)/\bar{P}(z)$.

Similarly for stems and trunk.

Also

$$\bar{D}_n(z) = \bar{I}(z)\,\bar{I}_n(z),$$

$$\bar{F}_n(0) = 1.0,$$

and $\bar{D}_n(0) = \bar{P}(0)$.

Scattering of Radiation by Needles

The reflectivity (Rf) and transmissivity (Tr) of the needles (Section 7) causes additional sources of radiation to each level. The additional source of scatter from above at z is

$$S\downarrow(z,\eta,\emptyset) = \int_z^{CH} Sc\downarrow(y,z)\,dy$$

, where $Sc\downarrow(y,z)$ is the scatter from level y to z. Now if the sources of diffuse and direct radiation from the sky are denoted D and I we have

$$\begin{aligned} Sc\downarrow(y,z) = \{[D \quad & \bar{D}_n(y) + I\,\hat{D}_n(y,\eta,\emptyset) \\ & + \bar{F}_r(y) \quad S\downarrow(y,\eta,\emptyset)]\ Tr \\ & + \bar{F}_n(y) \quad S\uparrow(y,\eta,\emptyset)\ Rf\ \}\ \text{view}\ (y,z). \end{aligned}$$

Then

$$S\downarrow(z,\eta,\phi) = D\int_{z}^{CH} \text{Tr view }(y,z)\ \bar{D}_n(y)\ dy$$

$$+\ I\int_{z}^{CH} \text{Tr view }(y,z)\ \hat{D}_n(y,\eta,\phi)\ dy$$

$$+\int_{z}^{CH} \text{view }(y,z)\quad \bar{F}_n(y)\ [\text{Tr } S\downarrow(y,\ ,\phi)$$

$$+\ \text{Rf } S\uparrow(y,\eta,\phi)]\ dy.$$

The additional source from scatter at z from below is

$$S\uparrow(z,\eta,\phi) = \int_{0}^{z} Sc\uparrow(y,z)\ dy$$

where

$$Sc\uparrow(y,z) = \{[D\ \bar{D}_n(y) = I\ \hat{D}_n(y,\eta,\phi)$$

$$+\ \bar{F}_n(y)\ S\downarrow(y,\eta,\phi)]\ \text{Rf}$$

$$+\ \bar{F}_n(y)\ S\uparrow(y,\eta,\phi)\ \text{Tr}\ \}\ \text{view }(y,z)$$

so

$$S\uparrow(z,\eta,\phi) = D\int_{0}^{z} \text{Rf view }(y,z)\ \bar{D}_n\ (y)\ dy$$

$$+\ I\int_{0}^{z} \text{Rf view }(y,z)\ \bar{D}_n\ (y)\ dy$$

$$+\int_{0}^{z} \text{view }(y,z)\ \bar{F}_n(y)\ [\text{Rf } S\downarrow(y,\eta,\phi) + \text{Tr } S\uparrow(y,\eta,\phi)]$$

Now defining the following integrals for diffuse radiation

$$\bar{A}_1(\alpha) = \int_{0}^{\alpha} \text{Rf view }(\beta,\alpha)\ \bar{D}_n(\beta)\ d\beta$$

$$\bar{A}_2(\alpha) = \int_{\alpha}^{CH} \text{Tr view } (\beta,\alpha)\ \bar{D}_n(\beta)\ d\beta$$

$$\bar{B}_1(\alpha) = \int_{0}^{\alpha} \text{view } (\beta,\alpha)\ \bar{F}_n\ (\beta)\ [\text{Tr } \bar{A}_1(\beta) + \text{Rf } \bar{A}_2(\beta)]\ d\beta$$

$$\bar{B}_2(\alpha) = \int_{\alpha}^{CH} \text{view } (\beta,\alpha)\ \bar{F}_n(\beta)\ [\text{Rf } \bar{A}_1(\beta) + \text{Tr } \bar{A}_2(\beta)]\ d\beta$$

$$\bar{C}_1(\alpha) = \int_{0}^{\alpha} \text{view } (\beta,\alpha)\ \bar{F}_n(\beta)\ [\text{Rf } \bar{B}_1(\beta) + \text{Tr } \bar{B}_2(\beta)]\ d\beta$$

$$\bar{C}_2(\alpha) = \int_{\alpha}^{CH} \text{view } (\beta,\alpha)\ \bar{F}_n(\beta)\ [\text{Tr } \bar{B}_1(\beta) + \text{Rf } \bar{B}_2(\beta)]\ d\beta$$

This accounts for up to third order scatter and the progression to higher orders is obvious. The integrals for direct radiation are defined similarly. Now, it can be shown that:

$$S{\downarrow}(z,\eta,\phi) \approx D\ [\bar{A}_2(z) + \bar{B}_2(z) + \bar{C}_2(z)]$$

$$+\ I\ [\hat{A}_2(z,\eta,\phi) + \hat{B}_2(z,\eta,\phi) + \hat{C}_2(z,\eta,\phi)]$$

and

$$S{\uparrow}(z,\eta,\phi) \approx D\ [\bar{A}_1(z) + \bar{B}_1(z) + \bar{C}_1(z)]$$

$$+\ I\ [\hat{A}_1(z,\eta,\phi) + \hat{B}_1(z,\eta,\phi) + \hat{C}_1(z,\eta,\phi)]$$

Therefore, the total fraction of the diffuse radiation penetrating to level z is

$$\bar{T}(z) = \bar{P}(z) + \bar{A}_1(z) + \bar{A}_2(z) + \bar{B}_1(z) + \bar{B}_2(z) + \bar{C}_1(z) + \bar{C}_2(z)$$

and the total fraction of direct radiation penetrating to level z is

$$\hat{T}(z,\eta,\emptyset) = \hat{P}(z,\eta,\emptyset) + \hat{A}_1(z,\eta,\emptyset) + \hat{A}_2(z,\eta,\emptyset) + \hat{B}_1(z,\eta,\emptyset) + \hat{B}_2(z,\eta,\emptyset) + \hat{C}_1(z,\eta,\emptyset) + \hat{C}_2(z,\eta,\emptyset).$$

Finally the absorption by needles (and similarly by trunk and stems) is given by:

$$Ab_n(z,\eta,\emptyset) = \bar{F}_n(z)\, \bar{T}(z)\, D + \hat{F}_n(z,\eta\emptyset)\, \hat{T}(z,\eta,\emptyset)\, I.$$

Therefore, the final results can be stored permanently in two tables for each element, one to obtain the fraction of diffuse radiation absorbed as a function of z and the other to obtain the fraction of direct radiation absorbed as a function of z, η, and $\emptyset$.

11.4 DISCUSSION

It is important that we know the radiation intercepted by the plant elements at different heights since the needle clump temperatures and hence the transpiration are critically dependent upon the radiation load.

Previous models have required that foliage be random, or clumped once, or clumped twice but into a two dimensional whorl, or clumped into uniform three dimensional shapes on a flat surface. This model allows for 2 levels of clumping - needle clumps and trees. It allows for different tree heights and radii and for the complications of the slope. Thus, it is a significant advance over previous models.

Obviously, this model also provides a more conceptually sound basis on which to model other situations, for example forest on level ground, agricultural row crops, etc.

Of course, as with any proposed model, the predictions of this model should be compared with measurements. However, the data for such tests were not available in time for this report.

11.5 FUTURE WORK

The details of the tree geometry are yet to be described in final form. When they are, we may find that a certain degree of asymmetry may have to be introduced. For example, the cone and cylinder may be eliptical rather than spherical and asimuthal asymmetry of the trees may be important.

11.6 REFERENCES

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12. PROJECT INTEGRATION

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12.1 INTRODUCTION

This project, VE6.1, is designed and carried out as an integrated whole. All subprojects have the same goals, which are to come to a comprehensive undertanding of the soil-plant-atmosphere system on a Jack pine forest, at the Richardson Study Site, to express this understanding in a mathematical model, and to employ this model to answer management questions about vegetation on deep sands. The model building is not separate from the field and laboratory rearch but is integrated with it in an intimate way. Model structures as well as parameters depend upon the results of measurement, and both the required inputs to the model and results from model runs have helped to determine field and lab measurement design.

In the case of the mycorrhizal study, much preliminary work must be done before model-directed research begins, but the ultimate aim is to incorporate this subproject directly into the model building effort.

Because the management questions which we are stressing are concerned with water use and the ability of plant communities to survive infrequent but severe droughts, the models developed have to do with water balance and, as a necessary corollary, energy balance. Section 10 of this report describes our current energy-water model, and Section 11 is an account of a sophisticated, new radiation model which is under development.

The energy-water model is still not in a finished form, but is at a stage where it can provide useful insights into the system under study.

12.2 MODEL RUNS

Besides the "normal" model run examined in detail in Section 10, which was designed to as closely as possible represent field conditions of the 1976 growing season, we carried out several runs to estimate the effects of changed cumulative leaf area index (CLAI) and precipitation (PPT) while keeping all other conditions the same. The CLAI was altered without changing other parameters; this is artificial, but a useful expedient. The precipitation was altered in two ways: First, every second precipitation event was discarded. Second, each rain event was reduced by 2/3. The latter resulted, because of interception by trees and lichens, in only 8.7 mm of water reaching the soil; the soil rapidly dried out to the point where the tree stomata were closed for nearly the whole summer, and transpiration was largely cuticular. No further results of this run will be presented.

Some results from all runs but the last one are presented in Table 1. As well as the effects on water balance, these runs indicate considerable physiological impact. Compared to the 1976 field conditions, the combination of reduced PPT and increased CLAI showed: 1) Greater duration of the times when stomata were closed because of low xylem tensions; 2) greater frequency of very low xylem tensions (13 days of less than -18 bars compared to only 1 day; 3) several periods during which night-time recovery of xylem tension was to only -12 bars or less (no such events occurred in the normal run); 4) one 24 hour period during which xylem tension varied only between about -17 to -21 bars.

12.3 DISCUSSION

The model run with 1976 field season conditions, as discussed in Section 10, gave reasonable agreement with field measurements, on both a diurnal and a seasonal basis.

Of particular interest is gross seasonal water balance. This run predicted a transpiration total (7 May-29 Aug.) of 100 mm and a change in storage in the upper 1 m of the soil of -3 mm, giving a total of 103 mm Over the same period, cumulative loss from the soil column to -6 m depth was 136 mm (Section 4), of which 37 mm were from the region -1 to -6 m; the difference, 99 mm, is assumed to have come from the top meter. If surface evaporation is negligible, which we take it to be because of the "mulch" effect of lichen and needle duff, then only 4 mm of water are unaccounted for, which is well within the limits of measurement error. We cannot dismiss the possibility that this good agreement arises from compounded measurement uncertainties, and another field season with more careful attention to water content changes in the upper meter of soil is necessary to further test our ability to properly calculate water balance. However, we now have the feeling that the various results which contribute to these calculations, from meteorology, plant physiology, lichen studies, soil physics and mathematical modelling agree in a very satisfactory and encouraging way.

The importance of the physiological effects predicted under conditions of reduced precipitation are difficult to judge at this time. Laboratory studies currently under way on the response of *Pinus banksiana* to extreme water stress will enable us to properly interpret these and other model runs in terms of sub-lethal effects and lethality.

This is a good point to note that examination of model output has suggested that there were times during the past field season during which

Table 1. The effects of altered cumulative leaf area index (CLAI) and precipitation (PPT) on transpiration and soil water storage (7 May - 29 Aug.).

Model Run Conditons		Seasonal total transpiration (mm)	Seasonal change in water content (0-1m depth) (mm)
Normal		100	-3
CLAI x .5,	PPT x 1	77	+20
CLAI x 1.5,	PPT x 1	112	-12
CLAI x 1,	PPT x .5	87	-24
CLAI x 1.5,	PPT x .5	92	-26

areas. In stating this, we realize that water relations do not tell even most of the story of a plant-soil community's structure and function, and urge that studies of nutrient relationships and soil processes be integrated into the modelling effort, as originally intended.