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TITLE OF THESIS/*TITRE DE LA THÈSE* AN ASCOMYCETOUS STUDY OF BARLEY SPECIES IN CENTRAL HABITAT

UNIVERSITY/*UNIVERSITÉ* UNIVERSITY OF AMBERTA

DEGREE FOR WHICH THESIS WAS PRESENTED/ *GRADE POUR LEQUEL CETTE THÈSE FUT PRÉSENTÉE* DOCTOR OF PHILOSOPHY

YEAR THIS DEGREE CONFERRED/*ANNÉE D'OBTENTION DE CE DEGRÉ* 1974

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THE UNIVERSITY OF ALBERTA

AN ECOPHYSIOLOGICAL STUDY OF BLACK SPRUCE IN CENTRAL ALBERTA

by

EDUARD MEINE VAN ZINDEREN BAKKER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

IN

ECOPHYSIOLOGY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

FALL, 1974

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "AN ECOPHYSIOLOGICAL STUDY OF BLACK SPRUCE IN CENTRAL ALBERTA" submitted by Eduard Meine van Zinderen Bakker in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Ecophysiology.

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ABSTRACT

The eco-physiology of black spruce (*Picea mariana* (Mill) BSP.) was investigated with respect to net assimilation and water relations both in the field near Edmonton, Alberta and laboratory.

Needle water potentials and its components were measured throughout the year at regular intervals. The data indicate that the species is hydrolabile with a maximum water potential of about -10 atm in June and a minimum of -35 atm in late March. A good relationship exists between air temperature and water potential for most of the year. In spring, needle water potentials rise with increasing temperatures as dormancy is terminated but then decrease due to a water deficit developing in the trees while the soil remains frozen till the end of May. This causes a severe drought condition, resulting in needle cast. On warm days during the summer the daily water potential exhibits a typical mid-day lag pattern as the stomata open and close in response to the water balance of the needles. Due to the lower temperatures in spring and fall, leading to lower transpiration rates this pattern is often not observed during these seasons. Throughout the dormancy period the stomata are closed and do not respond to light and temperature changes. The lowest needle infiltration pressure measured was 17 psi, agreeing well with the high diffusion resistance reported in the literature.

A maximum net assimilation rate of 7.0 mg CO_2/gm DWt/hr as measured by infra-red gas analysis was recorded in the field. Laboratory studies confirmed that the maximum fixation rate occurred at a needle temperature of 15°C with a light intensity of 450 μ E/m^2/sec or 0.2 cal/cm^2/min.

Lower light saturation values were obtained in the field at lower needle temperatures. Light compensation at 15°C needle temperature occurred at about 12 μ E/m^2/sec or 0.04 cal/cm^2/min. An increase or decrease of 10°C from the optimum temperature resulted in reducing the net assimilation rate by 50 percent. Frost at night reduced the maximum net assimilation rate on the following day even though temperatures rose to optimum and light was above saturation level. A relationship between net assimilation and water potential was also observed.

Evidence of the importance of soil temperature's role on the onset of dormancy was obtained both in the field and laboratory. Soil temperature was not as important as air temperature for the termination of dormancy. Throughout the dormant period the species did not respond to changes in the environmental parameters measured.

A series of hormone experiments was conducted to determine their influence on dormant branches. The transpiration data obtained from this hormone study is inconclusive. Both benzyladenine and abscisic acid at concentrations of 1×10^{-6} and 3.8×10^{-7} M respectively, however, had an enhancing effect on net assimilation.

Some of the principle findings were: frost during the summer severely inhibits net assimilation the next day; low water potentials are found even though the plant is growing on a site with soil water potential near zero; black spruce is subjected to especially severe drought conditions during May when the soil is still frozen; photosynthetic activity precedes bud break by several weeks; the stomata remain closed during the winter months while the trees are dormant; and dormancy is only terminated after temperatures have been above freezing for 4 to 5 days.

ACKNOWLEDGEMENTS

I would like to express my sincere appreciation to my supervisor, Dr. J. M. Mayo, for his continued encouragement and interest in this project. I am deeply indebted to him for his assistance in times of frustration and need.

This study could not have been conducted had Profs. P.R. Gorham and L.C. Bliss not put their equipment at my disposal. I gratefully acknowledge their support in doing so.

The hormone experiments were conducted under the guidance of Dr. G.D. Weston and I would like to thank him for making the different hormones available to me.

Finally, I would like to acknowledge my fellow graduate students, especially Toni Hartgerink and Sherman Nelson, for assistance and co-operation given during the execution of this project. They kindly acted as guinea pigs to many of my ideas and theories about the findings of my work.

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INTRODUCTION AND LITERATURE REVIEW

The greater part of the forested area of Canada consists of boreal forest, of various types, in which white and black spruce (*Picea glauca* (Moench) Voss and *P. mariana* (Mill) BSP, respectively) are characteristic species. While much information is available about the eco-physiology of the coniferous forests of the European Alps, particularly for *Pinus cembra* and *Picea excelsa*, very little is known about species of the Canadian north. A study of a closely related species could thus lead to interesting comparisons.

Picea mariana is one of the most important pulpwood species in Canada (Vincent, 1965). Relative to other species with which it occurs, black spruce increases in numbers northwards (Rowe, 1972). This may indicate that it is better adapted to the harsh climate.

The species ranges across the entire North American continent from east to west. The southern limit in the eastern U.S.A. corresponds roughly with the 21°C July isotherm while the northern limit in Ungava closely follows the 10°C July isotherm. It recedes south of this isotherm west of Hudson Bay (Vincent, 1965). In Alberta, it is considered the most common tree of the muskegs over the northern two-thirds of the province.

Black spruce forests occur on soils ranging from very wet peat bogs to deep sandy soils or gravel tills. It is absent or sparse on very dry sites. The species grows best on well drained loamy soils but, because it appears less competitive than other species, it cannot always occupy these soils.

> "Sites which it does occupy commonly, and those which are usually regarded as black spruce sites, it must be regarded as occupying by default." (Vincent, 1965)

The ability to produce adventitious roots appears to be the most important adaptive feature enabling the species to occupy peatlands. The root system is platelike and averages six meters in diameter for mature trees and rarely more than 60 cm deep, usually being confined to the upper 15 to 30 cm (Heinselman, 1961; Stanek, 1961 in Vincent, 1965).

Rowe (1972) has divided the boreal forest of Canada into 33 forest regions. The main forest type around Edmonton is the Aspen Grove (Rowe type B17). East of Edmonton is an outlier of Rowe's type B18a or Mixedwood. This latter type is recognized by an abundance of needle-leaved conifers. The lower positions and upper water catchment areas of the mixedwood forest develops into black spruce and tamarack (*Larix laricina*) muskeg with a limited accumulation of peat. The characteristic soil development in the outlier is podzolic consisting of 70% Cooking Lake Loam, 10% Uncas Loam and 20% Sloughs and organic soils (Bowser *et al.*, 1962) in the immediate vicinity of the study site, which was 20 km ESE of Edmonton. This locality is close to the southern distribution limit for the species in central Alberta. The trees studied were growing in a small swamp, about two ha in area.

The climate of the boreal forest can be considered as humid mesothermal. Edmonton is located in a zone with severe winters, moist all year around with short warm summers (Dbf according to the Köppen system of classification). All the regions north of Edmonton are in the subarctic zone (Dcf of Köppen) which has severe winters, moist all year round and short cool summers. "Klimadiagramme", following Walter and Leith (1967), have been drawn for Edmonton's two major meteorological

stations (The Edmonton International and Industrial Airports) and are given in Fig. 1. The figures are based on data published by the Atmospheric Environment Service of Canada (1972). Following this system Edmonton's climate belongs to type VII or cold boreal climate with a very long cold period and the monthly average temperature of the warmest month over 10°C. Temperatures at the International Airport are slightly lower than those at the Industrial. This can be ascribed to the latter airport being situated in the middle of the city while the former is located 20 km to the south. According to the "Klimadiagramme", the International Airport has two frost free months (July and August) while frost occurs during all months at the Industrial Airport. While this is contrary to expectation, it can be attributed to the records for the International Airport being only over a period of 13 years while those at the Industrial cover a 90-year period. Based on the same time period both localities have the months of July and August without frost.

The advantage evergreen species have over deciduous trees is that evergreens can fix carbon in early spring and late fall when the deciduous species are without leaves. These two periods were found to be extremely important to *Pinus cembra* and *Picea excelsa* by Pisek and Tranquillini (1951) as well as Zeller (1951). Daily temperatures are warm but not hot and thus high photosynthetic rates result. Night time temperatures are cool, and respiration rates are reduced to a minimum. After the first periods of frost in the fall, CO_2-assimilation is reduced but becomes inhibited only when true dormancy sets in at the beginning of the intense cold period. This is probably at the time the needles freeze. Zeller (1951) found that true dormancy in *Picea excelsa* never occurred during a very mild winter in the Austrian Alps and periods

of positive net assimilation were measured throughout. Parker (1953) was able to measure CO_2 uptake on warm clear days of November and early December even after severe frost had occurred. CO_2 fixation was not measured under similar conditions in late December and January, however. Ungerson and Scherdin (1965) measured positive net assimilation only at noon in late autumn, and none was measurable in midwinter. Similar results were obtained by Tranquillini and Machl-Ebner (1971) for *Pinus cembra*.

Tranquillini and Holzer (1958) have shown that respiration ceases in *Picea excelsa* and *Pinus cembra* at -6 and -8°C when all the water that can easily freeze in the cell has turned to ice. By reducing temperature to -40°C only a further 10% of the total water in the cells will freeze. Photosynthesis, on the other hand, is much more susceptible to cold. They found that photosynthesis ceased at the temperature that ice formation was initiated (-3 to -4°C). This temperature was undoubtedly to some extent dependent on the water and osmotic potentials of the needles.

The cessation of photosynthesis and onset of dormancy in winter can be explained in terms of profound changes in the plastid apparatus of the cell. Genkel and Barskaya (1961) found that needles of all age classes of dormant *Picea excelsa* exhibited marked aggregation of chloroplasts around the nuclei of the cells. Evidently this chloroplast aggregation leads to the establishment of a close contact between the nucleus and plastids as well as being the visible manifestation of complex processes developing in the resting cell. The nucleus undoubtedly plays a role in these changes of the plastid apparatus and the overwintering ability of the cells. Upon exposure to room temperature

for 3 to 5 days many cells showed disaggregation of the chloroplast mass and dispersion occurred. When this had taken place the needles began to metabolize actively again. A lowering of temperature to below freezing for long or short periods was not found to re-initiate aggregation of the plastids.

Tranquillini (1963) has shown that in both *Pinus cembra* and *Picea excelsa* photosynthesis and dry matter production are normal while the temperature remains above 0°C. As soon as temperatures drop to -4°C in the fall, however, the photosynthetic rate of the next day is below normal even though temperatures may be the same on the day before and after the frost. With temperatures dropping lower and lower at night, less fixation occurs until a point is reached when production ceases. This fairly well coincides with the time that the soil freezes and water lost during the day can no longer be replaced. Stomata close as a result of the water loss and remain so as dormancy sets in. In spring the temperatures rise, needles thaw, and respiration resumes. Initially, net assimilation is negative but gradually the photosynthetic apparatus comes into operation and dry matter production becomes positive. This sequence of events has also been observed by Weise (1961) who studied photosynthetic ra[illegible]ter artificial frost periods. While photosynthesis slowly increases [illegible]piration shows an initial strong increase and then gradually decr[illegible] to a lower level.

Zacharova (1929, in Walter, 96[illegible]as indicated that the onset of dormancy does not occur at the same t[illegible]or all species; for example, *Picea excelsa* fixed CO_2 later into w[illegible]ter than did *Pinus sylvestris* in the Moscow region. This was considered to be associated with changes in the plastid apparatus.

While photosynthesis thus shows a distinct cycle during the year, respiration does not and may continue, even in winter, whenever temperatures above freezing are reached and the needles thaw. Pisek and Winkler (1958), working on *Pinus cembra* and *Picea excelsa* were able to obtain about the same respiration rates for thawed out dormant needles as for summer needles at the same temperature. Thus warming of the needles in winter causes a release of carbon dioxide.

Throughout the dormancy period when photosynthesis has ceased the stomata are closed and transpiration rates are very low (Ivanoff, 1924 in Walter, 1968). Parker (1963) has indicated that the decline in transpiration is not associated with a decrease in leaf water content for *Pinus nigra* but with hardiness which causes an increase in sugars and thus a decrease in osmotic potential. Thus, while the water content did not change in the needles, the stomata could close due to a shortage of water because more was bound in the cells.

Frost hardened cells are less active photosynthetically than unhardened cells but have the advantage of being able to tolerate freezing temperatures (Zeller, 1951; Pisek and Tranquillini, 1951). Frost hardiness also shows a distinct annual cycle. It is initiated by the first frost in fall when the sugar content of the cell sap suddenly increases and the osmotic potential decreases (Pisek, 1950). The saccharose:glucose ratio simultaneously decreases. In spring, frost hardiness decreases after the first warm days while there is a simultaneous decrease in sugar levels and an increase in osmotic potential (Walter, 1960). Heber and Santarius (1964) have shown that the sugar content of the cytoplasm is important but not the sugar content of the cell sap. Sugars in the cytoplasm may prevent damage to the

phosphorylation system by low temperatures.

Direct frost damage to conifers is rarely found, even in Siberia where temperatures may go down to -60°C. This is largely because temperature changes in nature are slow enough to allow plants to adapt to the change (Levitt, 1972). Rapid cooling will increase freezing injury. There is, according to Levitt (1972), a critical freezing zone for any one hardy plant. Above and below this zone rates of cooling or warming have no effect. At temperatures above the zone a plant will survive regardless of the cooling (or warming) rate while below it the plant will be killed. Within the critical zone the rate of warming or cooling is of great importance to the survival of the species. Prolonged low temperatures in spring can, however, damage and even kill tissue. Due to higher solar radiation at that time and warm daily temperatures, needles become active and transpiration is initiated. The soil, however, remains frozen due to cold temperatures at night. Since roots cannot readily take up water from the frozen soil to replace that lost during the day, severe drought conditions can develop in the plant. Thus Goldsmith and Smith (in Walter, 1931) found the lowest osmotic potentials for *Picea engelmannii* not in midwinter as might be expected but in early spring.

Since the discovery of growth stimulating and inhibitory substances it was natural to propose that they played a major role in dormancy. Bud dormancy is thought to be controlled by a balance between them. In the preceding section, dormancy has been considered as the period when favorable conditions will not induce photosynthesis. This, however, needs closer examination when considering hormonal influences since photosynthesis continues long after active growth has ceased and starts

well before bud break in spring. Two main forms of dormancy can be distinguished, namely imposed or enforced dormancy which is caused by unfavourable environmental conditions and innate or spontaneous dormancy which is associated with the formation of resting buds in summer and autumn when growing conditions are still favourable (Wareing and Phillips, 1970). As there are different forms of dormancy, there are also different stages the plant goes through during the normal dormant period. Terminal buds, when first formed, can frequently be induced to resume growth by treatments such as defoliation. This is termed summer dormancy or predormancy. Conifers still actively photosynthesize during this period. Later in the season the same species will not respond to this treatment and then a state of winter or true dormancy is said to prevail. It is during this period that photosynthesis ceases and aggregation of the plastid apparatus around the nucleus takes place in conifers. After a certain time period, usually in late winter or early spring, buds can again be induced to resume growth. They are then in a postdormant stage. This is the period during which conifers photosynthesize before the buds have opened.

Garner and Allard (1920) indicated more than 50 years ago that day-length plays an important part in the control of dormancy. In most species long days will induce growth and short days cessation. Certain plants will grow continuously for eighteen months under warm, long day conditions while others show terminative growth by going into a pre-dormant stage after a certain long day period while conditions are still favourable for growth.

It is presently considered that the length of the dark period, rather than the length of the photoperiod is important. An interruption

of the dark period by a short "light-break" nullifies the effect of the short photoperiod and dormancy is delayed. The red region of the spectrum is the most effective which suggests the involvement of phytochrome.

Low temperatures and low light levels are as important as day length in initiating leaf senescence and abscission in deciduous species. Wide ranging species such as *Picea excelsa* show a marked ecotypic difference in their photoperiodic response in relation to latitude and the altitude at which they are growing (Wareing and Phillips, 1970).

The response of the shoot apex to a short day period is controlled primarily by the day length at which the leaves are maintained. This was determined by maintaining leaves in long day conditions and buds in short day conditions, resulting in continued growth of the buds. By placing the buds under long day and the leaves under short day conditions the buds remained dormant. This response can be the result of one of two possibilities; if we consider it in light of a hormonal balance. Either an inhibitor is produced in the leaves during short days and is transported to the buds or a growth substance ceases to be produced. Direct inhibition by the hormone abscisic acid (ABA) has been demonstrated in both *Betula* and *Cornus* (Wareing and Saunders, 1971).

Changes in growth promotors and inhibitors have been studied in leaves and buds of *Acer*, *Populus*, and *Salix*. An inhibitor was found to be present in all extracts made from *Acer* buds and leaves which exhibited quantitative changes throughout the course of the year. Apical extracts showed greatest inhibition in early winter, and least when active growth was taking place in May and June. In late summer and early autumn inhibitor levels increased until late August when there

began a gradual decrease to zero which is thought to be associated with the senescence of the leaves prior to abscission. The concentration of the inhibitor in the leaves was found to be less than 20% of that in the apex. *Populus*, on the other hand, exhibited much higher inhibition in the shoot in October after growth had stopped than in August. *Salix* phloem and xylem had an increase in an inhibitory factor throughout autumn. Between October and December it declined and disappeared from the xylem sap. Spiegel (in Samish, 1954), working on grape vines, showed that inhibitor concentrations increased during winter to a maximum in January and then fell to zero two weeks before bud swelling while auxin levels were rising sharply. Studies on mature trees, however, become much more complicated because other factors become important. Water stress, for instance, leads to a significant increase in the ABA concentration of the leaves. ABA may lead to the formation of quiescent buds and later true dormant buds. Little and Eidt (1968) have shown a distinct inhibitory effect on the transpiration rate and delayed bud break in white spruce (*Picea glauca*) due to ABA treatments. Working with wheat and barley, Mittelheuser and van Steveninck (1969) have shown that concentrations as low as 3.8×10^{-7} M of this hormone will cause stomatal closure and a reduction in transpiration.

As is clear from the above, buds are not in true dormancy throughout winter but tend to reach a quiescent state late in winter and remain so until conditions are favourable for growth. Fluctuations of growth-regulating substances in late winter and early spring occur but may be the result rather than the cause of emergence from dormancy (Wareing and Saunders, 1971). While the levels of growth inhibiting substances tend to decrease from February to April; growth promoting substances,

especially auxins, increase and reach a peak at the time of bud break. In *Syringa* and *Quercus*, however, no change in hormone levels were observed during this period. Gibberellins as well as auxin showed a peak at the time of bud break (Wareing and Phillips, 1971).

Returning to the question of day length and dormancy it is interesting to note that higher levels of growth-inhibitor were present in plants transferred to short day conditions than those that remained under long day conditions. This was found to be true for *Acer*, but not for *Betula* and *Robinia*. A further interesting fact in these experiments was that the change in level was detectable in leaves after two days and in the apex after five days before any marked effect of day length on growth could be noticed (Phillips and Wareing, 1959).

Until now hormones have been referred to as growth-promoting or growth-inhibiting. Only in the last twenty years has it been possible to separate and identify these hormones. The growth-inhibitor was initially named inhibitor fraction β, then dormin and abscisin II and is now identified as abscisic acid (ABA). The nature of abscisin I is still obscure. ABA cannot solely be concerned with dormancy regulation since it also occurs in active growing areas of plants. It has not been proven that the inhibitory effect of ABA is not overridden by other inhibitors or promotors mainly because ABA and some of the gibberellins that counteract it are difficult to seperate.

It is difficult to reconcile at present that some promotor might be present that has, until now, defied separation from ABA. It could be that ABA produced in the leaves under short day conditions is transported to the apex accompanied by a low level promotor with "anti-dormin" activity such as one of the gibberellins. Under long day conditions the

leaves could produce sufficient promotor to inhibit the action of ABA even though its levels have not changed.

Gibberellic acid (GA_3) is considered to be the growth-promotor involved with dormancy control since it will cause bud break if applied exogenously in some species. Furthermore the level of GA increases during the postdormant period while the ABA level decreases. It is thus possible to postulate that dormancy is induced by high ABA and low GA levels, while the converse could be true for emergence from dormancy.

Having considered the role of hormones in dormancy it would be approporiate to conclude with a brief section on how changes in hormone levels accomplish their control. Initially it was considered that with the onset of dormancy respiration was suppressed and thus made less energy available to the growing tissue. It has, however, recently been discovered that ABA directly inhibits RNA and DNA synthesis. Dormancy is maintained by blocking production of specific types of mRNA and thus specific proteins needed for growth (Wareing and Saunders, 1971). The action of GA is not fully understood although it is known to stimulate RNA synthesis. Auxins also stimulate RNA synthesis at low concentrations but inhibit it at higher concentrations. Interactions between growth-promoting and growth-inhibiting hormones can occur at many points and it is thus probably not surprising that opposing hormone actions have been recorded.

Very little is known about the eco-physiology of black spruce. The following research was therefore undertaken particularly with regard to:

A. Water Relations.

(i) annual fluctuations of water potential and its components.

Courtin and Mayo (1974) have stressed the lack of this type of

information for most species. These data also provide an indication of the degree of winter desiccation taking place.

(ii) diurnal water and component potential fluctuations.

(iii) stomatal opening on a year round basis particularly with regard to the dormant period.

B. Photosynthesis.

(i) a knowledge of net assimilation on an annual basis. Particular interest was paid to the winter period. Do the trees respond to short, warm periods in winter by initiating photosynthesis? When and what factors cause the onset and termination of dormancy?

(ii) laboratory studies on net assimilation with respect to light intensity and temperature. This supplements the field investigation and could lead to the determination of limiting factors for certain processes.

These investigations can lead to an understanding of how black ruce functions within its range.

MATERIAL AND METHODS

The Basic Gas Analysis System

An open gas-exchange system was used in which the incoming air stream was divided, with one portion going through the cuvette containing the branch and the other going directly to the infra-red gas analyser (IRGA) (Sestak, Catsky and Jarvis, 1971). The basic system for the gas exchange studies was designed in such a way that it could be used both in the field and laboratory with a minimum of change. A diagrammatic representation of the system is given in Fig. 2.

Field Studies

Three Reciprotor model 506R air pumps, whose speed was controlled by variable transformers, were used. The air intake was situated at the top of a 3.6 m dexion tower which supported the cuvette and other apparatus used in the field investigation.

All tubing used to connect the different components together was Polyvinylchloride of 0.6 cm I.D. and 0.15 cm wall. After pump #1 the intake line was split to the sample and blank reference cuvettes, the latter being added to the system to balance the volume of the two lines. It was of identical construction to the sample cuvette but without temperature control. Before and after the sample cuvette there were two Johnson type V-24 3-way solenoid air valves for switching the flow patterns. This made it possible to send ambient air through both cells of the gas analyser without altering the air flow through the sample cuvette. The method in which this was accomplished is shown in Fig. 3.

The solenoid valves were controlled by a Tork model 60M8001 timer with a 60-minute cycle. For reading the sample gas against the reference (Amb/Cuv) valves 1 and 2 were activated while 3 and 4 were deactivated. To obtain reference gas through both cells of the analyser (Amb/Amb) solenoids 3 and 4 were activated and 1 and 2 deactivated. The timer was set so that Amb/Cuv was read for 20 minutes followed by 10 minutes on Amb/Amb.

In the field the sample and reference cuvettes were joined to pumps #2 and #3 respectively by 45 m of tubing. After pumps 2 and 3 the air passed through Gilmont size 3 flow meters which monitored the total flow rate through the system. These were followed by needle valves (Whitey type 1VF2) through which a certain volume could be passed if necessary so that a constant, often slower, flow rate of 420 ml/min could be maintained through the analyser. A series of three further needle valves with interconnections made it possible to switch air streams manually from one side to the other. These were used to zero and span the analyser with standard gases. Gilmont size 2 flow meters were used to monitor the flow rate of the sample and reference gases through the analyser. The gases next passed through Drierite ($CaSO_4$) columns to remove water vapour and finally through Gamma 12 in - line filter units with grade 20 filter tubes to remove any dust before passing to the IRGA.

The gas analyser used for the majority of the study was a Mine Safety Model 200 LIRA (M.S.A.) with a maximum sensitivity of 100 parts per million (ppm) CO_2 full scale. Due to problems with the M.S.A. analyser (e.g. a faulty chopper motor) a UNOR model 2 and a Beckman model 865 analyser were occasionally used. Their sensitivity was set

to correspond to that of the M.S.A.

The analysers were set up in such a way that when ambient air was passed through both cells (Amb/Amb) it would give a mid-scale meter reading. This enabled measurement of both photosynthesis (a net uptake of CO_2) and respiration (a net production of CO_2) of the branch under investigation.

The output of the gas analyser was recorded on a Honeywell Electronik 16 dual range, 24 channel, strip chart recorder. Channels 1 to 8 inclusive were calibrated for inputs of 0-10 mV and channels 9 to 24 inclusive for copper-constantan thermocouples with a range from -10 to +40°C. By changing a range card, this recorder could be converted to ranges of -5 to +10 mV and -50 to +50°C, respectively.

In addition to the IRGA output, the following parameters were also recorded: solar radiation inside and out of the cuvette, soil temperature at 5 and 20 cm, air temperature inside and out of the cuvette, needle temperature in and out of the cuvette, tree root and tree trunk temperatures 2.5 cm from the surface.

Because no power was available in the field until 1973 the first three 24-hour investigations were conducted using an Onan 2.5 kW generator. This resulted in occasional frequency problems with the IRGA.

The dry weight of branches within the cuvette was determined by drying the sample for three days in an oven at 80°C. Longer drying periods at this temperature resulted in no further change of weight. Only needle dry weights were used in the calculation of net assimilation rates. No attempt was made to express the fixation data on a leaf area basis.

Laboratory Studies.

The basic gas analysis system used in the laboratory was the same as that described for the field with only minor changes. The air intake was positioned in the fresh air ventilation duct of the building coming into the room where the growth chamber was situated. The compressed air supply of the building was found to be too unstable for this purpose. The distance between the cuvettes and the analyser was reduced to 6 m from 45 m in the field. This reduced the lag time of the system. Due to the smaller size of the trees used in the laboratory study no measurements were made of root or trunk temperatures.

Cuvette Design

A cuvette with temperature control was designed and constructed for use in the net assimilation work (Fig. 4). Although needle temperature is very closely coupled to ambient air temperature (Miller and Gates, 1967), temperature control was considered necessary due to heat produced by the fan inside the cuvette and to solar heating.

The body of the cuvette consisted of a plexiglass tube 7.5 cm long with a 10 cm I.D. and 0.3 cm walls. The bottom was closed off by a sheet of plexiglass 0.3 cm thick in which an aluminum block 7.5 cm in diameter and 3 cm thick had been mounted. This served for pumping out heat produced in the cuvette. A heatsink, generally used to prevent power transistors from overheating, was mounted on top of the aluminum block with heatsink compound to facilitate better temperature exchange within the chamber.

The cuvette dome was sealed tightly to the base by the use of a plexiglass ring 15 cm O.D. and 2 cm thick mounted on top of the

plexiglass cylinder. On one side there was a 1 x 1 cm entrance in the ring through which wires and the branch were introduced into the cuvette. Suspended from the ring on the inside of the cuvette was a Pamotor miniature axial fan (model 8500 C) for stirring the air in the cuvette. This ensured proper mixing of the gas at all times and reduced the boundary layer around the needles. The fan motor was of an induction type and thus eliminated the possibility of ozone being produced by the brushes of conventional motors which might affect the net assimilation rates of the plants. The air speed within the cuvette was kept at a minimum velocity of 1.6 km/hr.

The cuvette dome was produced by heating a sheet of 0.3 cm plexiglass to 160°C in a mould and, while still hot, applying air pressure to it. This process produced a uniform hemisphere 10 cm in diameter that would provide a better light field within the cuvette than a flat surface with right angle corners. Fig. 5 shows the influence of the plexiglass dome on the spectrum of sunlight in wavelengths as measured with a spectroradiometer (Instrument Specialties Company, Lincoln, Nebraska). It is evident that there is no great shift in any particular wavelength but only a slight decrease in intensity over the whole spectrum (380 to 1550 nm).

The aluminum block was secured into the base of the cuvette with silicon rubber, General Electric Type RTV 102, while the base, cylinder and sealing ring were glued together with Devco clear epoxy. The dome was sealed onto the rest of the cuvette with Terostat type VII (Terson, Germany) and held in place by eight, 2.5 cm stove bolts with nuts.

A sheet of 2.5 cm styrofoam was placed between the cuvette base and the cooler top to ensure good thermal isolation. Good thermal contact

between the cold plate and aluminum block was obtained with heatsink compound between the two metal surfaces. The incoming and outgoing gas ports were situated half way up the cylinder on opposite sides of the fan housing. This prevented gas from passing through the cuvette in a straight line even if the fan was not in operation.

The circuit diagram used in the cuvette temperature controller was based on that described by Ashe (1972) and depicted in Fig. 6. The operational amplifier feedback resistor was changed from 1.0 meg ohm to 2.2 meg ohm, thus increasing the circuit gain and sensitivity of the controller. The second modification to the circuit was to switch the 110 V AC by means of two silicon controller rectifiers (SCR), the gates of which were connected to the relay. This eliminated the high voltage and current going through the relay and the possible arcing of its contacts. The reference diode was mounted in a plexiglass tube, that was painted white and covered with aluminum foil, on the incoming side of the cuvette and cuvette diode was mounted under the fan as shown in Fig. 7.

The cooler, a Peltier cold plate (Thermoelectrics model TCP 2), had its built-in fan wired separately from the cold plate so that it would run continuously irrespective of whether the plate was cooling or not. This reduced the sudden drain of current on the system to some extent with the result that the gas analyser gave a more stable operation. In the laboratory the cooler was capable of maintaining temperatures inside the cuvette to within 1°C of ambient. In the field, however, due to sudden and more frequent changes in ambient air temperatures a control of only ±2°C of ambient was possible. On a few occasions air temperatures within the cuvette rose to 10°C above ambient

because the fuse of the cooler blew due to sudden power surges and relay chatter. Under normal operating conditions the cooler was turned on and off about equal lengths of time.

Standard Gas Calibration

Bottles of standard gas were purchased at concentrations between 300 and 350 ppm CO_2 in air balance (Linde Specialty Gases). These gases were standardized against precisely mixed gases produced from pure carbon dioxide and carbon dioxide-free air, by four cascading Wösthoff precision mixing pumps (two type I SA 18/3a and two type I SA 27/3a pumps were used) as described by Bate, D'Aoust and Canvin (1969). The concentration of the two gases produced was chosen so that one would be higher and one lower than the gas to be standardized. Furthermore they had to be less than 30 ppm apart. A UNOR model 2 IRGA with a full scale span of 30 ppm was used to measure the unknown bottled gas against the primary standard produced by the pumps. The average of two values obtained, which usually differed by less than 0.5 ppm, was taken as the concentration of the unknown bottle. Periodically as the bottles were used they were reanalysed in the same manner to ensure as accurate a value as possible.

To ensure that the pumps were functioning properly gases produced by them were occasionally checked against a U.S. National Bureau of Standards gas guaranteed to be 308 ± 3 ppm CO_2 in nitrogen. For this purpose nitrogen was used as carrier gas in the pumps instead of air since oxygen causes a slight shift if present in only one of the analyser cells (D'Aoust, Bate and Canvin, 1971).

Controlled Environment Chamber

Laboratory studies of net assimilation were conducted in a chamber manufactured by Environmental Growth Chambers of Chagrin Falls, Ohio. The unit had a 2.75 x 3.6 m floor and a 3.6 m ceiling with a mylar barrier. Light was supplied by 84 F96T10/CW Fluorescent Tubes, 24; 100 watt incandescent bulbs and 8 Phillips model 133353E/44 infra-red lamps with an output of 250 watts each. A spectral analysis of the light made with the ISCO Spectroradiometer is given in Fig. 8. Light duration, temperature and humidity varied for different experiments and will be mentioned at the appropriate places. Temperature and humidity were controlled with a Honeywell Cam and Manual Programmer through a Honeywell Controller. The chamber controlled temperature within 1°C and relative humidity within ±5%.

The downward airflow in the chamber was at a rate of 30 m/min and the fresh air make-up fans provided ten changes of air per hour.

Small trees from 1 to 2 m high were collected at the field study site and grown in 36 cm diameter polyethylene pots in their natural soil. The plants were irrigated on alternate days with distilled water and once a month with a black spruce nutrient solution (Swann, 1960 in Hewitt, 1966) during the growing season. No watering was done during the dormant period.

Temperature Measurement

All temperature measurements were made with copper-constantan (T-type) thermocouples. During the 24-hour investigation periods as well as the growth chamber studies temperatures were continuously monitored

on a Honeywell Electronik 16 recorder. This instrument was calibrated against Brooklyn Thermometers with an accuracy of 0.01°C. Spot measurements were made using a Fluke Model 845 AB Microvoltmeter in conjunction with an Omega model CJ-T Cold Junction Compensator.

Soil temperatures were measured with 20 cm long T-type soil thermocouple probes.

Root, trunk and air temperatures were measured with thermocouples made from 5 mil teflon coated thermocouple wire. Thirty cm from the junction the wires were joined to 1 m of 26 gauge (15.9 ml) B. & S. thermocouple wire (Thermoelectric type GG-26-TT). The final connection between the recorder and the thermocouple (45 m in the field and 6 m in the laboratory) was made with 20 gauge (31.9 ml) B. & S. thermocouple lead wire (Thermoelectric type PP-20-TX). Both the root and the trunk thermocouples were inserted into the appropriate organs by drilling a small hole at the site of insertion and then plugging the hole with a match to ensure proper closure. Good contact between the thermocouple and surrounding wood was also achieved in this manner. The depth of insertion in both cases was about 2.5 cm. All bare thermocouples were sprayed with a urethane film to prevent loss of the signal.

Needle temperatures were measured with needle thermocouple clips made of 10 mil stainless steel wire and a nylon washer similar to that described by Fry (1965, pp. 109-110). Three mil copper and constantan wires were used for the construction of the junctions. These were joined to 5 mil teflon coated wires and lead wires as previously described.

Light Measurement

Four different methods were used in the laboratory and field to measure light intensities.

Kipp Solarimeter.

In the field and laboratory a Kipp solarimeter (pyranometer) was positioned as close to the cuvette as possible. The output of the specific pyranometer used was provided by the manufacturer as being 8.9 mV/cal/cm^2/min. Since this caused the recorder to drive off scale at light intensities of just over 1.1 cal/cm^2/min a voltage divider made of two 499 ohm 1% resistors was placed in the circuit. The pyranometer was then calibrated against another Kipp solarimeter (constant 8.3 mV/cal/cm^2/min) and an Eppley model 8-48 pyranometer with a constant of 7.95 mV/cal/cm^2/min in full sunlight on a clear day at various light intensities.

Silicon Blue Cell.

The pyranometer was too large to be placed inside the cuvette so it was placed about 10 cm to one side. This, however, created problems because at times the cuvette would be in full sunlight while the pyranometer was shaded and vice versa. Therefore a form of light sensor was sought that was small enough to fit inside the cuvette and at the same time not shade the branch being investigated. The Sharp model SBC-2020 photovoltaic cell was chosen because it had a spectral response peak in the visible region. Fifty-five percent of the voltage output was due to light between the wavelengths 400 to 700 nm, wit peak between 600 and 700 nm.

Due to the high output of these sensors, two 10 ohm 1% resistors were connected to the leads as a voltage divider so that 1.6 cal/cm^2/min would produce an emf of 10 mV or 100 scale divisions on the recorder. Like the altered Kipp solarimeter, this photocell was calibrated against the Eppley pyranometer and unaltered Kipp solarimeter in sunlight of varying intensities during the day. Thus, at any moment during a 24-hour field study or in the growth chamber, a measure was obtained of the light intensity within the cuvette. The calibration of the various light sensors against one another is given in Fig. 9.

Spectral Analysis.

At four-hour intervals throughout the light period of a 24-hour investigation period in the field, a spectral analysis of the incoming radiation was made with the ISCO spectroradiometer. Spectra were also obtained at different light intensities in the growth chamber studies. Periodically the instrument was recalibrated with the aid of an ISCO model SRC Spectroradiometer Calibrator.

Lambda Meter

At the four-hour intervals when light readings were made with the spectroradiometer, measurements were also taken with all three sensors of a Lambda model LI-185 Quantum/Radiometer/Photometer.

Photosynthetically active radiation (PAR) was measured with a model LI-190S Quantum sensor which had cut-off wavelengths of 400 and 700 nm. Solar radiation was measured using a LI-200S pyranometer. These readings were converted to cal/cm^2/min using the correction factor 1.43197×10^{-3} so that they could be checked against the Kipp solarimeter and silicon blue cell values.

Since many authors still report light values in Lux, a model LI-210S photometric sensor was used with the Lambda meter which produced direct readouts in these units.

Water Relations

Water Potentials

Water potentials of the needles were measured by two different methods. In the field, a Wescor HR-33 Dew Point Microvoltmeter was used in conjunction with a Wescor model C-51 Sample Chamber. The method employed to obtain standard readings was to cool the junction for five seconds and take the reading after a further 30 seconds. This procedure was used to eliminate a slight drift on the meter which sometimes occurred. The sample equilibration time was two hours for the total water potential measurements. Three readings taken five minutes apart were averaged. Extreme variation among the three readings would be 1.0 μV or 2.0 atm. Normal variations for the same sample were 0.5 μV or 1.0 atm for a -30 atm sample. During the 24-hour investigation periods in the field, samples for water potential determination were taken every four hours.

In the laboratory a constant temperature bath was used in conjunction with sample chambers as described by Mayo (1974). A cooling current of 4 mA was used for 15 sec and the measurement was made on a Fluke model 845 AB Microvoltmeter or the microvoltmeter of the Wescor HR-33 dew point meter.

Component Potentials

After readings of total water potential were taken the samples were

removed, together with the sample holder, wrapped in aluminum foil, and immersed in liquid nitrogen for five minutes. The samples were then allowed to warm up to room temperature for ten minutes, care being taken that no condensation could take place before the foil was removed. The sample was then replaced in the bath in the same sample chamber and three further readings were made, five minutes apart, after an equilibration of one hour. The values obtained in this manner are defined as a combined measure of "osmotic and matric" potentials, since both components would influence readings taken as described above.

Periodically a large sample of needles was taken in the field and placed in liquid nitrogen while wrapped in foil. Upon returning to the laboratory a few needles were removed and measurements of combined "osmotic and matric" made on them. Hereafter the remainder of the sample was allowed to thaw and the sap extracted from it with the aid of a hydraulic press. Values obtained for these samples gave the osmotic potential.

Turgor pressure was always determined by the difference between the total water potential and the combined "osmotic and matric" potentials. Matric potentials were calculated from the combined "osmotic and matric" and osmotic values. In the equation:

$$\Psi = \Psi_p + \Psi_\pi + \Psi_\tau \quad \text{.....equation 1.}$$

the following measurements were thus taken: Ψ, $(\Psi_\pi + \Psi_\tau)$ and Ψ_π

where: Ψ = water potential

Ψ_π = osmotic potential

Ψ_τ = matric potential

Ψ_p = turgor or pressure potential

Sample Chamber Calibration

The sample chambers were calibrated with sucrose, mannitol or potassium chloride solutions having potentials of the following values: -1.8, -8.8, -22.6, and -42.1 atm at 30°C. Three readings five minutes apart were made after 1, 2, 3, 4, 5 and 6 hours in the constant temperature bath. The change in output of the psychrometer is shown against time in Fig. 10. These data were used to draw calibration curves for the chambers used after equilibration times of one and two hours, which were the times used when making the actual measurements (Fig. 11). Due to very negative water potentials being found towards the end of the winter the sample chambers were later also calibrated to -90 atm for use in this range.

Soil Water Potential

Soil water potentials were measured at two depths with the aid of Wescor model PT-51-05 soil psychrometers. Measurements were made with the Wescor model HR-33 Dew Point Microvoltmeter as previously described. The soil psychrometers were positioned under the tree at depths of 5 and 20 cm in such a way that water would not be conducted down the wire to the cup.

Needle Infiltration Pressure

Concurrent with taking samples for water potential measurements, samples were also taken for the estimation of stomatal aperture. Needle infiltration pressures were determined with a pressure chamber as described by Lopushinsky (1969a) with 57% ethanol as the infiltration

fluid. Five readings were made at a time and the average value reported.

Hormone Experiments

During recent years much work has been done on the influence of plant hormones on growth, development and dormancy. Two sets of experiments were conducted to investigate the importance of selected hormones on the breaking of dormancy; as indicated by an increase in transpiration, net assimilation and the effect upon stomatal aperture.

Dormant branches were collected in the field and brought into the laboratory. Small branches were cut off and placed in individual containers of hormone solution. The tops of the contrainers around the branches were closed off with aluminium foil to minimize evaporation. Treatments were replicated and various concentrations of gibberellic acid (GA_3), kinetin, abscisic acid (ABA), benzyladenine (BA), and napthalene acetic acid (NAA) were studied.

Measurements made on the branches included: transpiration, needle dry weight, water potential and its components, and CO_2 assimilation.

Specific details concerning hormone concentration, type of measurement made, and conditions under which the experiments were carried out are described for each experiment in the Results Section.

EXPERIMENTAL RESULTS - NET ASSIMILATION

Field Studies

Net Assimilation

Field data were taken periodically between October 13, 1972 and April 19, 1974.

Due to the very open canopy in black spruce bogs, no distinction between sun and shade leaves was made in this study because all needles were exposed to full sunlight at various times of the day. The results presented here are examples of days during spring (prior to bud break), summer and fall (onset of dormancy). The effects of drought (low water potential) and frost during the summer are also illustrated. Additional data can be found in Appendix A.

The daily maximum and minimum temperatures for the Edmonton International and Industrial Airports from September, 1972 through May, 1974 are given in Figs. 12 and 13. During March minimum temperatures gradually increased and in early April the first frost free day was recorded. The last frost of spring was recorded on April 30 at the Industrial Airport and on May 12 at the International.

A minimum cuvette temperature of -1.0°C was recorded in the field during the night of 6 to 7 May. This had no influence on the net assimilation rate which became positive at sunrise (Fig. 14). A maximum rate of 4.8 mg CO_2/gm DWt/hr was recorded at 10.5°C needle temperature and a light intensity of over 1.10 cal/cm^2/min. At this stage bud swelling had just started and a net gain of 34.2 mg CO_2 was fixed over the 24 hours (Table 1). The loss in CO_2 during the night was

replaced within 2.5 hours the next morning.

At the end of May, when the next field experiment was conducted, frost no longer occurred. The buds were very swollen and in the stage just prior to opening. Considerable problems were experienced with the Peltier cooler, resulting in cuvette air temperatures at one stage rising to a maximum of 8°C over the ambient air temperature. Notwithstanding this a maximum net assimilation rate of 4.56 mg CO_2/gm DWt/hr was recorded at 18.5°C and 0.39 cal/cm^2/min (Fig. 15). An hour later light intensity had increased to 0.94 cal/cm^2/min but temperatures of both the cuvette and ambient air had increased from 10°C to 29° and 28°, respectively, resulting in a fixation rate of only 3.47 mg CO^2/gm DWt/hr. For most of the remainder of that day temperatures and light intensities stayed high and net assimilation rates decreased showing a marked mid-day lag due to high temperatures. Although the CO_2 lost at night was double the amount of three weeks earlier (1.59 compared to 0.72 mg CO_2), mainly due to higher nighttime temperatures, it still only required two hours to replace the amount lost. An overall gain of 28.91 mg CO_2 was recorded for the 24 hours. This is markedly less than that observed three weeks before.

Toward the end of June maximum and minimum temperatures were very similar to those at the end of May. The new shoots were now up to 7.5 cm in length and made up the majority of the plant material in the cuvette. A maximum net assimilation rate of 6.01 mg CO_2/gm DWt/hr was recorded at 25.5°C and 0.56 cal/cm^2/min (Fig. 16). During this investigation it was found, like the month before, that temperatures over 30°C resulted in a marked drop in net assimilation. A maximum net gain of 48.67 mg CO_2 was found during the 24-hour period. The high assimilation

rate is ascribed to a high water potential that created favourable conditions for photosynthesis. Due to the high minimum temperature at night (10.5°C) high respiration rates were recorded and a total of 5.76 mg CO_2 was lost. This was, however, regained after 3 hours of positive fixation.

A heavy overcast sky with intermittent rain prevailed on July 22 when the next investigation was conducted. There was only a 5.5°C difference between the maximum (16.5°) and minimum (11.0°) temperatures recorded. The overall result was that the maximum fixation rate (7.00 mg CO_2/gm DWt/hr) was recorded at the time of maximum light intensity (0.23 cal/cm^2/min) and temperature in the cuvette (16.0°C) (Fig. 17). Respiration at night was still relatively high (3.07 mg CO_2 lost) and it took 4 hours to replace the CO_2 lost mainly due to low light levels until noon (less than 0.1 cal/cm^2/min).

In mid-August temperatures suddenly began to decrease and frost occurred on the 18th and 19th. The influence of the frost was very evident on the 19th when a maximum net assimilation rate of only 3.74 mg CO_2/gm DWt/hr was recorded at 22.5°C and 0.8 cal/cm^2/min of light (Fig. 18). Two hours prior to the occurrence of the maximum fixation rate (at 12.30) only 2.35 mg CO_2/gm DWt/hr was fixed at a temperature of 19.5°C and a light intensity of 0.6 cal/cm^2/min. This indicates that the low fixation rate was not due to a temperature above optimum for fixation but to some other factor. Pharis, Helmers and Schuurmans (1970) have shown that subfreezing temperatures of -2°C during the 16 hour night will depress the photosynthetic rate the following day at +3°C in both *Pinus ponderosa* and *Pseudotsuga menziesii*. The rate of temperature ascent from the subfreezing temperature was found to be critical in the

degree of depression. With a rise of temperature to +11°C the recovery was enhanced. Compared with the data obtained on 22 July, the amount of CO_2 fixed during the 24 hours was halved (20.79 mg CO_2) and only one quarter as much respiration took place at night (0.75 mg CO_2 lost). Nevertheless, 4 hours was still required to replace the CO_2 lost at night. This is largely because low light levels prevailed (below 0.1 cal/cm^2/min) for most of the morning.

By the middle of October frost occurred nightly and minimum temperatures had reached -8°C. Definite signs of dormancy were by now evident. Although the minimum temperature was only 0°C fixation rates did not exceed 1.79 mg CO_2/gm DWt/hr at 12.0°C and 0.26 cal/cm^2/min (Fig. 19). Respiration at night resulted in a loss of 1.48 mg CO_2 which was similar to the amount respired on October 2nd and 3rd at a similar temperature. After 2.5 hours of positive fixation the CO_2 had been regained and a total net gain of 7.09 mg CO_2 was found over the 24 hours.

In early November temperatures decreased sharply and no more field investigations were conducted. No work could be undertaken during the warm periods in winter because the gas analyser did not work properly.

Light Response

On July 22, October 2 and 18, in the field, light intensity suddenly decreased from a relatively high value and then increased again within an hour while temperatures remained virtually unaltered. This made it possible to draw light response curves for these occasions (Fig. 20). The three curves differ markedly. On October 18, light saturation was reached at 0.1 cal/cm^2/min with a needle temperature

between 4.5 and 6.0°C. At needle temperatures between 7.5 and 10.0°C on October 2, light saturation was reached at almost 0.15 cal/cm^2/min; the data for July 22 shows a light saturation at 0.20 cal/cm^2/min at needle temperatures between 13.0 and 14.5°C. The differences in the curves may partially be due to the differences in needle temperature at which they were obtained but also to the phenologic state of the tree at the time. In July the new shoots were a month and a half old and the needles were at their maximum photosynthetic capacity. In October, however, the trees were gradually going into dormancy, daylength was reduced and frost occurred at night. This could result in a decrease in light saturation level while photosynthetic rates are also reduced.

Laboratory Studies

Dormancy Termination and Net Assimilation

Early in February, 1973, several small trees were collected at the study site, potted, and maintained in a growth chamber at temperatures of 0 to -5°C. From February 18 to March 4 one of these trees was brought out of dormancy while net assimilation measurements were made continuously. Maximum net assimilation rates taken at 12.00 noon from February 18 to March 3 are given in Fig. 21. There was an initial burst of respiration followed by a gradual activation of the photosynthetic apparatus. The light regime, temperatures and net assimilation data from February 22 to March 3 are given in Appendix B. No positive net assimilation was recorded and only minimal respiration was observed between February 18 and 21 and therefore these data are not presented graphically. Throughout this period minimum temperatures reached -5.5°C at night and maximum temperatures +4.0°C under the full light load.

Light periods and intensities are given in Appendix B for the period of investigation.

On February 22 net assimilation was still negative except for the reading at 12.00 when a positive fixation rate of 0.02 mg CO_2/gm DWt/hr. was measured. A certain amount of photosynthesis was, however, taking place during most of the light period since net assimilation values were higher during the light period than the dark period (0.00 in the light compared to -0.04 mg CO_2/gm DWt/hr in the dark). Positive net assimilation rates were measured from 09.00 to 16.00 on 23 February, that is throughout the perioc when light intensities were over 0.03 cal/ m^2/min. Hereafter net assimilation rates gradually increased until a maximum value of 1.03 mg CO_2/gm DWt/hr was attained on March 2. The reason for the lower absolute fixation rate on March 3 is not evident.

The first positive fixation was measured on the fifth day after temperatures had risen above freezing. This evidence would support that reported by Genkel and Barskaya (1961) who found that dormant *Picea excelsa* became metabolically active after three to five days of exposure to room temperature.

Temperature Response of Dormant Trees

In the preceding experiment it was shown that photosynthesis would not be initiated in a dormant tree if the temperature rises to above freezing during one day only. On the first four days of the experiment the temperature did not exceed +4°C. Higher temperatures could possibly have led to a positive CO_2 fixation and this was tested on three occasions. Frozen pots of soil with dormant trees were placed in large containers and surrounded by vermiculite. This insulated the pots and

prevented the soil from thawing during the experiments. Ambient air temperatures were then gradually increased from 0 to over 30°C in 5° steps over 32 hours while net assimilation was monitored both in the light and dark. During the trials, each of which was conducted on a different tree, no sign of photosynthesis was observed. Figure 22 gives the results. A marked difference in respiration rates is evident. This can be directly attributed to the water potential of the needles. The respiration rate at 30°C of a tree with a water potential of -40 atm was 0.58 mg CO_2/gm DWt/hr and that of another with a water potential of less than -90 atm was 0.32 mg CO_2/gm DWt/hr. Only at temperatures below 5°C was there no appreciable difference in the respiration rates.

Temperature Response of Non-dormant Trees

The photosynthetic response of one-year-old and new needles was investigated in the growth chamber. During the bud swelling stage branches were brought into the laboratory from the field and, with maximum light intensity in the growth chamber (0.21 cal/cm^2/min), net assimilation and respiration rates were measured at temperatures between 0° and 30°C. The data obtained for one of these branches, in which only one-year-old needles were used, are given in Fig. 23. Between 0° and 10°C net assimilation increases sharply and dark respiration started to increase at temperatures over 5°C. An optimum net assimilation rate of slightly over 6 mg CO_2/gm DWt/hr was attained at 15°C; temperatures above this level caused a rapid decrease. Between 10° and 30°C respiration increases virtually in a straight line. Gross photosynthesis, calculated from the net assimilation and respiration data, also showed a maximum at 15°C. It is interesting to note that net assimilation rates

at 0° and 30°C are similar. Unfortunately temperatures below 0°C could not be achieved in the growth chamber under a full light load. The minimum temperature at which positive net assimilation ceases was thus not determined. By extrapolation it could be in the region of -5°C. Freeland (1944) contends that black spruce can photosynthesize to a temperature of -6°C.

Light Response at Optimum Temperature

The influence of light on net assimilation was determined on branches brought in from the field and maintained at 15 ± 1°C in the growth chamber. From Fig. 24, which gives the light response of a branch with swelling buds, it can be concluded that photosynthesis starts at very low light intensities. At a light intensity of 0.01 cal/cm^2/min (7.0μ E/m^2/sec) 0.42 mg CO_2 /gm DWt/hr was being fixed. Light compensation occurred at about 12μ E/m^2/sec (0.04 cal/cm^2/min) and light saturation at about 450μ E/m^2/sec (0.20 cal/cm^2/min).

EXPERIMENTAL RESULTS - WATER RELATIONS

Annual Cycle of Water Potential and its Component Potentials

Samples for determination of water and component potentials were taken around solar noon at fairly regular intervals from ealy May 1973 to the end of May 1974. Osmotic potential measurements were also made and it was then possible to estimate the matric potential. Annual water potential and "combined osmotic and matric" potential cycles for the youngest needles on the tree are given in Fig. 25. Readings taken in early May 1973 were made on 1972 needles which were nearly one year old at that stage. The new needles emerged from the buds in early June 1973 and the readings from then to the end of May 1974 were made on needles increasing in age from one week to one year. In March 1974, an additional sample chamber became available and readings were subsequently also made on needles one year older.

The most striking features of Fig. 25 are the great fluctuations in water potential and "combined osmotic and matric" potentials which occur throughout the year. Between May 2 and May 16 1974 the water potential changed 13.5 atm (from -14.4 to -27.9). Over the same period the "combined osmotic and matric" potentials changed 15.1 atm (from -19.7 to -34.8). This suggests that the species is hydrolable according to the classification of Walter (1931).

When water potential data are compared with maximum and minimum temperature data (Figs. 12 and 13) it becomes clear that a strong correlation exists between them for most of the year. The only exceptions are in May of both years and July 1973. While air

temperatures were rising, water potential dropped sharply in May 1973. Soil temperatures between +2.5 and 7.5°C were recorded at a depth of 5 cm while 0°C was recorded at 20 cm throughout May (Table 2). This led to difficulties in replacing the water lost by transpiration and resulted in low values for May. June readings were made on young needles that were still expanding and very succulent; thus the high water potential. By this stage the soil at 20 cm was no longer frozen.

On July 22 water potentials were lower than at the end of June and temperatures remained unaltered. This drop in water potential is ascribed to the ageing of needles which had by then ceased to grow and were in their stage of full photosynthetic activity. In mid-August temperatures decreased to freezing and water potential also declined. This is considered to be the direct reaction to the lowering of the temperature and the frost hardening of the needles. In early September temperatures were again above freezing and the water potential had increased from the values measured in August. Hereafter, water potentials closely followed changes in temperature. The water potential measurement for early February 1974 seems high. This might be because the snow was not completely removed from the needles before they were placed in the sample chamber. By late March, a minimum water potential was reached. Daily maximum temperatures were around 0°C and the soil at both 5 and 20 cm was frozen.

On all days during April the maximum daily temperature was above 0°C and the tree trunk temperatures were also measured above 0°C by the 9th. Turrell and Austin (1965), working on citrus trees, have shown that branches up to 10.5 cm in diameter exhibit no significant difference from air temperature in their centre during the course of the day.

The tree trunks might thaw during this time with generally rising temperatures. The sharp increase in water potential during April could result from mobilization of water stored in the xylem. Wilner (1952), in Saskatchewan, found that the water content of twigs attached to trees increased during the periods of above-freezing temperatures in late March and April. They did not exhibit an increase in water content from January through March. Detached twigs showed a decrease in water content during both periods. While no mention is made of soil temperatures, it can be assumed that they were below freezing at that time of year. This tends to substantiate the idea that water movement is initiated within the trees in spring before the soil thaws. The field station was dismantled on May 23, 1974 and on that day soil at 5 cm depth was unfrozen. The soil at a depth of 20 cm, however, was still frozen. This implies that roots at a depth of 20 cm were unable to take up water. If, however, the water supply in the trunk had decreased sufficiently due to transpiration of the actively photosynthesizing needles at that stage a deficit could develop and lead to a lowering of the water potential in the needles such as was observed during May in both 1973 and 1974. That the trees were under stress was evident because extensive needle-cast occurred in late May of both years. By early June, when the buds start swelling, the soil usually is unfrozen and water is again available to the roots. This leads to a rise in water potential.

The difference between the curves of Fig. 25 illustrates the magnitude of the turgor pressure in the cells as indicated in Equation (1) on page 26. The average annual turgor pressur of 4.0 atm is low. It varies from a minimum of 0.5 to a maximum of 8.4 atm. A minimum

turgor pressure of 0.5 atm was measured on two occasions. The first in early May 1973, when the soil was frozen and the tree was actively photosynthesizing. This was undoubtedly caused by a water deficit in the needles. In early November 1973, when daily maximum temperatures suddenly decreased from about 0° to -18°C in four days, a turgor pressure of 0.5 atm was again measured. This was probably caused by an abrupt cut-off of the water supply to the needles. The maximum turgor pressure of 8.4 atm was measured in the new, expanding needles just after bud break occurred. A high turgor pressure in this actively growing tissue would be advantageous for cell expansion. Cleland (1967) contended that maximum turgor causes maximum enlargement. While this is judged not to be entirely correct, as water flux has not been considered, higher turgor pressures do tend to promote expansion (Boyer, 1968). The next highest turgor pressure (8.2 atm) was measured in mid April when water potentials were rising sharply with increasing temperatures.

Occasionally measurements of osmotic potentials were made. These data together with the "combined osmotic and matric" potential measurements on the same days are depicted in Fig. 26. The difference between the two curves in this case gives an estimate of matric potential (Equation (1) page 26). The smallest matric potential, -3.0 atm was measured in young expanding needles. The value gradually increased with the ageing of the needles to a minimum of -13.4 atm in late March. By early May matric potential had been increased to twice this value.

Daily Cycle of Water Potential and Needle Infiltration Pressures

The daily cycle of water potential and its component potentials was measured every four hours, where possible, during the 24-hour field investigation periods. Generally, water potentials were high early in the morning, then decreased as the day progressed reaching a minimum around noon. This resulted in higher readings of needle infiltration pressure and indicated that the stomata were probably closed. Then water potential increased because transpiration had decreased.

The data presented here are for representative days during the year indicating the diurnal pattern of water potentials and needle infiltration pressures in the spring before bud break while the soil is still frozen at 20 cm, during the spring drought period, mid-summer with thawed soil and high water potentials, and the influence of the first frost in the fall. Additional data for the other field investigation periods can be found in Appendix C.

The lowest needle infiltration pressures measured were in the region of 17 psi (Fig. 27) and this value was taken to represent open stomata. Pressures in the infiltration chamber were increased up to 40 psi and values of this magnitude represented closed stomata. Lopushinsky (1969b) gave a value of 13 psi for open stomata of *Picea engelmannii*. He also considers stomata to cause no further change in transpiration when infiltration pressures reached 30 psi. Miller and Gates (1967) found that the minimum diffusion resistance to water vapour in the field and laboratory for black spruce was 50 sec cm^{-1}. This high value agrees well with the high minimum needle infiltration pressure measured on the trees studied.

On May 6 and 7, 1973 needle infiltration pressures varied between 17 and 23 psi. This indicates that the stomata were almost fully open most of the day (Fig. 27). Water potentials started at about -13 atm by 20.00 in the evening on May 6 and then increased to a maximum of -11 atm at 04.00 in the morning. With the complete opening of the stomata, the value decreased to a minimum of -22 atm at noon on May 7. Although stomata were not closed at midday on the 7th, water potentials had started to increase by 16.00. The "combined osmotic and matric" potential exhibited a similar response to the water potential but a greater change occurred during the night. Turgor pressures were high (12.5 atm) at 20.00 on May 6 and decreased steadily to about 0 atm by 08.00 on May 7. It remained at a low value for the rest of the day. At this stage the soil at 5 cm had thawed but was still frozen at a depth of 20 cm (Table 2).

The needle infiltration pressures on May 29 and 30 indicated that the stomata went from fully open to closed (18 to 40 psi, Fig. 28). At 18.00 on May 29 the stomata were nearly closed and four hours later they were fully closed. The water potential as well as the "combined osmotic and matric" potential increased until 04.00 the next morning when the stomata had opened again. After 08.00 on May 30 the water potential decreased and reached a minimum value at noon. Needle infiltration pressures increased after 14.00 and water potentials were higher when measured at 16.00.

Water potential was subsequently measured on June 27 and 28 and little variation occurred in the course of the 24 hours (Fig. 29). The stomata, however, still displayed their normal pattern by being open late in the afternoon of June 27, closing to some extent during the

night and reopening next morning. During this 24-hour period the highest water potential was measured in the field, namely -8.5 atm and at 04.00 on the morning of June 28.

The first frost of autumn was recorded on the night of August 18 to 19 and this had a marked effect on the water potentials as well as on the stomata (Fig. 30). The stomata were partially open for most of the night but they closed suddenly once frost occurred at 02.00 on August 19. When the temperature rose above freezing the stomata again reopened. Instead of increasing, as expected, water potentials decreased during the night. Once the stomata were closed there was, however, a slight increase but this reversed itself again as soon as the stomata reopened. Water potentials were thus not restored during the night and a general decrease prevailed over the 24-hour period.

EXPERIMENTAL RESULTS - HORMONES

The Influence of Various Hormones on Transpiration

Experiment No. 1

The first experiment on the influence of hormones upon transpiration of dormant branches was carried out in 1972. The samples were kept in a growth chamber with 16°C day temperatures (8 hr) and 6°C nights (12 hr) with 2 hour change over periods. Light duration and intensities are given in Table 3.

The vials containing the branches were weighed on a Metler (model balance each morning at 08.00, refilled with the same hormone solution, reweighed, and replaced in the chamber.

Throughout the course of the experiment notes were kept on signs of bud swelling and colour changes of the needles. The experiment was terminated after 30 days. Needle dry weights were determined for each branch and the transpiration rates calculated on a dry weight basis.

The treatment and results of the first transpiration experiment are summarized in Table 4. After 30 days the average amount transpired by the three controls and the benzyladenine (BA) 1×10^{-6}M treatment was greater than in any of the other treatments, including the BA 1×10^{-5}M. This was the only treatment in which a large difference in rate was observed between the two concentrations. BA 1×10^{-6} appeared to enhance transpiration slightly, but BA 1×10^{-5} appeared to suppress it distinctly. Abscisic acid (ABA) in both concentrations showed the greatest suppression and all the other treatments exhibited varying degrees of suppression. Sometimes these were dependent on the

concentration and sometimes not.

The data obtained are depicted graphically in Figs. 31 through 35 plotted in cumulative totals for average values at five day intervals.

Experiment No 2

Because of the results obtained in experiment No. 1, it was considered important to examine further the influence of ABA and BA on transpiration, net assimilation, and water potentials. The temperature of the growth chamber was maintained at a constant 10°C with a relative humidity of 60 percent. Light duration and intensities are given in Table 5.

Transpiration was measured by filling 25 ml measuring cylinders to the same mark with the original solution every evening at 20.00. This was done with a 2 ml pipette and the volume added was recorded to the nearest 0.01 ml. At the end of the experiment the branches were dried and the transpiration rates calculated on a needle dry weight basis.

Water potentials and component potentials were measured as described previously. Only needles from the control, ABA 3.8×10^{-7}M and BA 1×10^{-6}M treatments were used for this.

Net assimilation and respiration measurements were similarily made on the control, ABA 3.8×10^{-7}, and BA 1×10^{-6} treatments. On alternating days a branch of one of the treatments was placed in the cuvette and its net assimilation and respiration rates monitored over a 24 hour period with the base of the branch remaining in the treatment solution. In this manner the same branch for each treatment was measured 5 times over the 15 day duration of the experiment. The

method in which the gas analysis study was conducted has been described previously.

The treatments and transpiration data obtained are summarized in Table 6. While this experiment was conducted only over a 15 day period, there was a big difference if compared with the 1972 data (Expt. No. 1) over a similar time period with the same treatments and the same concentrations. Both ABA and BA showed suppressed transpiration slightly. The only treatment that exhibited a slight enhancement of transpiration was ABA + BA 1×10^{-6}. All treatments showed a general increase over the first week followed by a decrease the next.

Figures 36 through 38 give the results graphically for the different sets of treatments. Both ABA + BA 5×10^{-5} and ABA + BA 5×10^{-6} have final values very close to that found in the control. The treatment with ABA + BA 1×10^{-6} had a higher total than the control but not significantly so. On the other hand ABA + BA 1×10^{-5} was significantly lower than any of the other treatments in this group and similar to that obtained for BA 1×10^{-6} by itself.

Throughout both the transpiration experiments with hormones great variability was found among the three replicates of each treatment. In the extreme case the difference between the highest and the lowest value for the same day as 8x.

The Influence of Hormone Treatments on Water Potential and its Component Potentials

Water potentials of the three treatments studied in experiment No. 2 varied greatly from day to day (Fig. 39). This was surprising since the samples were all taken at 11.00 in the morning and temperatures, relative humidity, light intensity, and photoperiod remained constant for the duration of the experiment. The only conclusion that can be drawn from the water potential data is that the BA treatment had an average value of 5 atm lower than the other two treatments over the 15 day investigation period. This could be due to enhanced stomatal opening and increased transpiration. Pallas and Box (1970) have shown an increase in transpiration rate and a decrease in stomatal resistance in *Avena* after treatment with cytokinins.

Although "combined osmotic and matric" potentials also varied, their amplitude of variation was much smaller. Considerable difficulty was experienced when making these readings and six values were not available.

The Influence of Hormone Treatments on Net Assimilation

The three treatments in experiment No. 2 were conducted simultaneously, but since net assimilation was investigated only on alternating days direct comparisons cannot be made. Appendix D gives the net assimilation data as obtained on the individual days for the 24-hour investigation periods.

The control branches (H_2O measured on days 1, 4, 7, 10 and 13) exhibited maximum fixation rates during the third investigation period

and thereafter a decrease (Fig. 40). With respect to the net gain in CO_2 fixed, equal quantities were fixed on days 1 and 7 and the smallest net gain was recorded on day 13 (Fig. 41).

The ABA 3.8×10^{-7}M treatment (measured on days 2, 5, 8, 11, and 14) showed a general increase in maximum fixation rate for the first four periods and then a decrease (Fig. 40). Net gains on the other hand increased over the first three periods and then decreased (Fig. 41). Although the highest fixation rate was recorded on day 11, this rate was maintained only for a short period and was then followed by a sudden decrease to just above compensation point.

The BA 1×10^{-6}M treatment (measured on days 3, 6, 9, 12, and 15) started with the highest fixation rate and generally decreased thereafter (Fig. 40). Daily gains in net fixation exhibited a similar trend (Fig. 41).

When the net gains are plotted on an accumulative basis (Fig. 42), it is evident that the control gained nearly 20 mg CO_2/gm DWt on the five days measured and the branch subjected to the BA treatment fixed a total of 40 mg CO_2/gm DWt. For the branch give the ABA treatment the total fixed as 60 mg CO_2/gm DWt (Fig. 42). This indicates that both hormones enhanced net assimilation but not to the same extent. Adedipe, Hunt and Fletcher (1971) have shown that a BA solution applied to the leaves of red kedney bean plants will enhance photosynthesis.

DISCUSSION

Black spruce is well adapted to the environment in which it occurs with a maximum net assimilation rate at 15°C under low light intensities (Fig. 23). The evergreen nature of the species makes it possible to exhibit positive net assimilation until late in the autumn, long after deciduous species have lost their leaves. Similarily, net assimilation can commence before the new leaves have developed on deciduous species. Because net assimilation is positive for more than a month before bud swelling is initiated, energy reserves which have to be brought through the long, harsh winters to maintain vital processes do not have to be large since little, if any, are needed for the development of the new leaves in spring.

Ideal growing conditions, as indicated by both the field and laboratory investigations, would consist of maximum daily temperatures between 12 and 18°C and minimum night-time temperatures from 0 to +5°C. This would ensure a maximum net assimilation during the day and a minimum CO_2 loss at night due to respiration. Furthermore, if temperatures remain above freezing at night, photosynthesis would not be impaired during the subsequent day. Light intensities of one-tenth the solar constant ensure light saturation for photosynthesis provided that the water potential of the needles is not too low (Fig. 24).

Net assimilation rates of evergreen conifers varies between 5 and 15 mg CO_2/gm DWt/hr (Sestak, Catsky and Jarvis, 1971). Small (1972a) published an extrapolated maximum mean net photosynthesis rate of 4.32 mg CO_2/gm DWt/hr for black spruce. This mean was derived from two

determinations in each of June, July, and August. Branches were brought into the laboratory and net assimilation rates determined under standard conditions. No mention is made, however, of the environmental conditions at the time, the age of the needles used in the study or the phenological state of the tree from which the branches were taken. This is less than the 7.0 mg CO_2/gm DWt/hr measured in this study. The only other data that are available on the photosynthetic rate of black spruce is that of Clark and Bonga (1970), which was also conducted on branches brought into the laboratory. A maximum fixation rate of approximately 1.3 mg CO_2/gm DWt/hr was measured at 20°C and a light intensity of 0.058 cal/cm^2/min. The very low maximum net assimilation rates reported in this study are due to the very low light levels used. The present investigation indicates that a fixation rate of only 0.29 mg CO_2/gm DWt/hr occurs at a light intensity of 0.05 cal/cm^2/min (Fig. 24).

The general pattern of photosynthesis as found in this study over the seasons is given in Fig. 43. All the data collected in the field were combined to indicate the influence of temperature and light intensity on net assimilation. This combined information is presented in Fig. 44.

Miller and Gates (1967) have stated that the finely divided needles of conifers have large convection coefficients and a strong convective heat exchange due to their small diameters which cause the needles to be strongly coupled to air temperature. Even under a full light load of 1.3 cal/cm^2/min in mid-summer, needle temperatures were not found to deviate more than 1°C from air temperature. While this phenomenon can be advantageous to a species by preventing high temperatures from developing in the leaves under conditions of high light intensities and

high air temperatures, it can also be disadvantageous by depressing photosynthesis during periods of low ambient air temperatures and high light intensities. In black spruce, an increase or decrease of about 10°C from the optimum net assimilation temperature of 15°C results in halving the fixation rate (Fig. [redacted] while conditions are suitable for photosynthesis during [redacted] and late autumn, maximum fixation rates are lower than [redacted] summer at the same light intensity (Table I). This is also reflected in the CO_2 balance for the field investigation periods during the spring and fall when it took longer to replace the CO_2 lost at night by respiration. The time taken varied from 2 to 5 hours; the longer periods being after cold nights when less CO_2 was lost by respiration.

Frost during the summer, as occurred on August 18 and 19, 1973, causes a drastic reduction in fixation over the next 24 hours even though temperatures may return to optimum with light intensities well above saturation (Fig. 18). Tranquillini (1963) has shown that net assimilation is depressed on days following frost of -4°C or more for *Picea excelsa*. This phenomenon is considered to be associated with frost hardiness and the water relations of the species since it does not occur during spring and fall when frost occurs regularly at night. Pisek and Tranquillini (1951) and Zeller (1951) have shown that frost-hardened cells are less active photosynthetically than unhardened cells. The depression of net assimilation during the summer after frost at night in *Pinus ponderosa* and *Pseudotsuga menziesii* has been shown by Pharis, Helmers and Schuurmans (1970).

As with temperatures below optimum, temperatures above optimum cause a decrease in fixation. This decrease is due to a higher

respiration rate, and desiccation which leads to lower water potentials and closure of the stomata. Data obtained in the field on May 30, 1973, exemplify this phenomenon when needle temperatures rose to over 30°C in the cuvette during the afternoon resulting in lower net assimilation rates than during the morning (Fig. 15).

Vincent (1965) contends that soil temperatures do not appear to be a controlling factor in bud break since this happens when the soil temperature varied between 38 and 46°F (+3 and 8°C, respectively). This investigation would, however, indicate that soil temperature is of great importance in spring due to its direct influence on water relations and thus indirectly on bud swelling and net assimilation. Bud swelling was initiated during early May when water potentials were high (Fig. 25). The decreasing water potentials in late May, due to transpiration while the soil is still frozen (Table 2), cause a cessation in bud swelling. The buds break in early June when soil temperatures are above 0°C and when water potentials are higher due to water being available to the roots.

Conceivably, soil temperatures also play an important part in determining the initiation of dormancy in the fall. Soil temperatures were still a few degrees above freezing at both 5 and 20 cm below the surface during the second field investigation of October 1973, but were rapidly decreasing (Table 2). Two weeks later air temperature dropped sharply and soil temperatures probably reached freezing temperatures soon thereafter (Fig. 13). Dormancy must have set in at this stage as maximum air temperatures thereafter did not exceed -10°C. Due to the den change in air temperatures in 1973 it is difficult to ascribe the onset of dormancy in that year to either air or soil temperatures. In 1972, however, air temperatures decreased gradually

and then increased again in late November to just above freezing (Fig. 12). Throughout October and November that year soil temperatures at a depth of 20 cm below the surface were at 0°C or slightly above freezing. Positive net assimilation was still measured on November 23 when air and needle temperatures reached a maximum of +6.5°C. Fixation rates were, however, extremely low, suggesting the onset of dormancy.

Additional information on dormancy and frost hardiness was obtained during one of the transpiration experiments (discussed in Appendix E) when a growth chamber went out of contol. A tree with its soil frozen and maintained at -5°C with a cold plate, after it had been used in the transpiration experiments, and another that was still to be used were placed in a growth chamber for investigation the next day. During the night, temperatures in the chamber inadvertently dropped to -20°C for a few hours. The following day efforts were made to sustain the two trees by placing them under optimal conditions and allowing the soil in the one pot to thaw. After a few weeks, however, the tree that was still to be used in the transpiration experiment showed no sign of survival while the other, which had the frozen soil, had initiated new growth and subsequently overcame the setback. This indicates that soil temperature probably has a very important function in regulating both frost hardiness and dormancy.

Data obtained in the field indicate that temperatures also influence light saturation levels of the needles (Fig. 20). At needle temperatures between 4.5 and 6.0°C, light saturation was reached at 0.1 cal/cm^2/min. Needle temperatures from 7.5 to 10°C gave light saturation values of 0.15 cal/cm^2/min, and 0.20 cal/cm^2/min was needed to saturate needles at a temperature of 13 to 14.5°C. Growth chamber

studies conducted at a needle temperature of 15°C also indicate light saturation at an intensity of 0.20 cal/cm^2/min which corresponded to about 450 μ Einsteins/m^2/sec (Fig. 24). Even on overcast rainy days this light intensity was reached suggesting that light is rarely a limiting factor for net assimilation. Small (1972) found that light saturation had been reached at 185 W/m^2 (0.265 cal/cm^2/min) at a temperature of 25°C. Comparing these results with those reported for comparable species (Larcher, 1969) it is evident that a good agreement exists (Table 7). The light compensation value obtained was on the high side while the light saturation level is below the average. The data published by Larcher (1969) take sun and shade leaves into consideration but due to the very open nature of the canopy in a black spruce swamp no distinction between sun and shade leaves was made in this study as all the needles were exposed to full sunlight at various times of the day. Both the maximum fixation rate and the optimum temperature for fixation agree well with species growing under comparable conditions. Growth chamber studies indicate that, at a needle temperature of 15°C, light compensation occurs at about 0.04 cal/cm^2/min or 12 μ E/m^2/sec (Fig. 24). It can be assumed that this value will not be higher at lower needle temperatures. This would ensure that, even though maximum fixation might not occur on the dullest days, positive fixation would still occur. Similarily a positive fixation was often measured in the field before sunrise in the morning and after sunset in the evening.

The very low light saturation and low light compensation levels are of great importance to a species inhabiting high latitudes where long twilight hours exist during spring, summer and fall. At latitudes north of 60°N this could lead to a positive fixation throughout the

24-hour day of continuous daylight in mid summer. A great enhancement in the amount of CO_2 fixed during the summer months would result with more storage of reserves and the possibility of the species being able to inhabit otherwise unfavourable climates where the summers are too short for replacing the energy lost during the long winters.

The measurement of water potential and its component potentials over the seasons indicates that black spruce is hydrolabile. Water potential measurements taken at noon vary from -8.5 to -35 atm while "combined osmotic and matric" potentials fluctuate from -14 to -38 atm (Figs. 25 and 26). Small (1972b) obtained an average water potential of about -19 atm, ranging from -17 to -21 atm, for six measurements taken during June, July and August. These values are surprisingly low for a bog plant that is standing with its roots in contact with available water for more than half the year. Both water and osmotic potentials exhibit a good correlation with temperature over most of the year. A maximum noon value of -8.5 atm was obtained in late June 1973 when the new needles had reached full development. Minimum values at noon of less than -30 atm were found in early November 1973, due to a sudden increase in air and needle temperatures, and in late March, 1974, owing to maximum temperatures being above freezing while the soil remained frozen. Winter dehydration has been shown to occur in *Picea glauca* by Fraser (1966) and [illegible] by Lindsay (1971). Increased air temperatures in April lead to the mobilization of water in the xylem of the trees resulting in higher water potentials. The soil at a depth of 20 cm, however, remained frozen until the end of May and caused a drought condition to develop once no more water was available to be moved into the needles. Water and osmotic potentials subsequently dropped to a

final minimum value with resulting needle cast before the soil thawed. Denyer and Riley (1964) have reported needle cast in black spruce due to drought conditions in summer. They indicate that the older needles are more affected than the younger needles. In early June the soil thawed and made water available for uptake by the roots. It was only when this occurred that new growth was initiated. Belyea *et al.* (1951) found radial growth to be initiated in black spruce towards the end of May in northern Ontario (40°N). This corresponds well with the time of bud break observed in the Edmonton region.

Daily fluctuations in water and "combined osmotic and matric" potentials showed a distinct pattern in summer. During the early morning hours before sunrise the stomata open and water potentials tend to decrease gradually to a minimum value at noon (Fig. 28). The guard cells then close and water potentials rise. The stomata may open again in the late afternoon, but this usually has little effect on the water potentials. After sunset, the stomata close again and water potentials rise to a maximum value at night. Noon values of water potentials are usually 5 to 10 atm lower than night-time values. The "combined osmotic and matric" potentials exhibit a similar fluctuation during the day but with a smaller amplitude.

The highest turgor potential (8 atm) was measured in young growing needles. Once the needles were fully extended turgor diminished considerably. Turgor pressures generally varied from 2 to 5 atm with occasional values outside this range due to sudden changes in the environmental conditions. Young growing needles also had high matric potentials (-3 atm) compared to the average value which was between -6 and -12 atm.

Soil water potentials measured at both 5 and 20 cm below the surface throughout the summer never fell below -2 atm. This indicated that water is always abundantly available for uptake by the roots while the soil is not frozen. The present study indicates a high root resistance to water uptake, because soil water potentials are high throughout the year while needle water potentials remain low even under the most favourable conditions.

Ahlgren and Hansen (1957) studied the effect of temporary flooding on black spruce and found that nearly 100 percent survived for all periods of flooding up to 48 days. The shallow, plate-like root system the species exhibits throughout its range may be an advantage. Oxygen tensions in the soil would be higher close to the water surface than deeper down. Furthermore, a plate-like root system would be advantageous in the arctic region where a shallow active layer prevails over the permafrost. A shallow root system could, however, be disadvantageous in dry, sandy soils where the species would suffer from dessiccation long before a deep-rooted species. This could possibly be the reason for black spruce showing a distinct preference for wetter sites throughout its range. Greater competition for available nutrients and water could also take place between a shallow-rooted species and the shrubs and herbs growing around it, which due to their smaller size generally have superficial roots.

Evidence was obtained indicating there is a relationship between the maximum photosynthetic and respiratory rates and water potential. During both field investigations in May 1973 net assimilation rates of only 60 percent of maximum were obtained under favourable conditions. This cannot be ascribed to the needle age class because needles of the

same age in a growth chamber study, but with high water potentials, gave maximum fixation rates. Comparing the maximum net assimilation rates as obtained in the field (Table 1) with the annual cycle of water potential (Fig. 25) it is evident that net assimilation was suppressed by water potentials below -20 atm. However, high fixation rates were measured at water potentials above -20 atm indicating the ability to fix carbon at a relative low water potential. Similarly the respiration rate of a dormant tree with a water potential of less than -90 atm was only 55 percent of that of a dormant tree with a water potential of -40 atm at the same temperature (Fig. 22). The lowest water potential at which signs of photosynthesis were still evident was -54 atm while respiration was measured at a water potential of less than -90 atm. In both these cases the trees were in a growth chamber and subsequently died.

Studies conducted on dormant trees indicate that photosynthesis was not initiated by short periods of temperatures above freezing as was reported by Clark and Bonga (1970). It was only after a period of four days with maximum temperatures up to +4°C that photosynthesis was initiated (Fig. 21). Apparently during Chinook periods of short duration photosynthesis does not take place but respiration does. Chinooks can, however, cause severe damage due to an increased transpiration rate with the higher temperature and thus consumption of the reserve water supply. Christersson (1972) found a maximum transpiration rate in spruce seedlings (*Picea excelsa*) only after 3 to 5 days of conditions favourable for the termination of dormancy. Under similar conditions *Pinus sylvestris* needed 10 to 14 days to reach a maximum transpiration rate.

Throughout the winter while the trees were dormant, needle

infiltration pressures greater than 40 psi were always measured. This indicates that the stomata were constantly closed. The lowest needle infiltration pressure measured was 17 psi and this was taken to represent fully open stomata. This figure agrees well with the very high diffusion resistance value obtained by Miller and Gates (1967).

The results of the hormone experiments are inconsistant; for example transpiration results obtained for the BA 1 x 10^{-6} treatment contradict one another on the two years, the one enhancing transpiration and the other inhibiting (Figs. 34 and 36). ABA at all concentrations tested, however, reduced water loss (Figs. 35 and 36). In the transpiration experiments with ABA and various concentrations of BA, and BA conflicting results were obtained. ABA and BA 1 x 10^{-6} enhanced transpiration while both ABA and BA 5 x 10^{-5} and 5 x 10^{-6} gave values similar to the control. ABA and BA 1 x 10^{-5} suppressed transpiration. Both BA and ABA enhanced net assimilation which is surprising since ABA is known to cause stomatal closure (Figs. 41 and 42). Ludlow and Jarvis (1971) found that the mesophyll resistance to CO_2 transfer in Sitka spruce was much higher than the stomatal resistance (minimum values of 6.0 and 1.8 sec/cm, respectively). The enhancing effect of both ABA and BA on net assimilation could be due to a decrease in the mesophyll resistance caused by these hormones. This would lead to a more efficient transfer of CO_2 to the chloroplasts and thus enhance fixation. This contradictory evidence needs a more detailed investigation.

Recently a study has been completed on the eco-physiology of black spruce near its northern limit of distribution at Schefferville, Quebec for which complete data are at present available (Vowinckel et al., 1974). Daily gains in CO_2 during the summer are reported to vary

from 2.5 to 3.5 mg CO_2/gm DWt at Schefferville while similar values for the Edmonton region were found to be between 30 and 50 mg CO_2/gm DWt/day. While the relevant data are not available, this is thought to be due to the needles being frost-hardy throughout the summer, resulting in the lower fixation rates. The temperature for maximum fixation at the tree-line was reported at 15°C, the same as that found in this study. Light saturation, however, only occurred at 0.8 cal/cm^2/min (1.0 μ E/cm^2/sec, their given figure) while this was found to occur at 0.20 cal/cm^2/min (450 μ E/m^2/sec) at Edmonton.

It would be appropriate to consider what distributional barriers would prevent this species from extending its range. It has been shown that frost during the summer greatly reduces net assimilation. The further north the species grows, the greater is the possibility of it being exposed to frost in summer. Summers are also generally shorter and colder farther north. A zone is reached where the amount of energy that can be stored during the summer is not sufficient to sustain the species during the winter. An additional problem for black spruce is the rise and fall in water potential that occurs in April and May. Should the soil not thaw for a long time after air temperatures rise above freezing, drought conditions may cause death due to its intensification. The plate-like root system is undoubtedly an advantage in this respect.

Vincent (1965) has stressed the fact that black spruce does not tolerate competition for growing space. Travelling towards the equator, floras become richer and the species more diverse in adaptations to specific environments. This results in greater competition, which causes black spruce to be confined to unfavourable localities. In

addition to this the higher temperatures in summer cause a decrease in net assimilation while night time respiration rates are also high due to the higher night time temperatures. Again a zone is reached where fixation rates during the summer become limiting. While the latter condition is of some importance in limiting black spruce from spreading further south, competition and the availability of suitable habitats are thought to be more important restraints.

In Alberta, Chinooks increase in frequency and duration towards the south. This would cause the trees to break dormancy in late winter only to be confronted with extended periods of temperatures below freezing once the Chinook conditions are over. This could have a very adverse effect on the survival of the species since much energy which cannot be replaced will be lost during respiration.

The following are the major contributions of this study to an understanding of black spruce. Both in the field and laboratory investigations the maximum net assimilation rate was measured at a needle temperature of 15°C. An increase or decrease in temperature of 10°C reduced the fixation rate by about 50 percent. Light compensation for net assimilation was found to be at 0.04 cal/cm^2/min (12 μ E/m^2/sec) at a temperature of 15°C while light saturation occurred at 0.20 cal/cm^2/min (450 μ E/m^2/sec). The maximum fixation rate recorded in summer was 7.0 mg CO_2/gm DWt/hr, which resulted in between 30 to 50 mg CO_2/gm DWt/day being fixed by the trees. During late summer, frost at night drastically reduced the net assimilation rate of the following morning even though temperature and light intensity returned to an optimum. A relationship was found to exist between needle water potential and net assimilation. Water potentials below -20 atm had an inhibito

effect on fixation.

The trees were found to be hydrolabile exhibiting a fluctuation in needle water potential between -8 and -35 atm over the seasons. "Combined osmotic and matric" potentials varied from -14 to -38 atm over the same period. Minimum needle water potentials were measured at noon and were generally 5 to 10 atm lower than values obtained at mid-night when the highest measurements were obtained. Turgor pressure in the cells fluctuated from 2 to 5 atm. The matric potential of young, growing needles was very high (-3 atm) but decreased with age to between -6 and -12 atm. Soil water potentials were always found to be higher than -2 atm.

Winter desiccation takes place and is followed by a spring drought period when the trees are out of dormancy, actively photosynthesizing, but unable to take up water from the frozen soil. During dormancy the stomata are closed and do not respond to changes in light or temperature of short duration. Photosynthesis was only induced after 3 to 5 days of temperatures above freezing by which time the stomata were again active. Needle infiltration measurements taken with fully open stomata indicate a high diffusion resistance to water loss.

The following question, which warrant further investigation, have arisen, or remained unanswered by this study:

1. New assimilation studies could only be conducted to a temperature a few degrees above freezing. At this temperature fixation was still positive. It would be important for an understanding of black spruce to determine the lowest temperature at which a positive net assimilation still occurs.

2. Indications are that root resistance to water uptake is high.

This, however, needs verification.

3. The occurrence of the plate-like root system throughout the range of the species suggests that this phenomenon is genetically controlled. No genetic studies have at present been undertaken to test this hypothesis.

4. Dormancy tends to set in at the time that the soil freezes in the fall instead of being controlled by air temperature. This needs further investigation.

5. A study of the spring drought period would be rewarding. The occurrence of the drought has been established but its overall influence on the trees needs further study.

6. A correlation has been shown to exist between needle water potential and net assimilation rate. It is, however, not known if the decrease in fixation is due to desiccation of the cytoplasm or other changes within the cells.

7. Water and osmotic potentials were found to change rapidly in the cells. Is this accomplished by hydrolysis of starch to sugars or by other means?

8. An increase in net assimilation was reported with the hormone experiments. It was suggested that this might be due to changes of the mesophyll resistance, but no proof is available for this at present.

TABLE 1. Maximum net assimilation, CO_2 balance and temperature data for the field studies.

Date	Max. N.A. mg/gm/hr	Temp °C	Light cal/cm²/min	Min. Cuv. Temp°C	CO_2 balance mg CO_2/gm DWt/day	Remarks
14 Oct. 72	0.31	+6.0	0.72	-10.0	-0.834	1972 needles
20 Oct. 72	1.84	+5.5	0.18	-5.0	+5.804	1972 needles
23 Nov. 72	0.34	+6.5	0.11	-3.5	--	1972 needles
7 May 73	4.48	+10.5	1.20	-1.0	+34.150	1972 needles buds swelling
30 May 73	4.56	+18.5	0.39	+7.0	+28.910	1972 needles buds ± open
28 June 73	6.01	+22.5	0.56	+10.5	+48.67	1972 needles 1/4 1973 needles 3/4
22 July 73	7.00	+16.[illegible]	0.23	+9.0	+42.42	1973 needles
19 Aug. 73	3.74	+22.5	0.80	-3.5	+20.79	1973 needles first frost
7 Sept. 73	5.43	+14.0	0.20	+9.5	+26.26	1973 needles
3 Oct. 73	5.67	+14.0	0.23	-0.5	+28.70	1973 needles
18 Oct. 73	1.79	+12.0	0.26	0.0	+7.09	1973 needles

TABLE 2. Average soil temperatures in °C during the field investigation periods and supplemental noon readings during 1974.

Date	5 cm depth	20 cm depth
14 October 1972	0°C	+0.5°C
20 October 1972	-1°	0°
23 November 1972	-1°	0°
7 May 1973	+2.5°	0°
30 May 1973	7.5°	0°
14 June 1973	10°	1°
28 June 1973	10°	+2°
22 July 1973	10°	3.5°
19 August 1973	5°	7.5°
7 September 1973	10°	7.5°
3 October 1973	2°	4.5°
18 October 1973	2.5°	3°
4 February 1974	-6°	-2.5°
12 March 1974	-3.5°	-2°
9 April 1974	-1.3°	-1.3°
19 April 1974	-0.5°	-0.5°

TABLE 3. Radiation intensity and duration, and photosynthetically active radiation (PAR, 400-700 nm) in hormone experiment No. 1.

Time period	Incandescent	Fluorescent	Radiation cal/cm^2/min	PAR μE/m^2/sec
00.00 - 06.00	1/3	1/3	0.08	160
06.00 - 10.00	3/3	1/3	0.10	175
10.00 - 18.00	3/3	3/3	0.21	400
18.00 - 22.00	3/3	1/3	0.10	175
22.00 - 24.00	1/3	1/3	0.08	160

TABLE 4. Summarized results on the effect of hormones upon transpiration. Experiment No. 1. Average of 3 replicates over a 30 day period. Transpiration in ml/gm DWt at various hormone concentrations (M).

Treatment	1×10^{-5}	1×10^{-6}	3.8×10^{-6}	3.8×10^{-7}
GA	21.68	17.01		
Kinetin	19.73	19.70		
BA	18.77	29.19		
NAA	22.39	16.24		
ABA			15.42	13.05
H_2O		26.72		

TABLE 5. Radiation intensity and duration, and photosynthetically active ratiation (PAR, 400-700 nm) in hormone experiment No. 2.

Time period	Incandescent	Fluorescent	Radiation cal/cm^2/min	PAR µE/m^2/sec
00.00 - 06.00	--	--	--	--
06.00 - 08.00	1/3	--	0.03	10
08.00 - 10.00	1/3	1/3	0.08	160
10.00 - 14.00	3/3	3/3	0.21	400
14.00 - 16.00	1/3	1/3	0.08	160
16.00 - 18.00	1/3	--	0.03	10
18.00 - 24.00	--	--	--	--

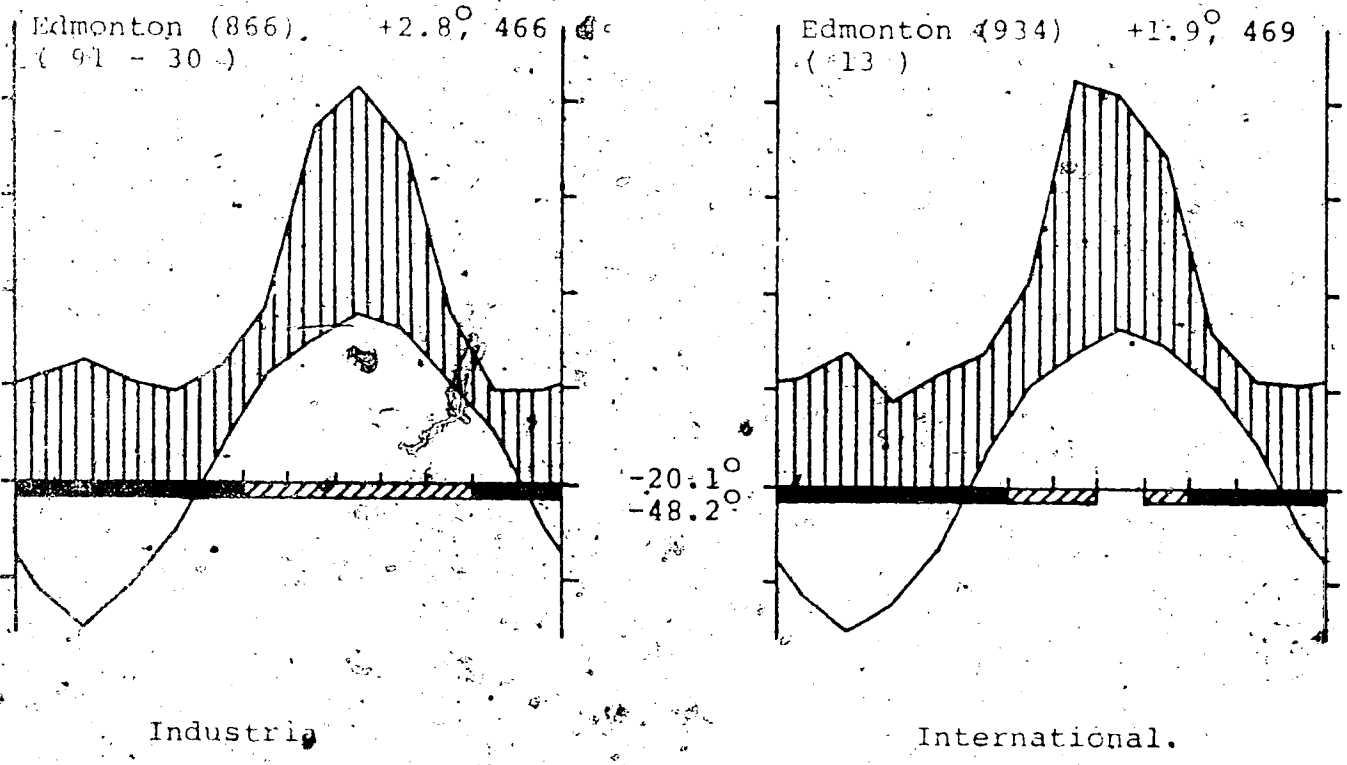
TABLE 6. Summarized results on the effect of hormones upon transpiration. Experiment No. 2. Average of 3 replicates over a 15 day period. Transpiration in ml/gm DWt at various hormone concentrations (M).

Treatment		1973	1972
H_2O (Control)		13.17	17.15
ABA 3.8×10^{-7}		12.45	9.09
BA 5×10^{-9}		11.01	
1×10^{-6}		10.43	19.14
5×10^{-7}		11.64	
ABA 2.8×10^{-7} + BA 5×10^{-9}		13.20	
	1×10^{-5}	10.88	
	5×10^{-6}	13.09	
	1×10^{-6}	13.99	

BLE 7. Net assimilation, optimum temperature, light compensation, and light saturation levels for four different conifers as reported by Larcher (1969) and black spruce as found in this study.

Species	Maximum fixation mg CO_2/gm DWt/hr	Optimum Temperature in °C	Light compensation cal/cm^2/min	Light saturation cal/cm^2/min
Picea glauca	3.0 - 5.0	18 - 20	0.012 - 0.02	0.80 - 1.30
Picea expelsa	4.0 - 6.0	12 - 18	0.008 - 0.04	0.12 - 1.00
Pinus cembra	6.0 - 12.0	12 - 16	0.003 - 0.032	0.36 - 0.60
Pseudotsuga menziesii	6.0 - 8.0	18 - 22	0.006 - 0.30	0.18 - 0.70
Picea mariana	7.0	12 - 18	0.04	0.20

Figure 1. "Klimadiagramme" for the Edmonton International and Industrial Airports (after Walter and Lieth, 1967).



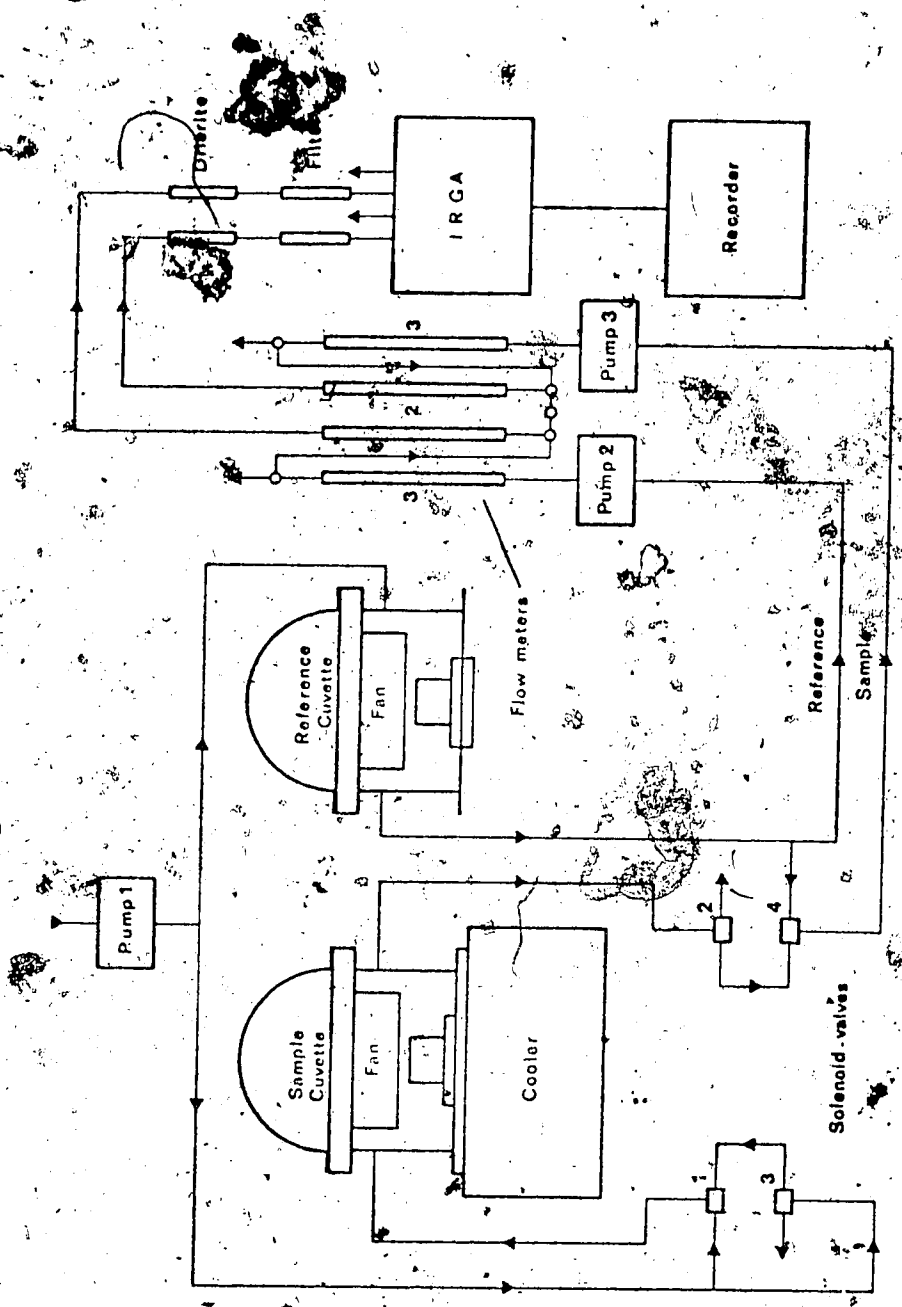


Figure 2. Diagramatic representation of the basic gas analysis system.

Figure 3: Method employed for switching from Amb/Amb to Amb/Cuv without changing flow rates.
S sample; R reference; 1 - 4 solenoid valves.

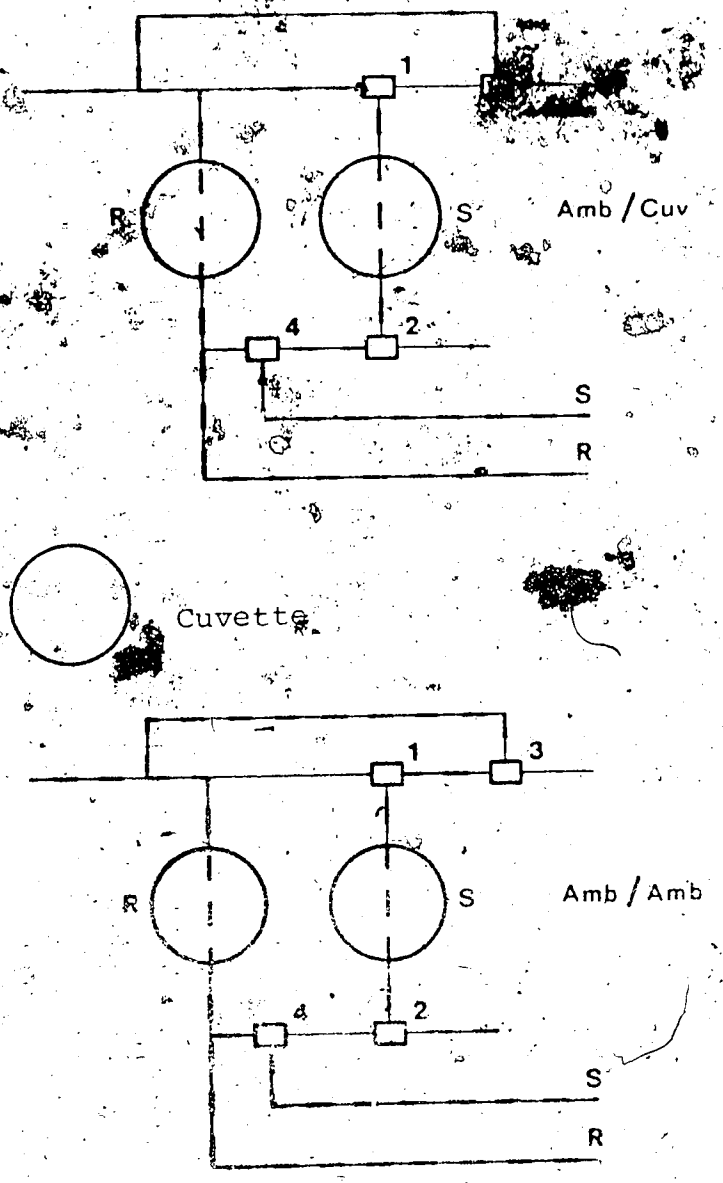


Figure 4. Cuvette as used in the field with Kipp solarimeter on the left.

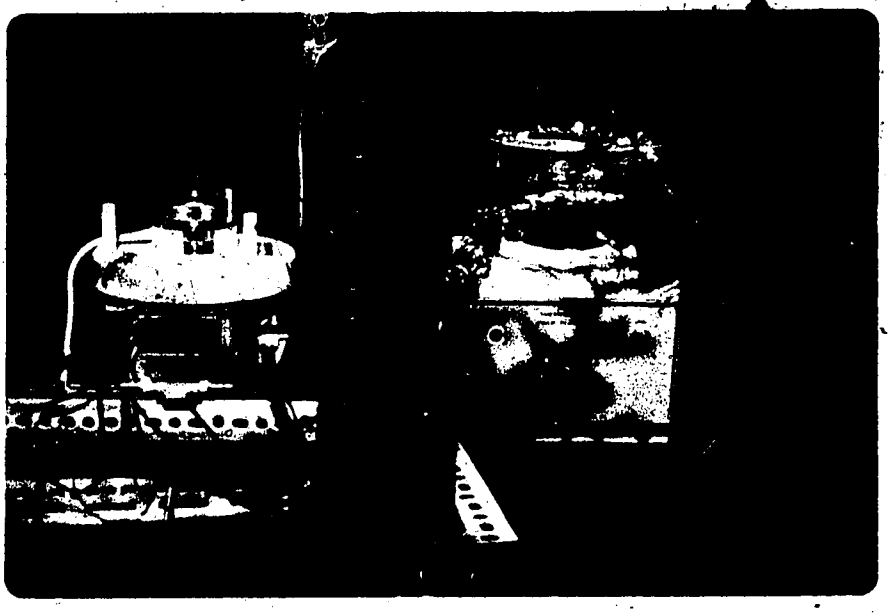
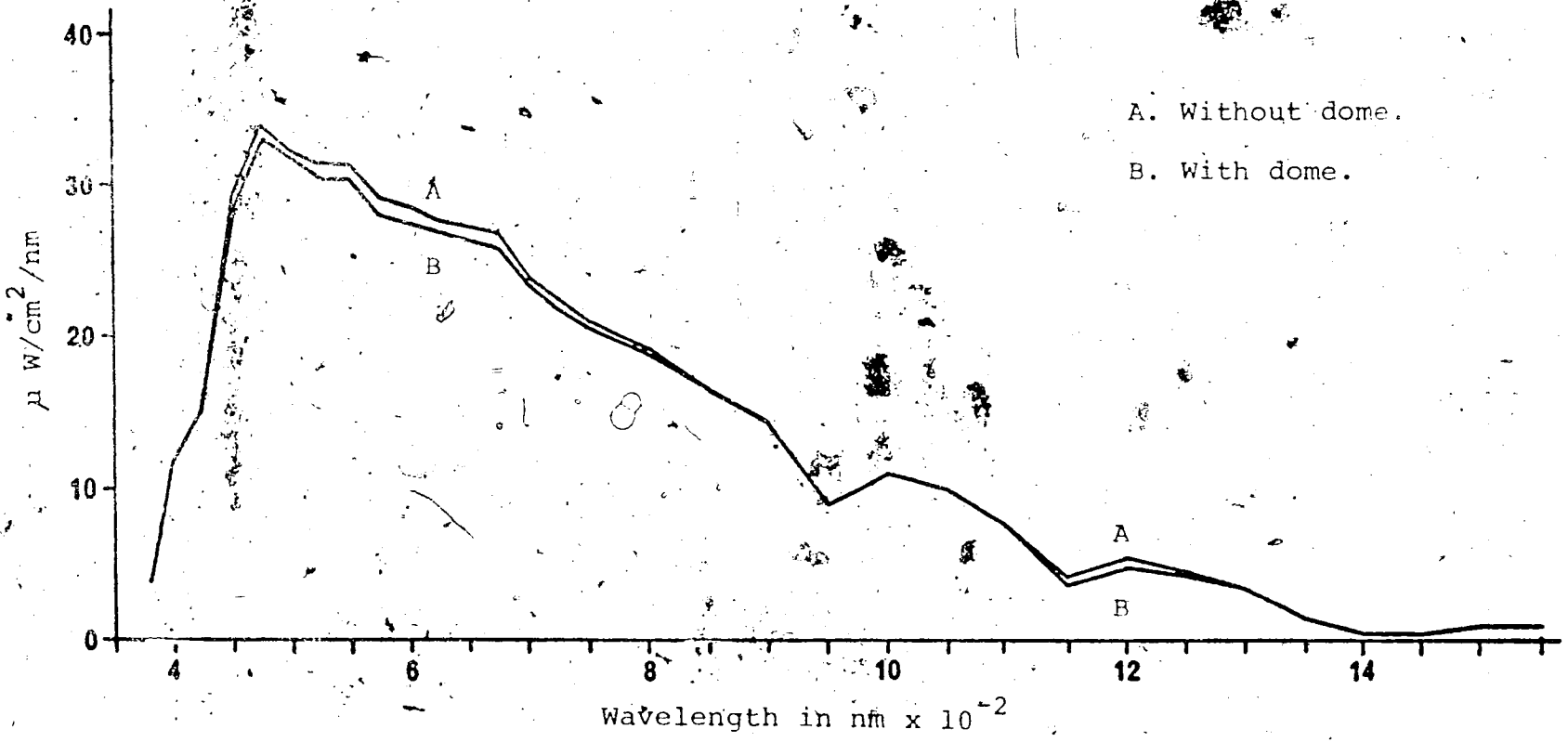


Figure 5. The effect of the plexiglass cuvette dome on sunlight as measured with the ISCO Spectroradiometer. (12.00 on Febr[illegible] 21, 1974 with clear sky).



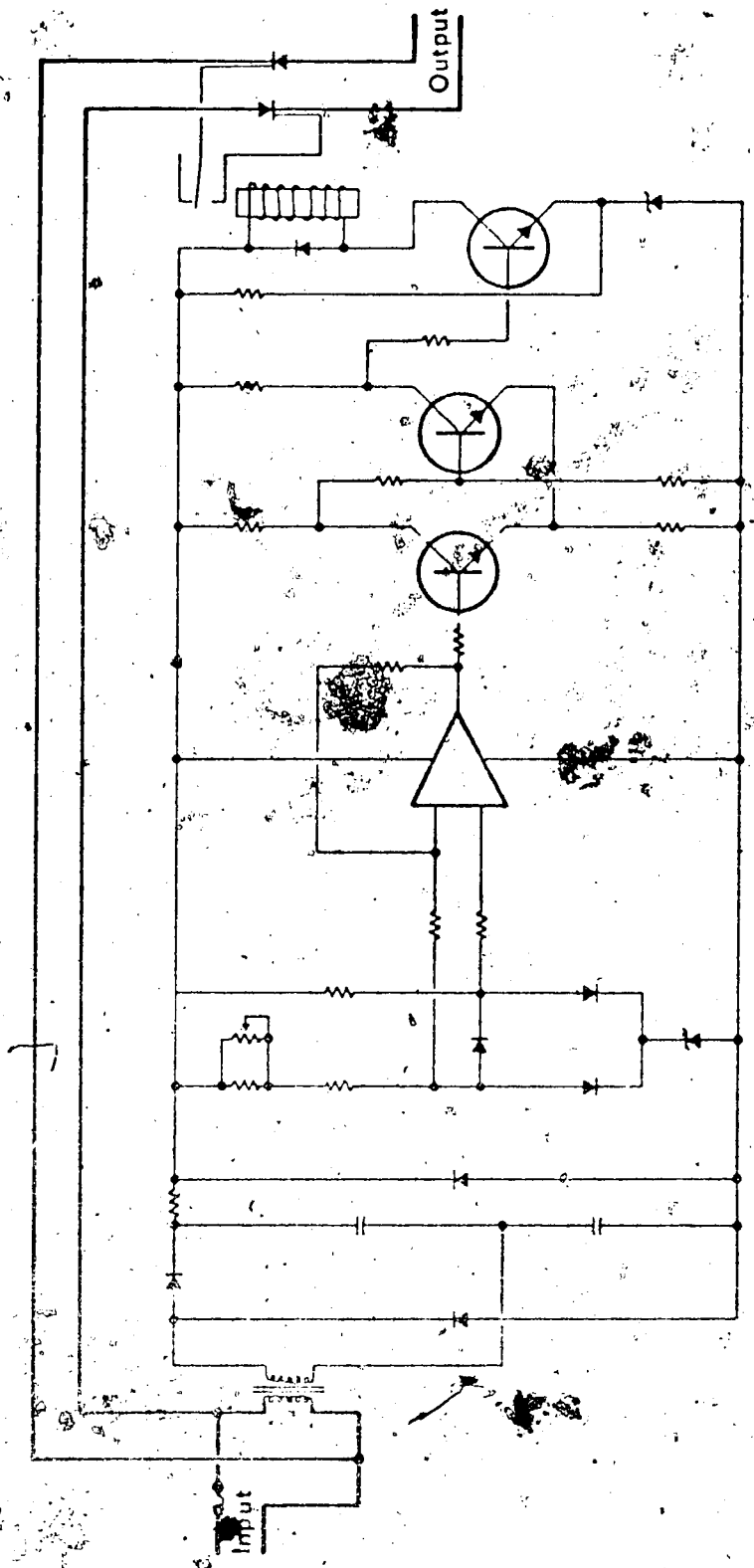


Figure 6. Circuit diagram for the cuvette temperature controller (after Ashe, 1972).

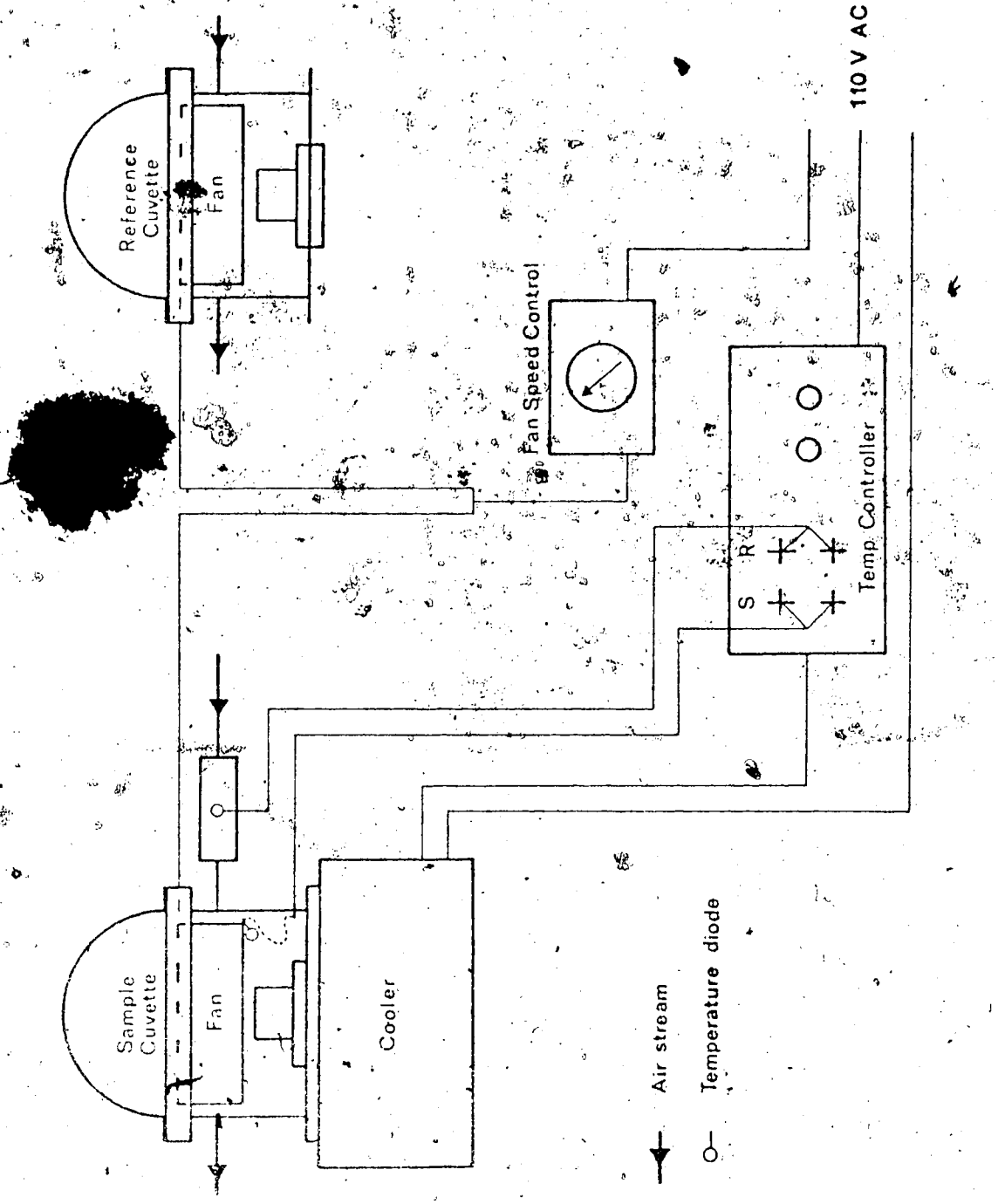


Figure 7. Diagramatic representation of the temperature control system of the cuvette

Figure 8. The spectral analysis of radiant energy in the growth chamber used in the study.

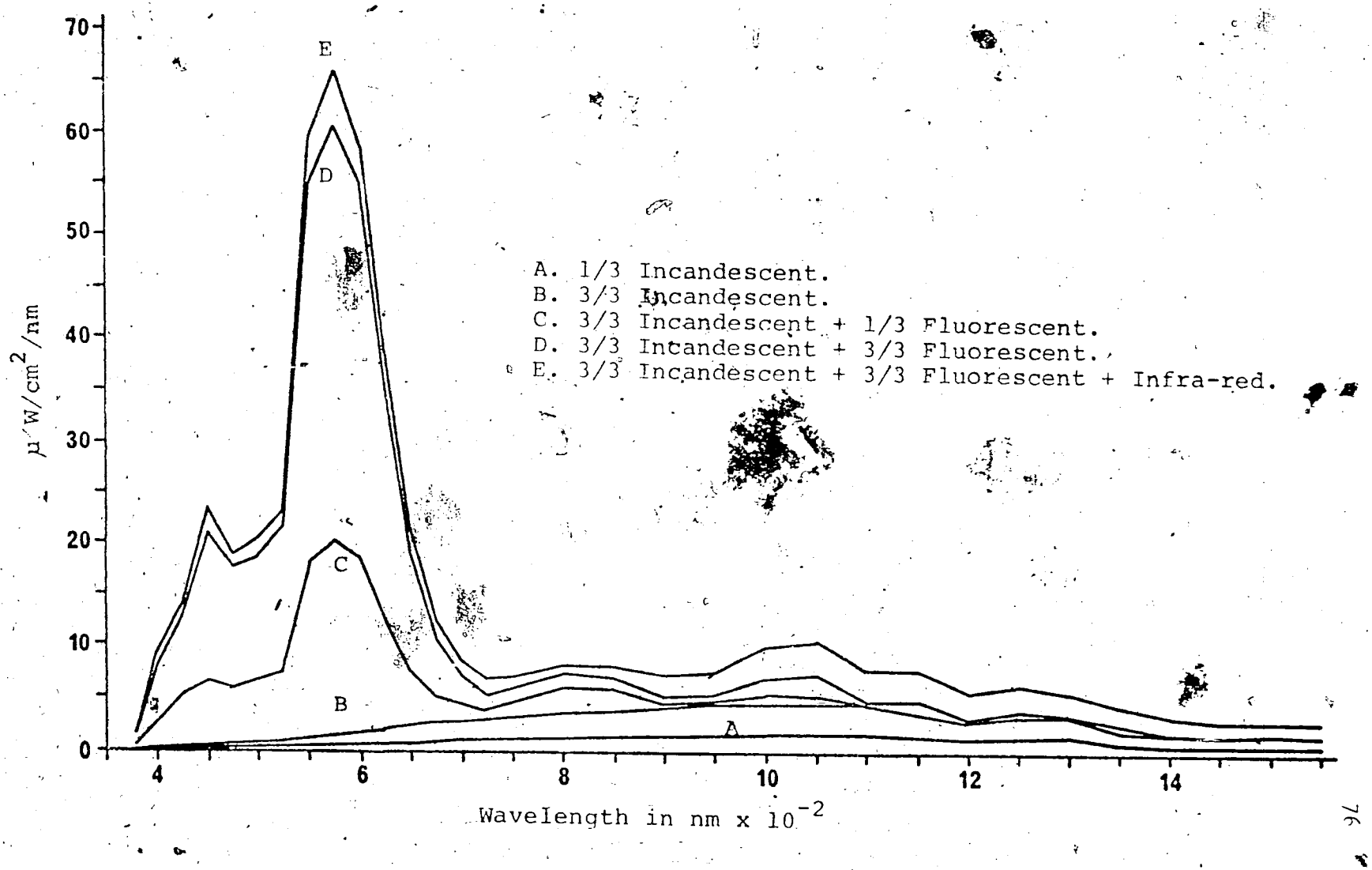


Figure 9. Calibration of the radiation sensors used in the study.

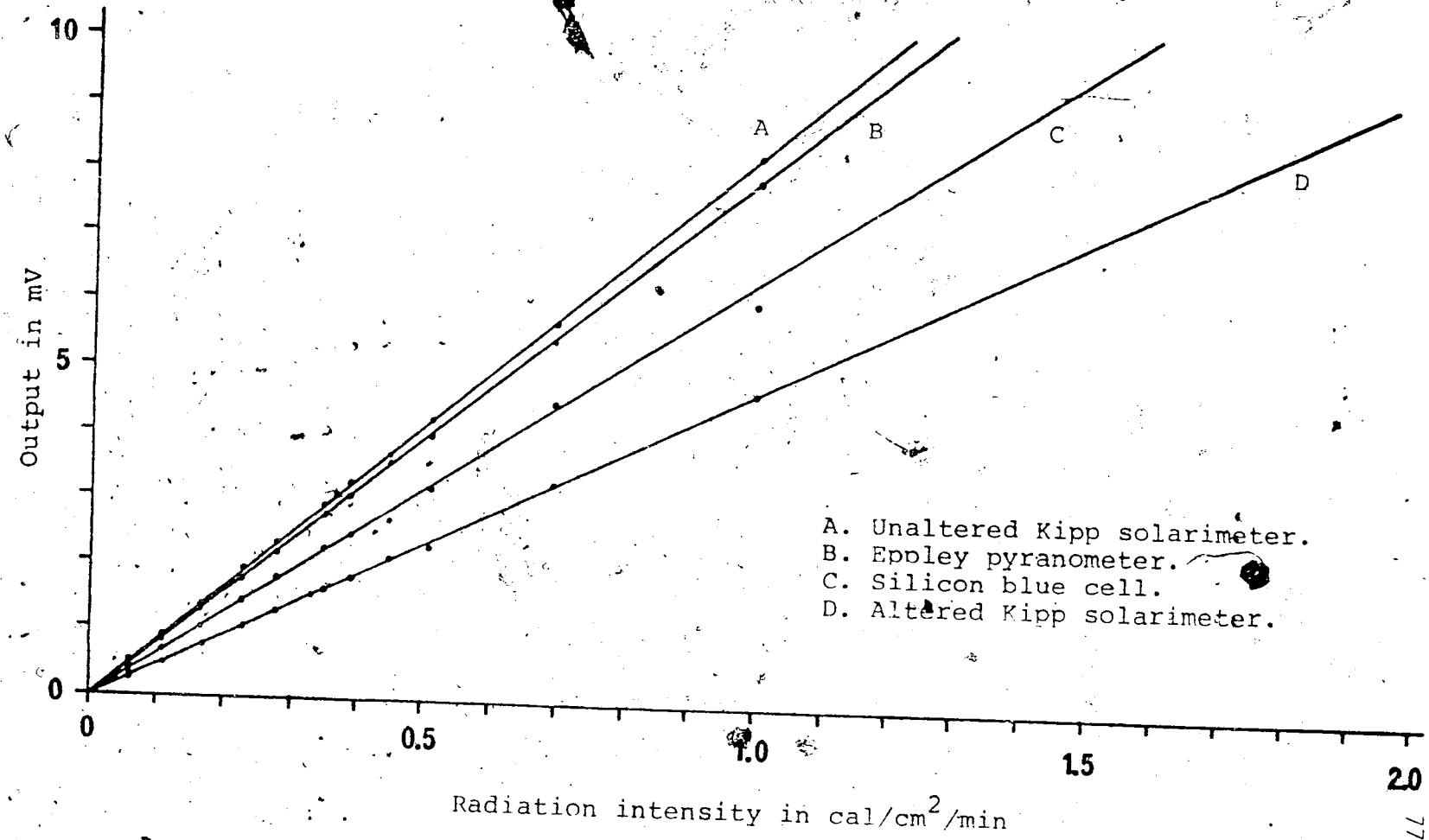


Figure 10. The effect of equilibration time on thermocouple psychrometer output.

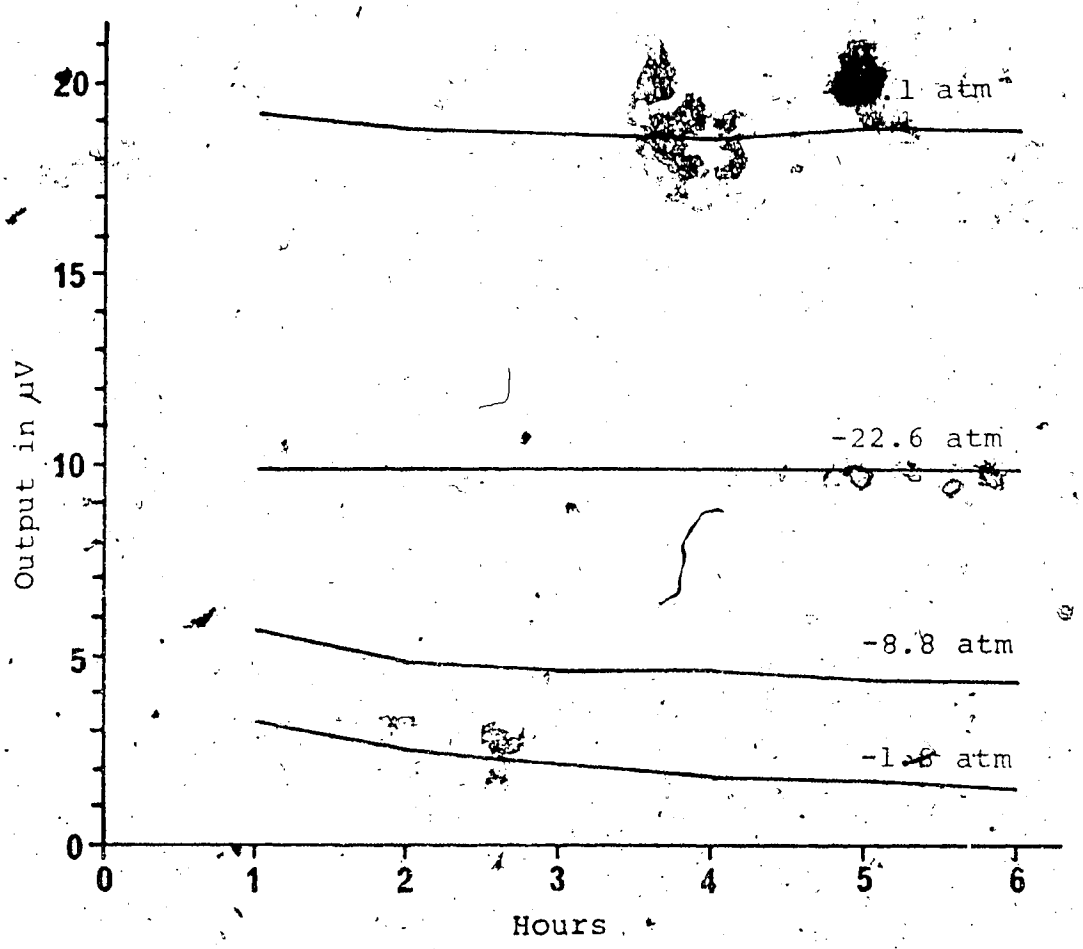


Figure 11. Example thermocouple psychrometer calibration.

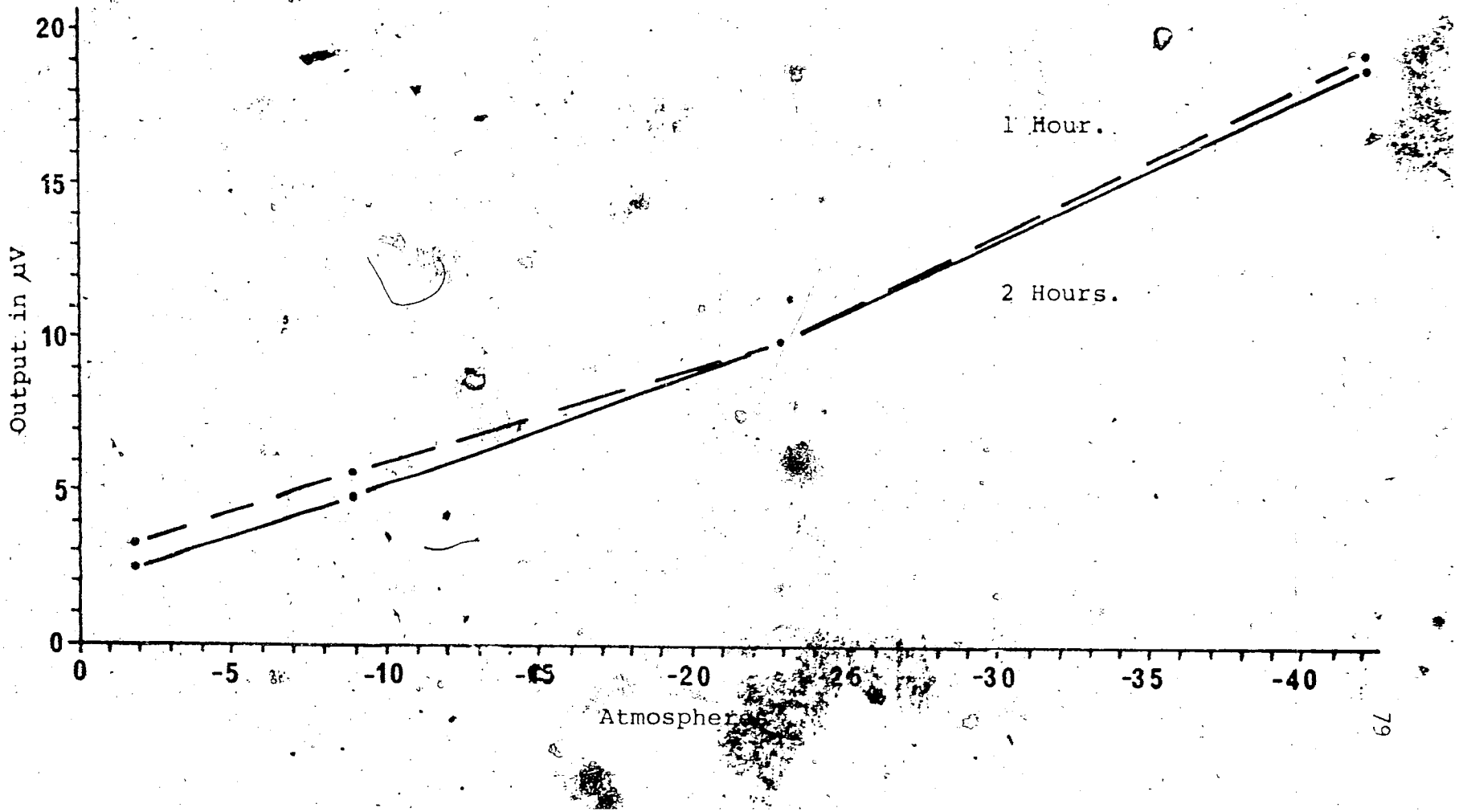


Figure 12. Daily maximum and minimum temperatures for the Edmonton International and Industrial Airports from September 1972 to July 1973.

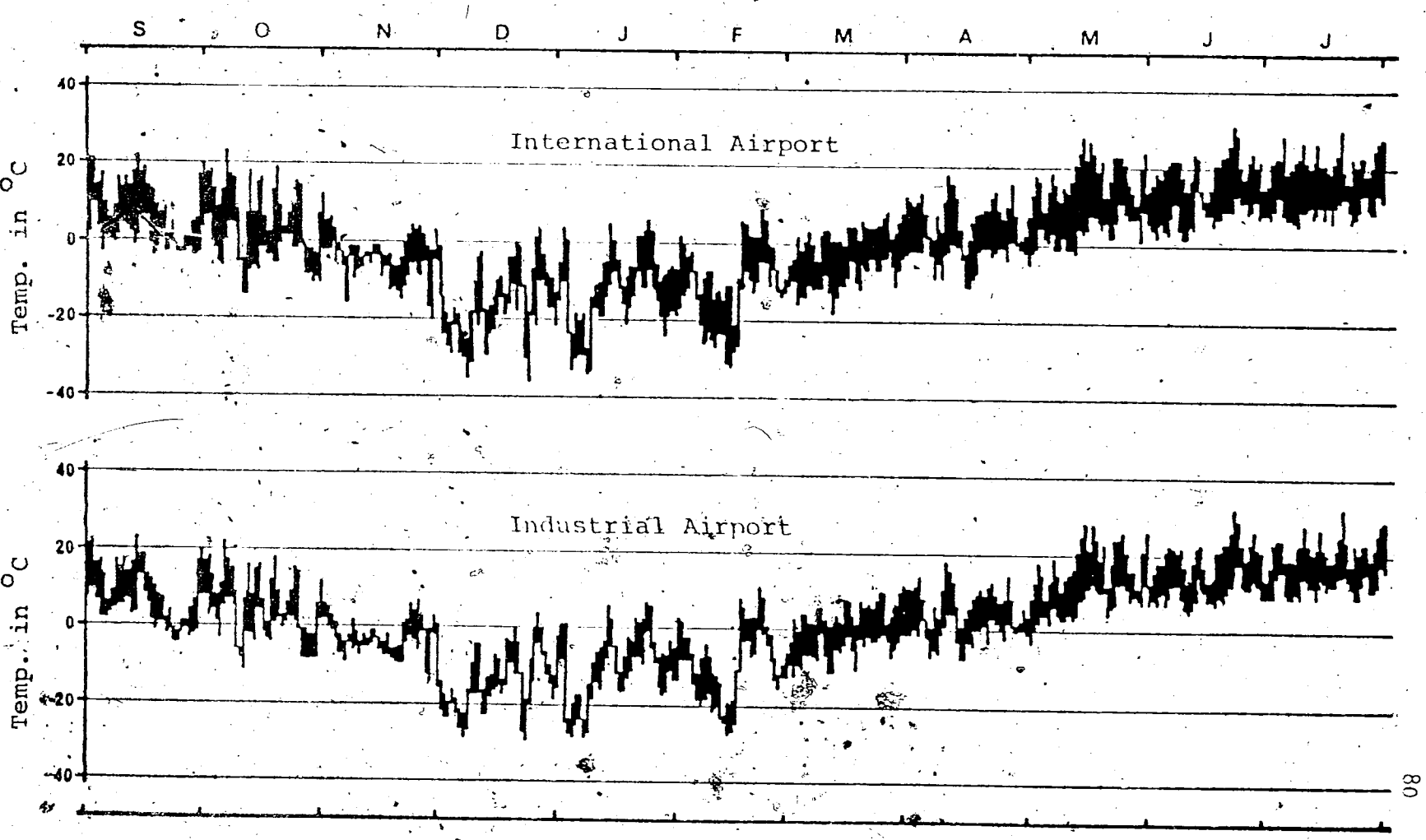


Figure 13. Daily maximum and minimum temperatures for the Edmonton International and Industrail Airports from July 1973 to May 1974.

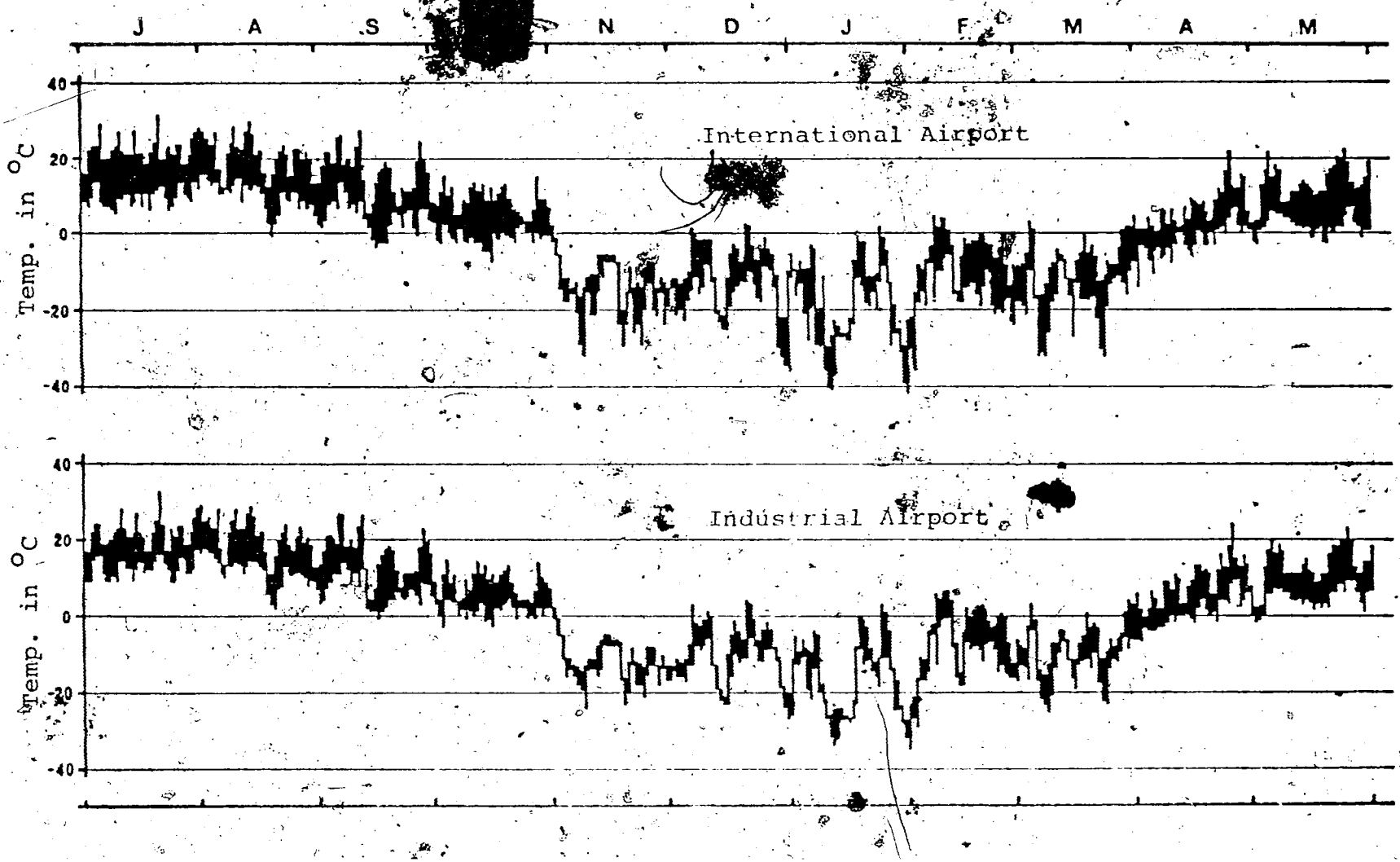


Figure 14. Radiation, needle temperature, and net assimilation (N.A.) as measured in the field on 6 and 7 May, 1973 before bud-break. The soil is still frozen at 20 cm.

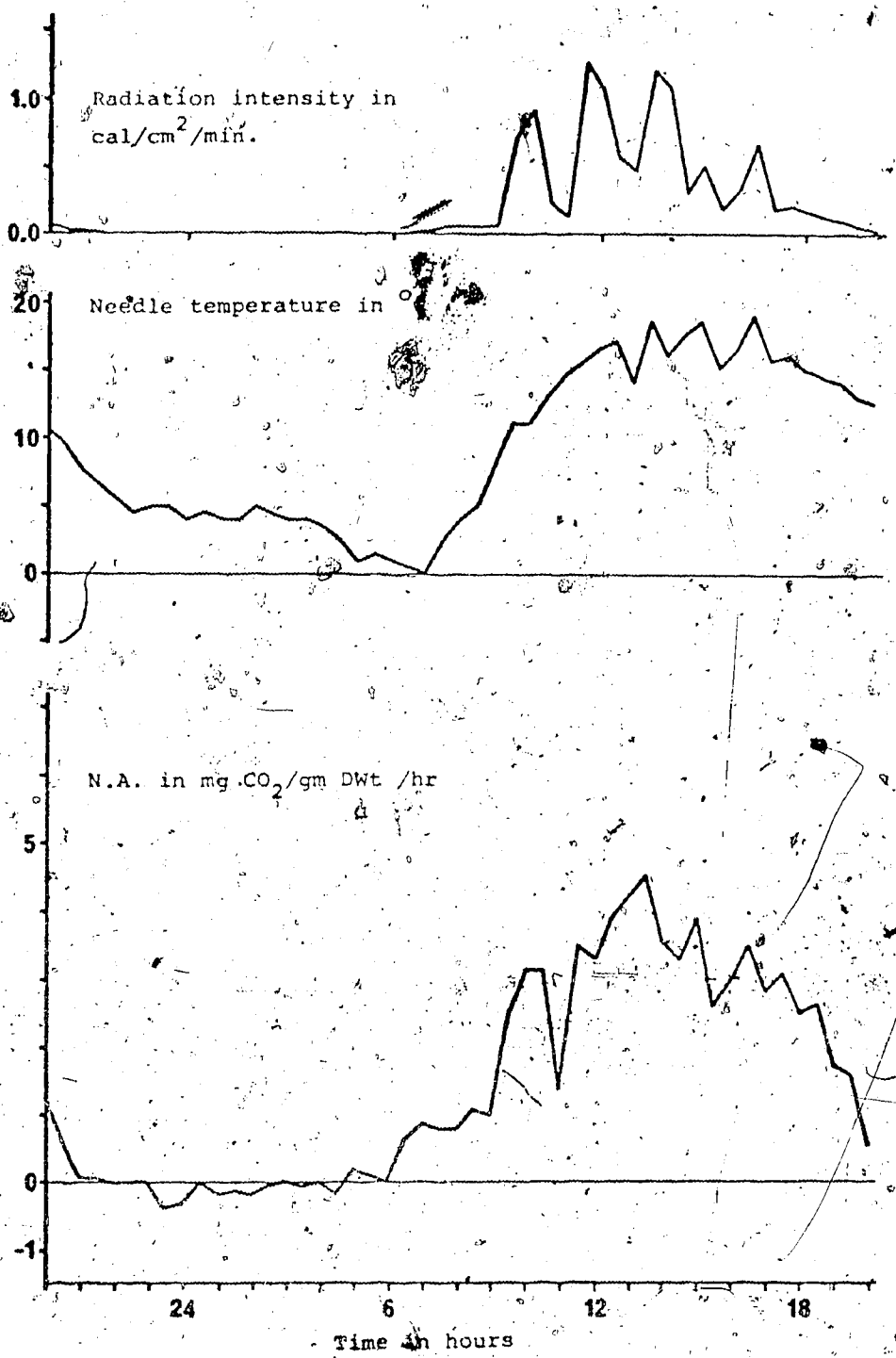


Figure 15. Radiation, needle temperature, and net assimilation (N.A.) as measured in the field on 29 and 30 May, 1973 indicating mid-day lag. The soil is still frozen at 20 cm; needles one year old.

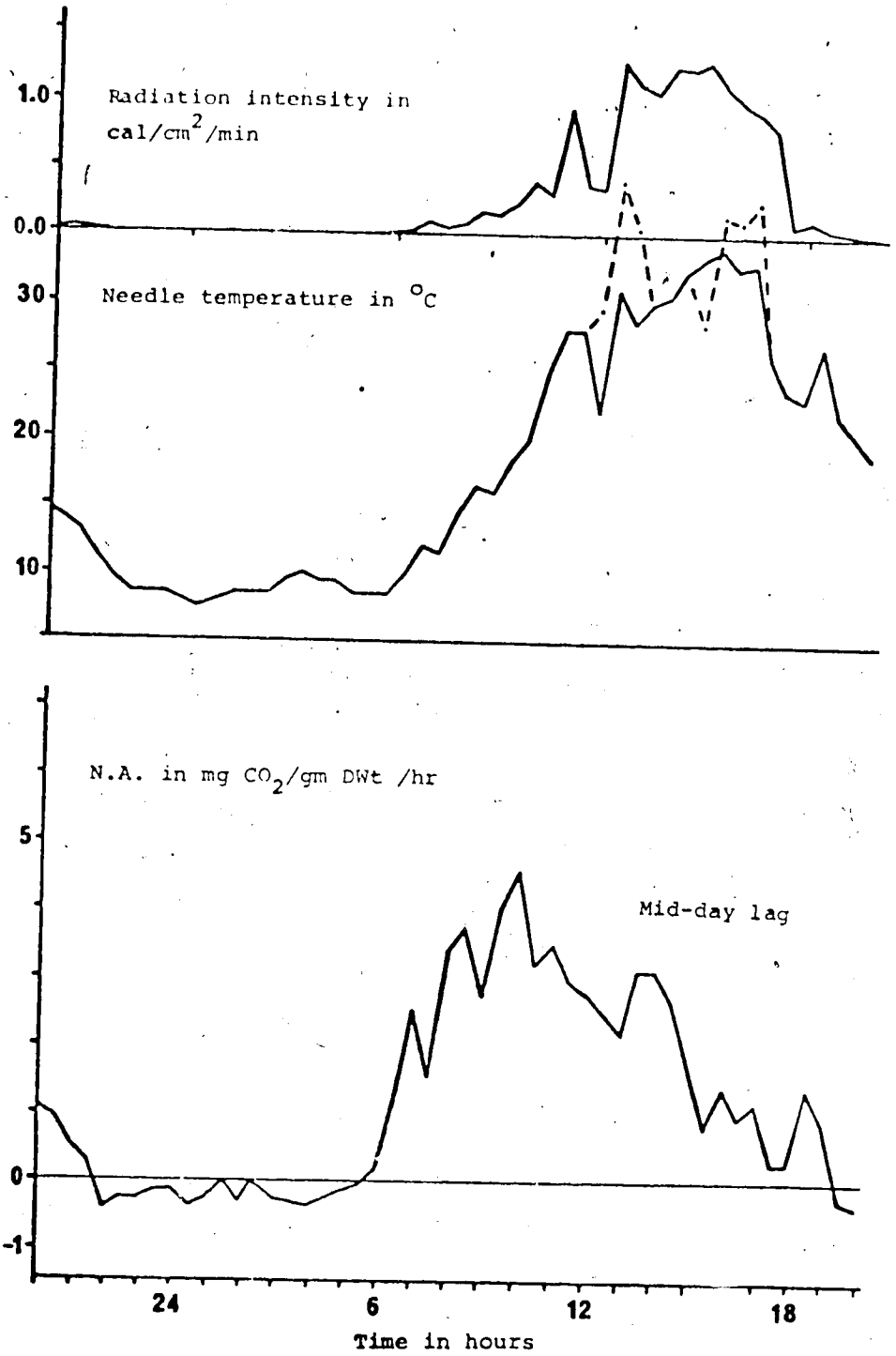


Figure 16. Radiation, needle temperature, and net assimilation (N.A.) as measured in the field on 27 and 28 June, 1973 showing high fixation rate with high water potentials. Current year's needles.

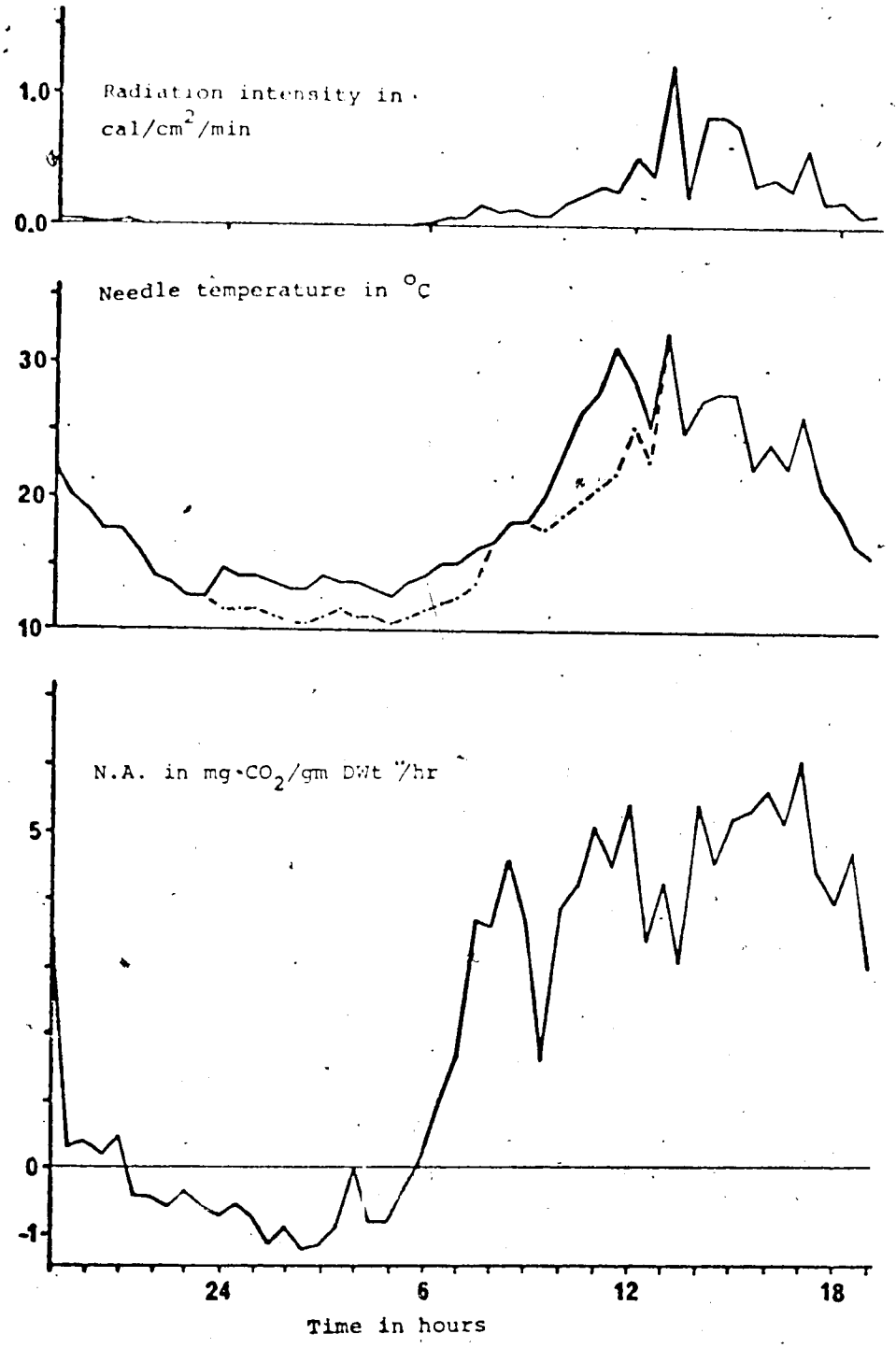


Figure 17. Radiation, needle temperature, and net assimilation (N.A.) as measured in the field on 21 and 22 July, 1973 showing maximum fixation rate.

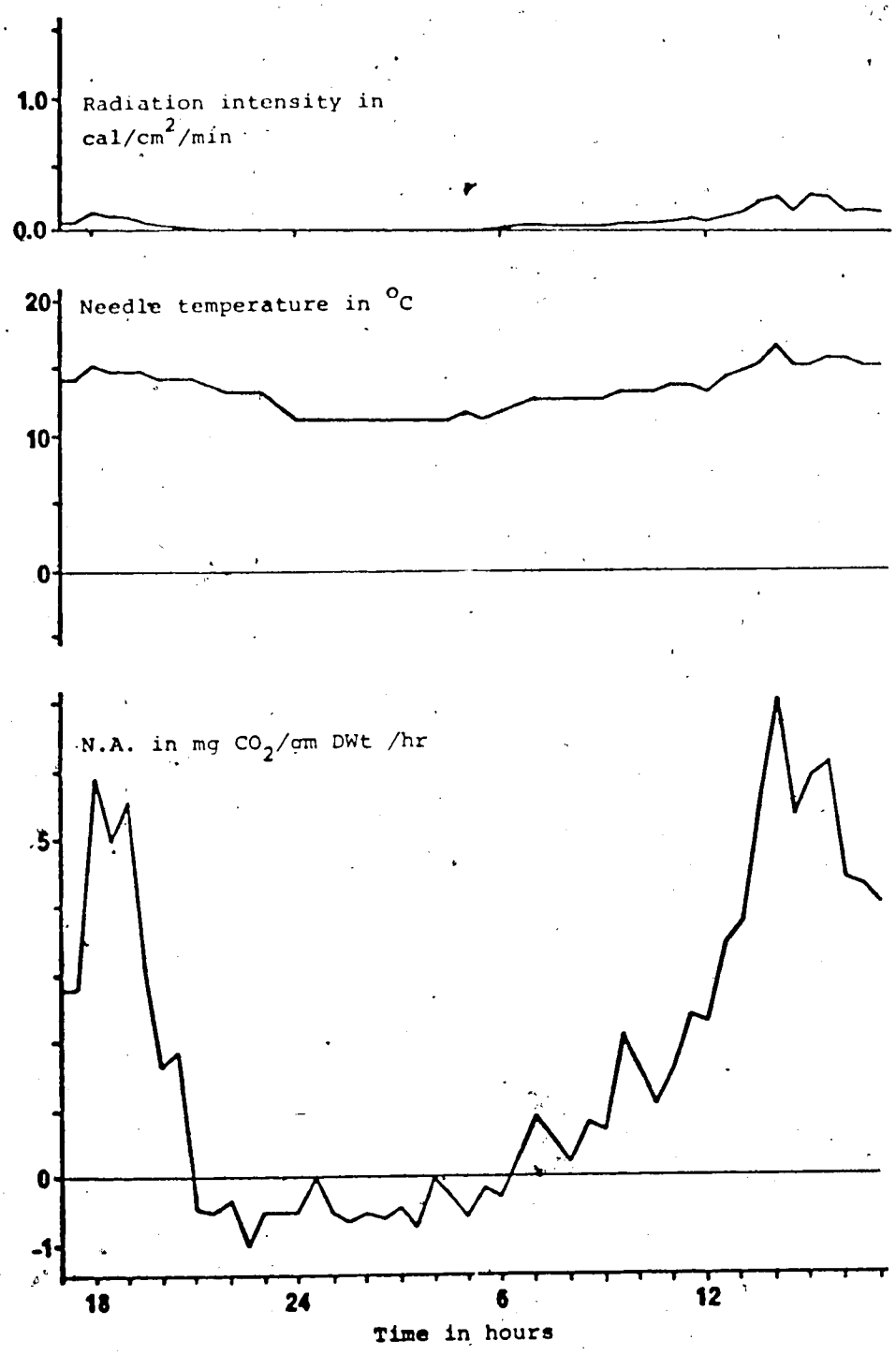


Figure 18. Radiation, needle temperature, and net assimilation (N.A.) as measured in the field on 18 and 19 August, 1973 indicating the effect of frost on fixation.

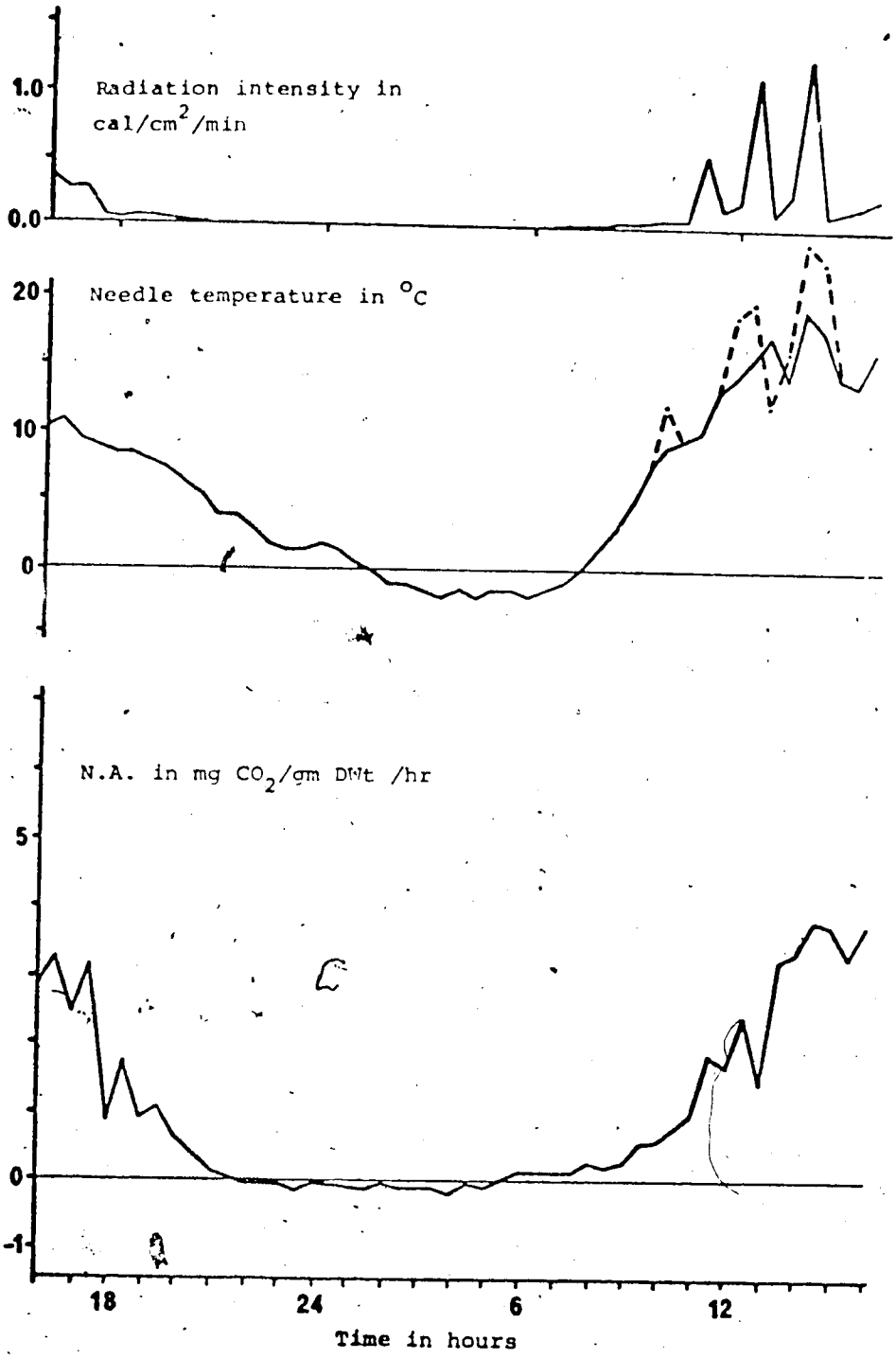


Figure 19. Radiation, needle temperature, and net assimilation (N.A.) as measured in the field on 17 and 18 October, 1973 indicating the onset of dormancy.

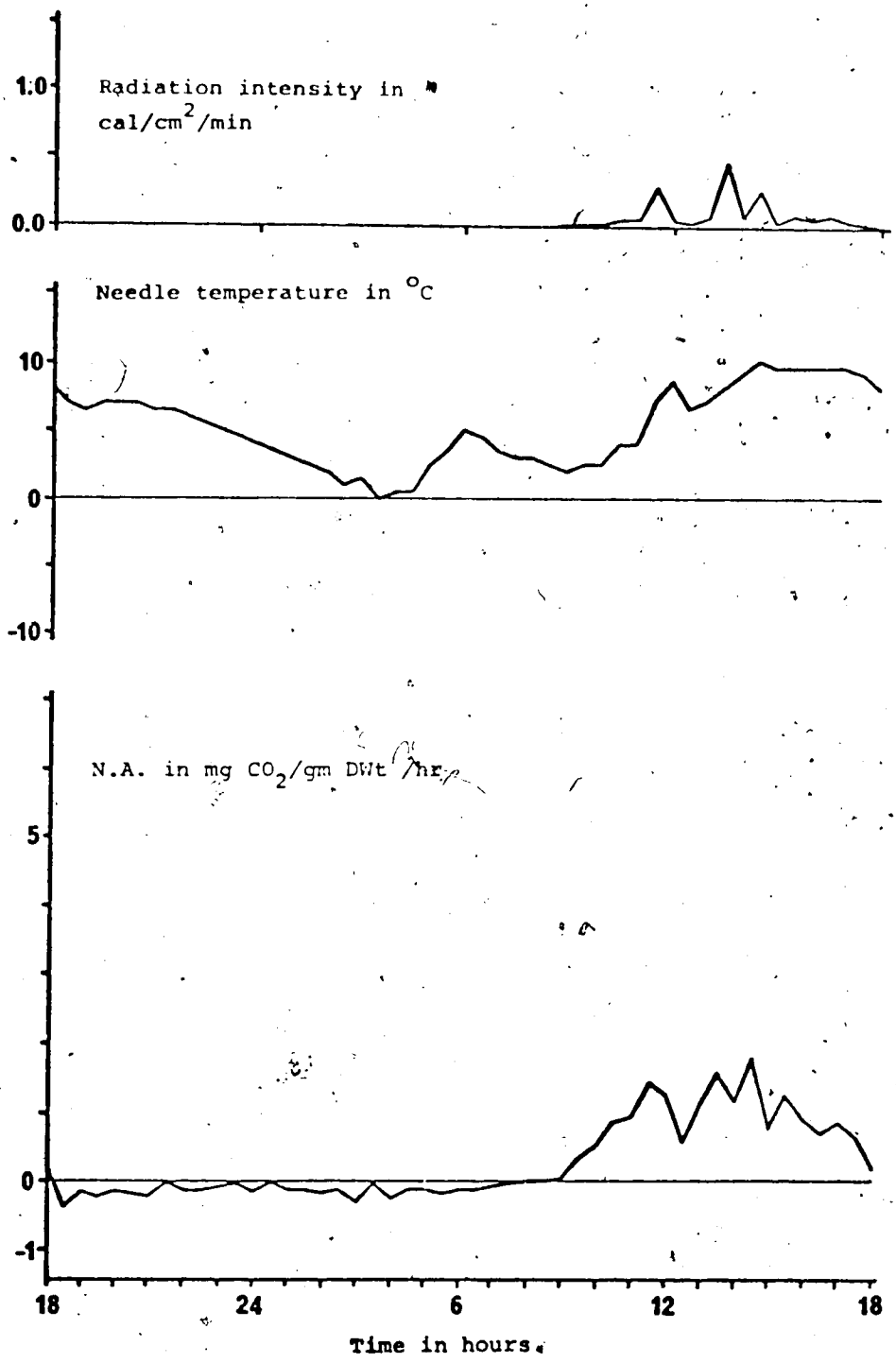


Figure 20. Net assimilation response to radiation as measured in the field at different temperatures.

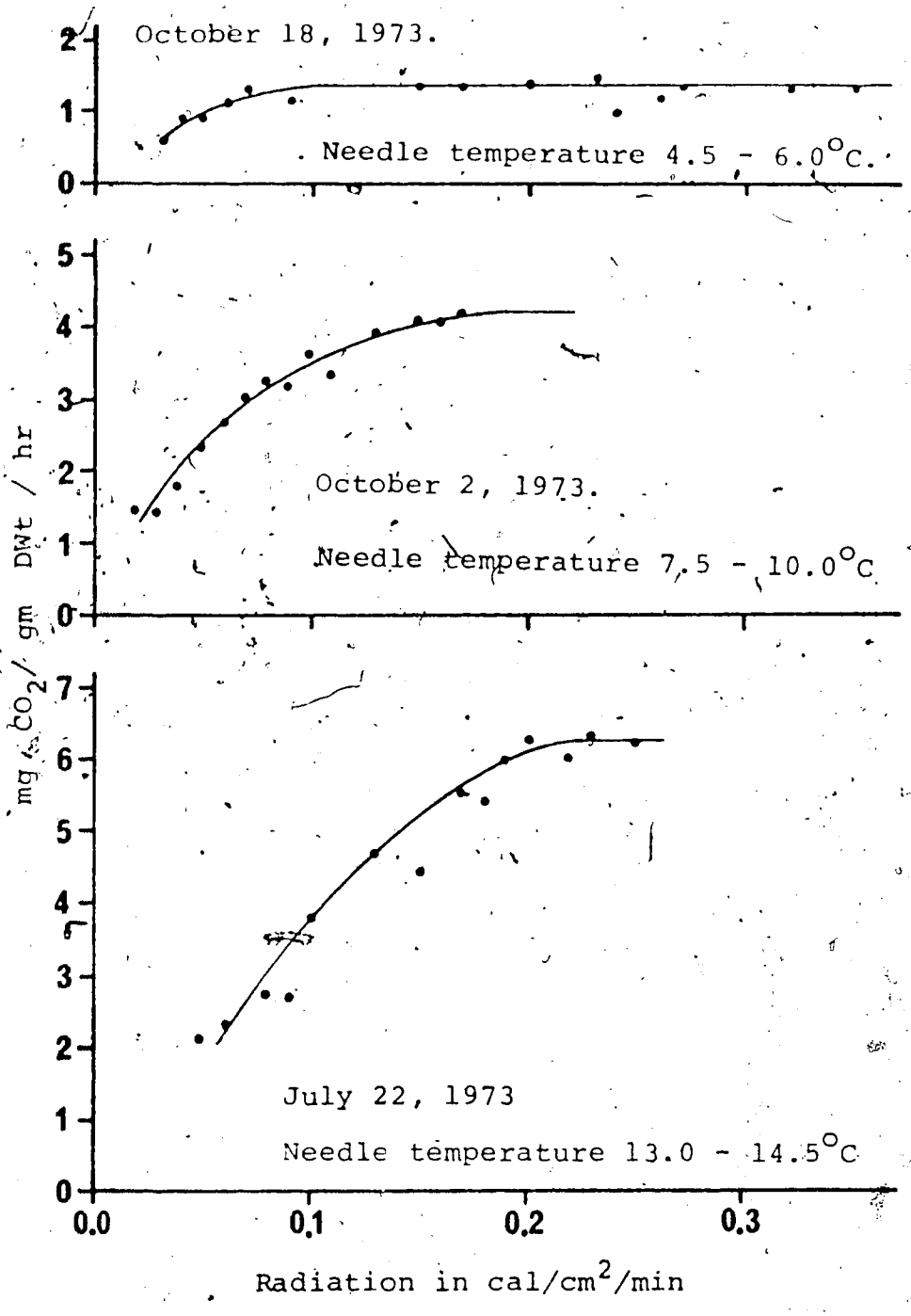


Figure 21. Maximum noon net assimilation rate of a tree breaking dormancy under growth chamber conditions.

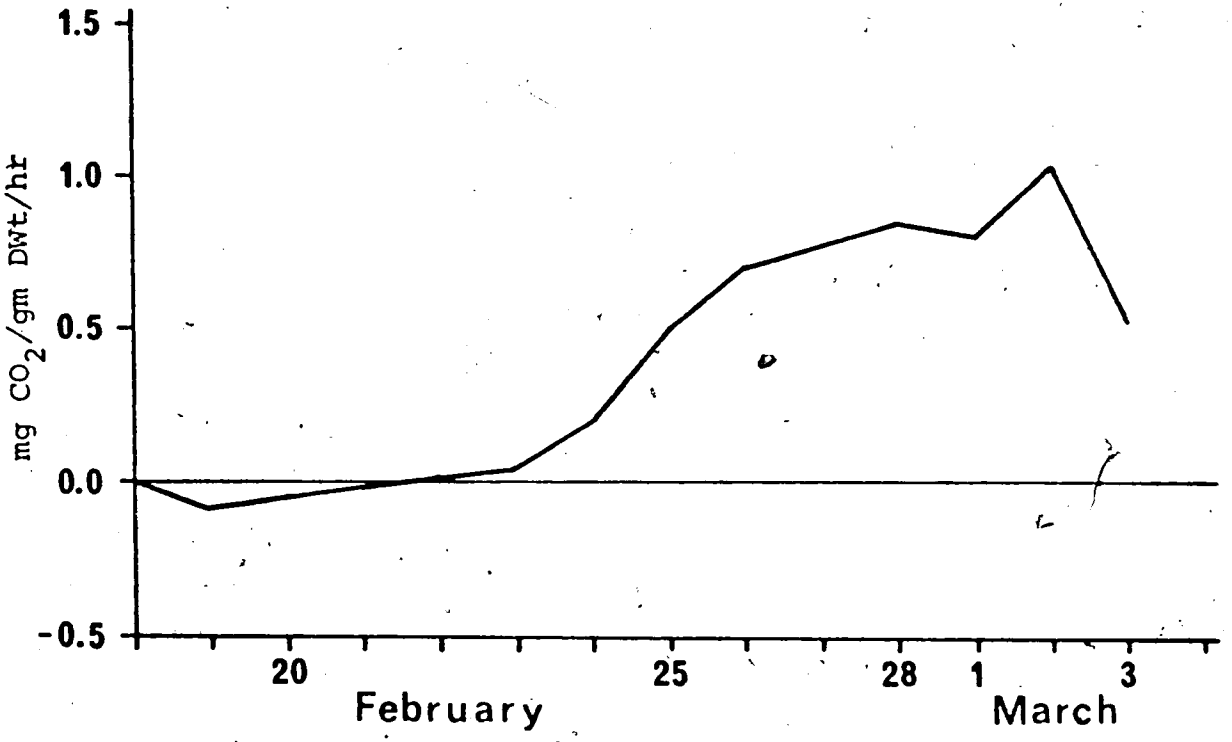


Figure 22. Respiration response to temperature of a dormant tree with a water potential of -40 atm and less than -90 atm.

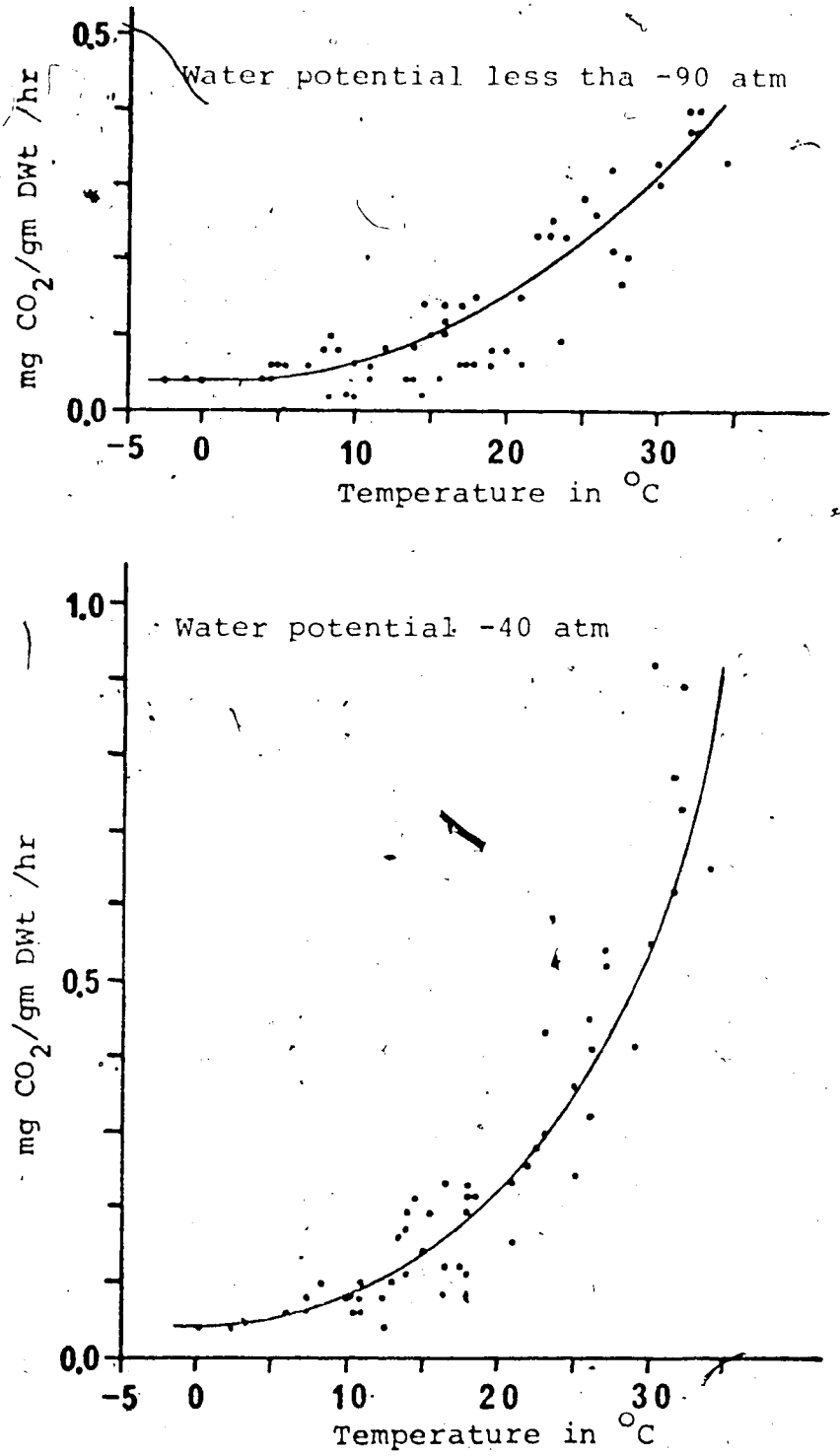


Figure 23. Net assimilation and respiration response of a non-dormant tree to various temperatures.

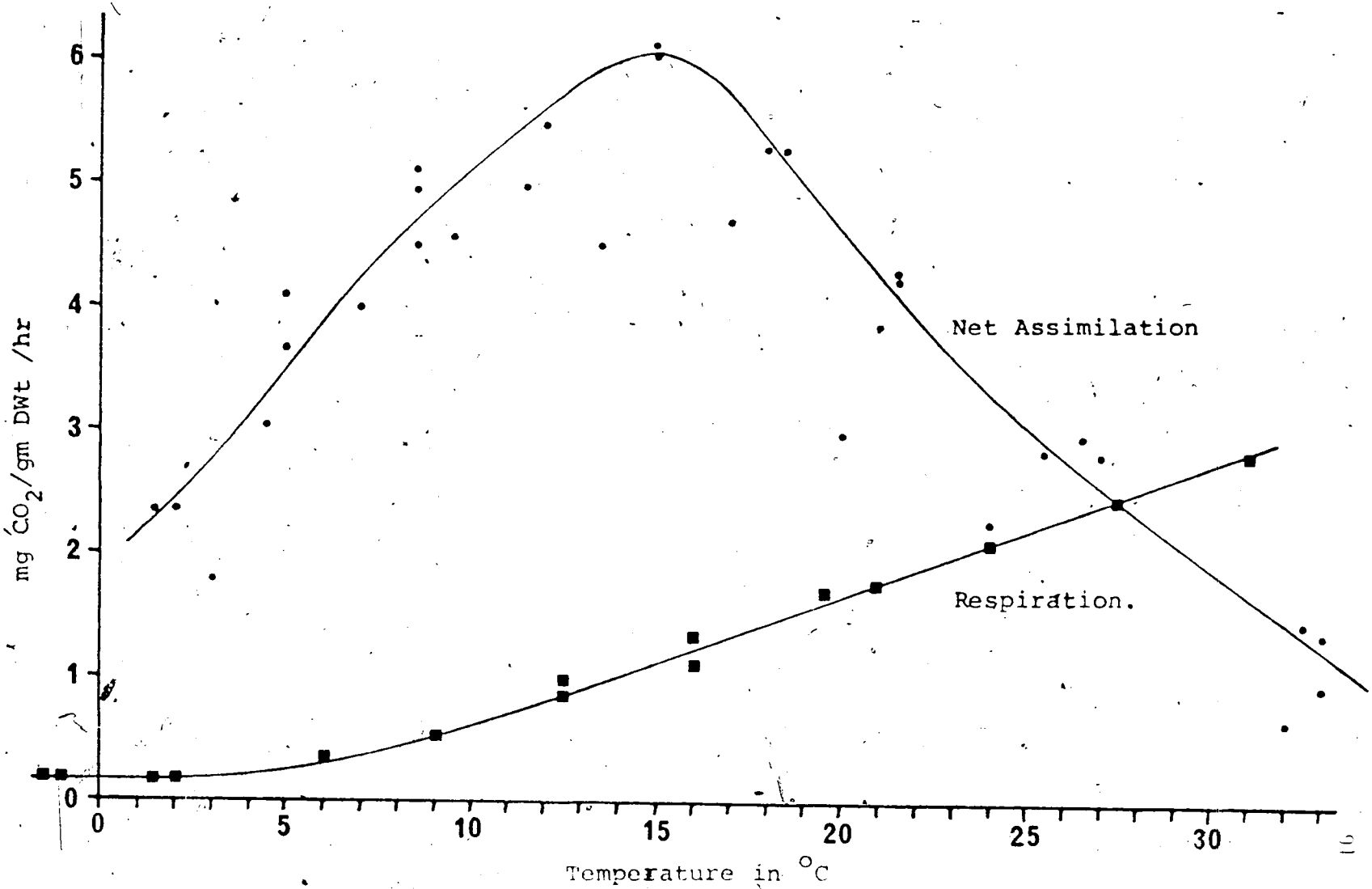


Figure 24. Net assimilation response to PAR (400 - 700 nm) of a non-dormant tree at 15 ± 1°C. Each light response measured three times.

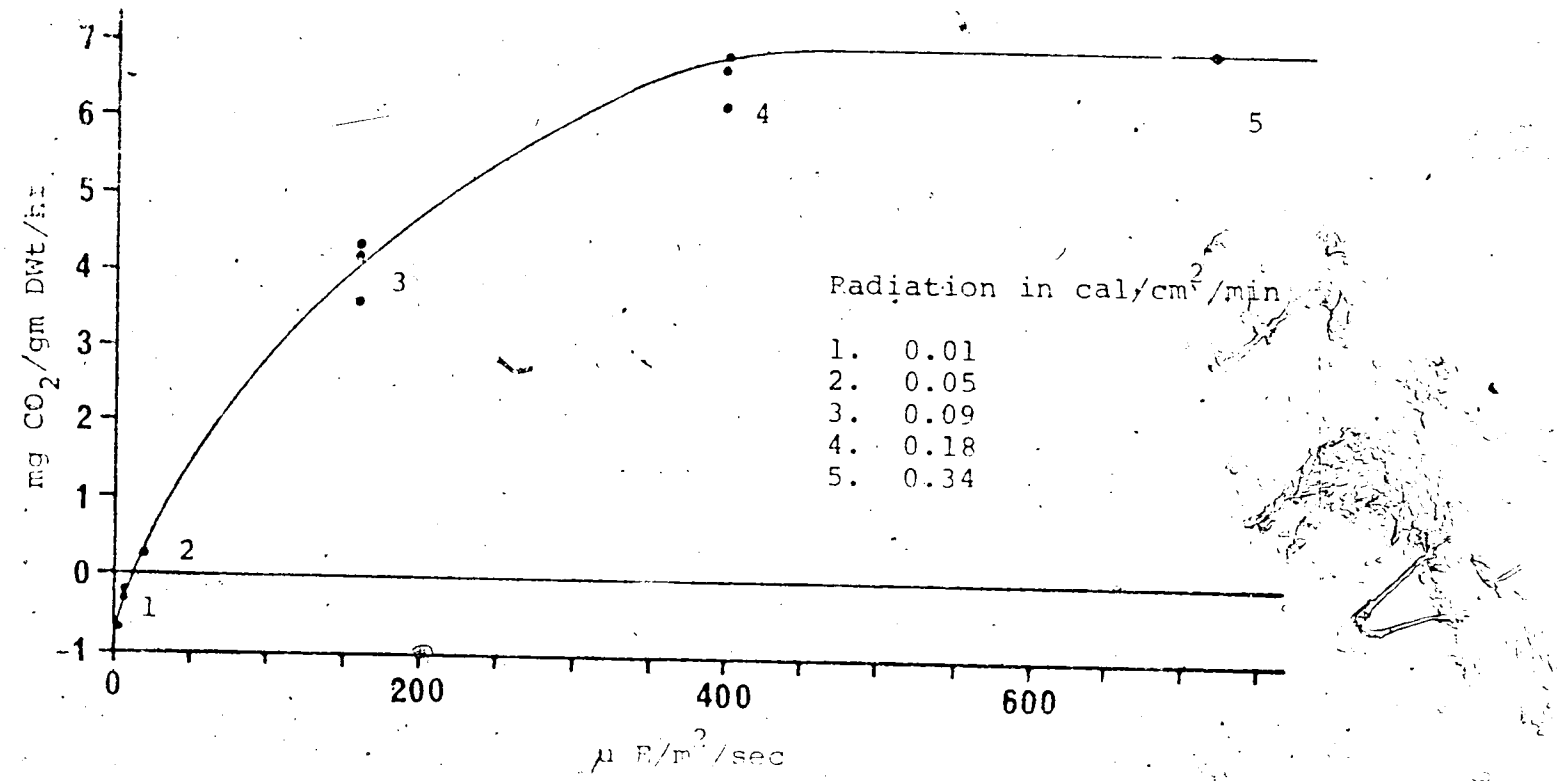


Figure 25. Minimum mid-day needle water potentials and "combined osmotic and matric potentials" from May 1973 to June 1974.
Ψ = water potential; $\Psi_{\pi+\tau}$ = "combined osmotic and matric potentials".
The difference between the two curves represents turgor pressure.

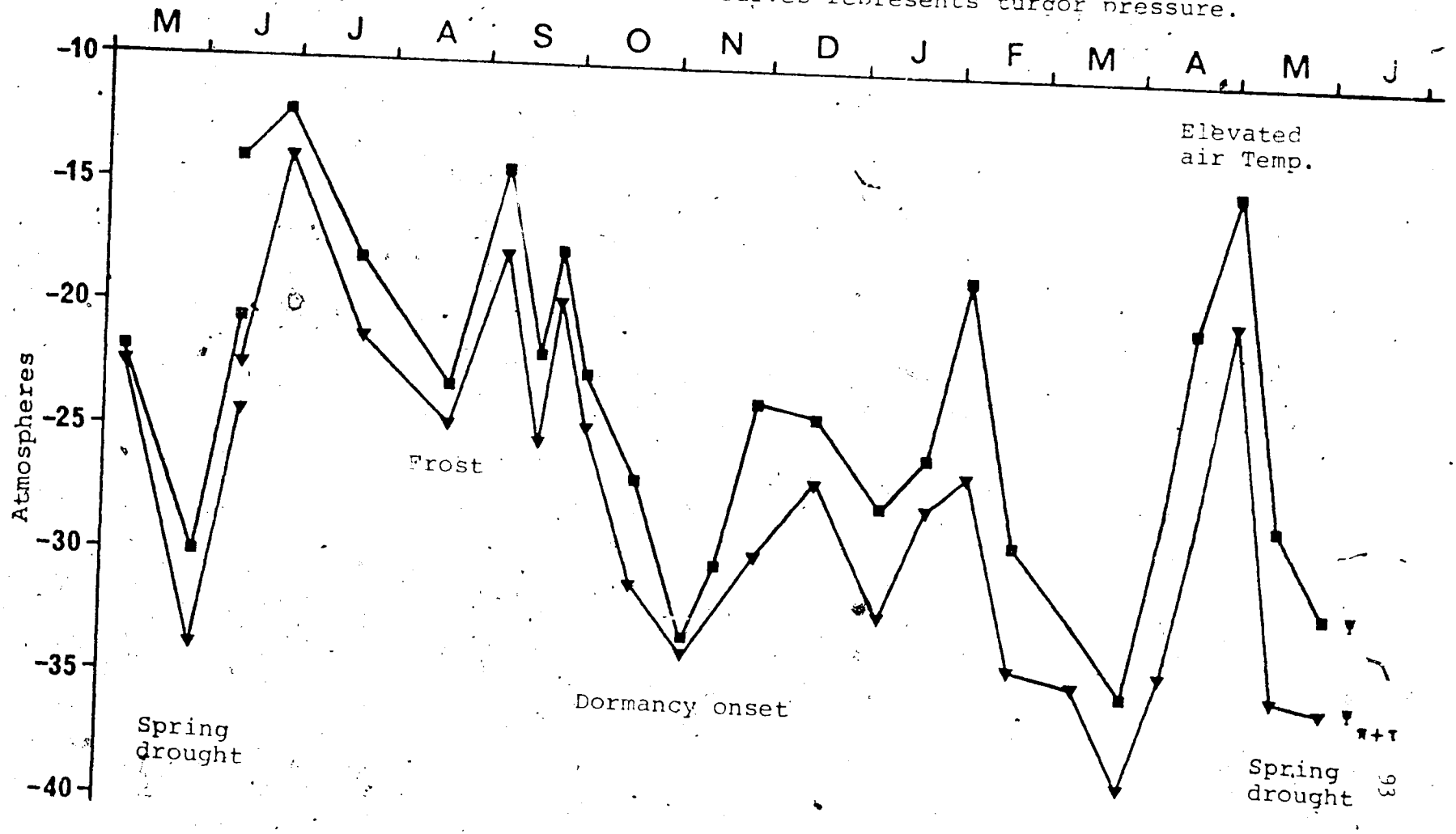


Figure 26. Annual cycle of needle component potentials. June 1973 to May 1974. Ψ_π = osmotic potential; $\Psi_{\pi+\tau}$ = "combined osmotic and matric potentials". The difference between the two curves represents the matric potential.

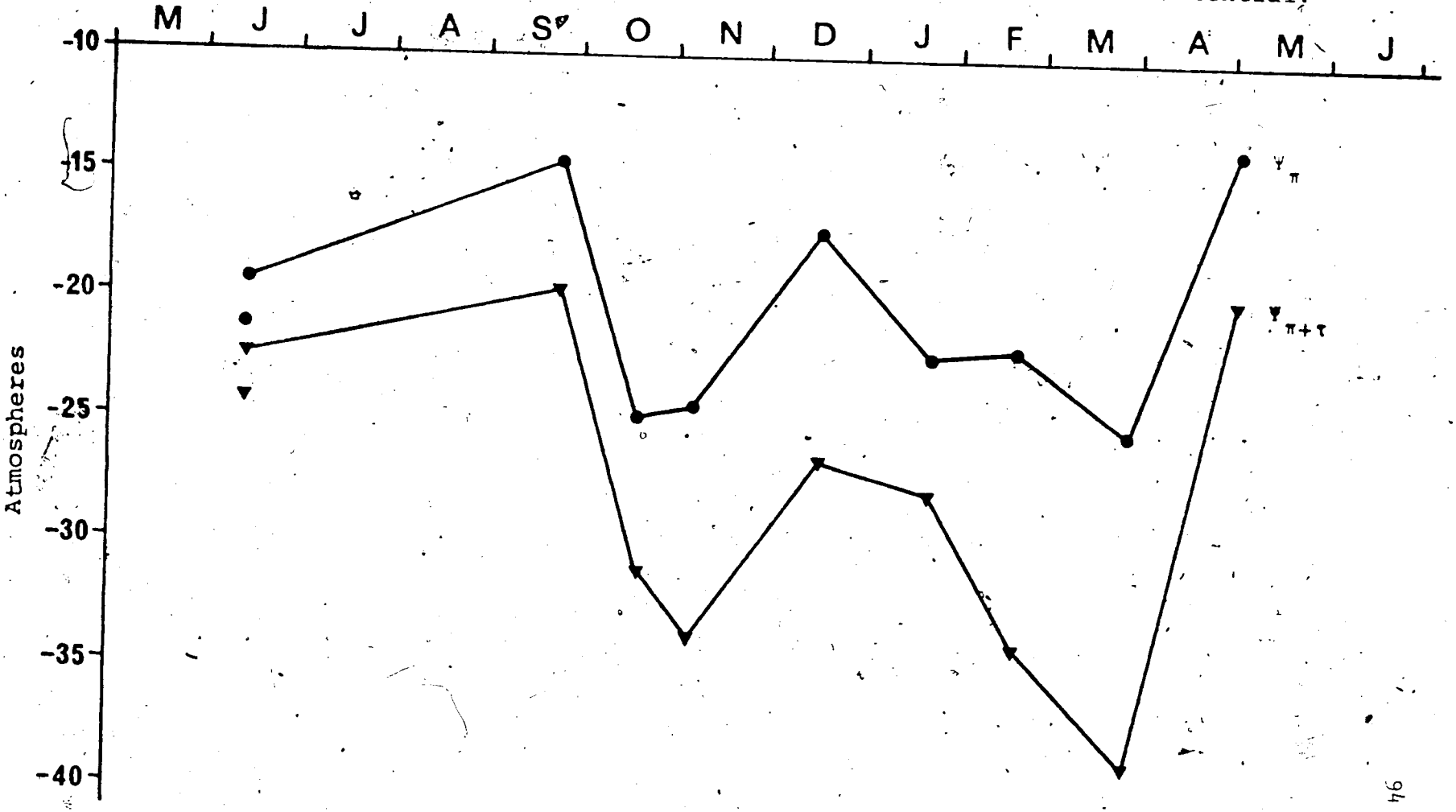


Figure 27. Springtime daily cycle of water potential and its components while soil is frozen; and needle infiltration pressures (N.I.). 6 and 7 May, 1973. Ψ = water potential; $\Psi_{\pi+\tau}$ = "combined osmotic and matric potentials."

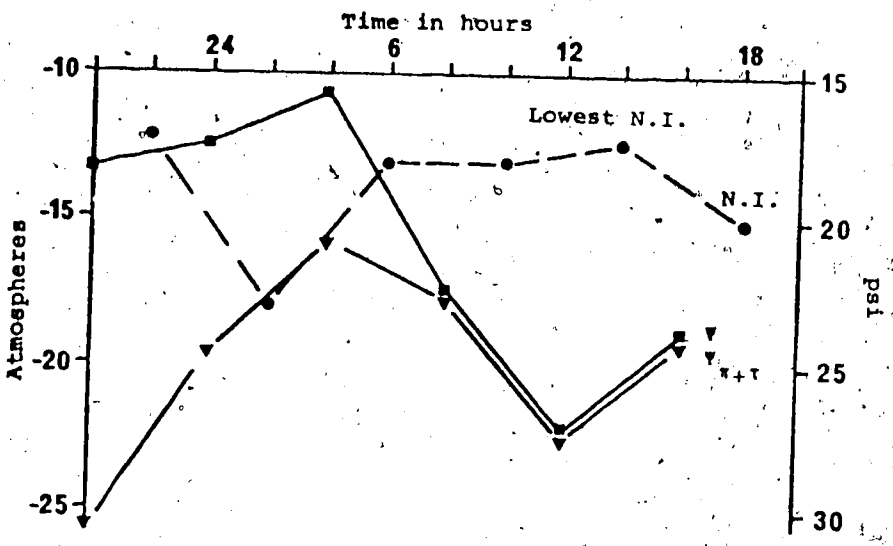


Figure 28. Daily cycle of water potential and its components while soil is frozen; and needle infiltration pressures (N.I.). 29 and 30 May, 1973. Ψ = water potential; $\Psi_{\pi+\tau}$ = "combined osmotic and matric potentials."

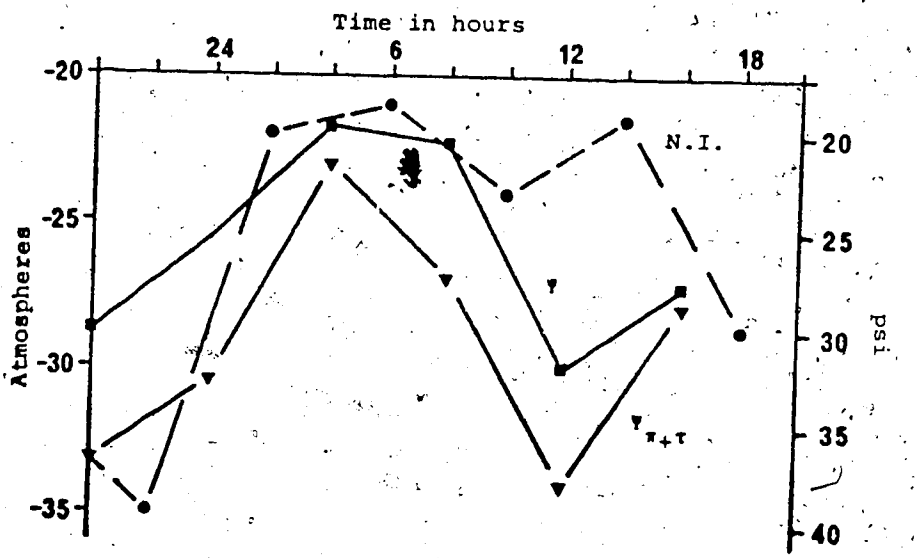


Figure 29. Summer daily cycle of water potential and its components; and needle infiltration pressures (N.I.). 27 and 28 June, 1973.
Ψ = water potential; $\Psi_{\pi+\tau}$ = "combined osmotic and matric potentials."

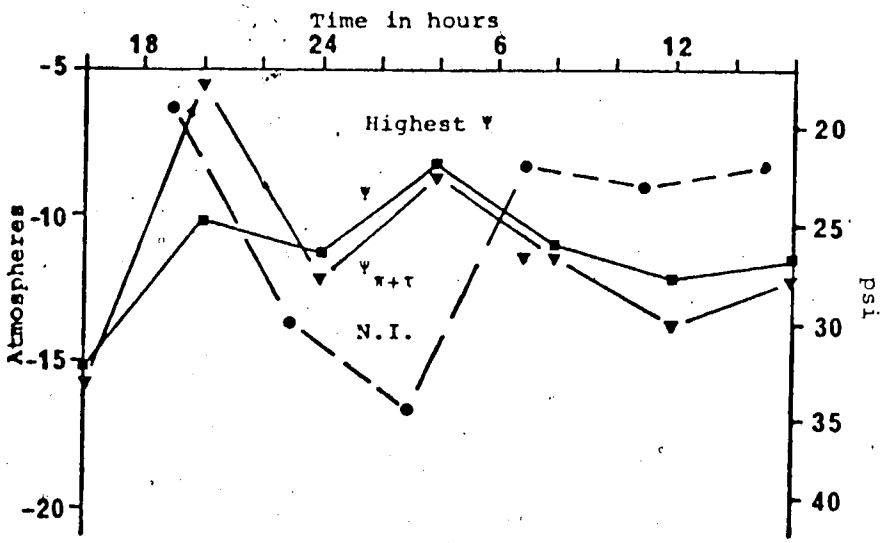


Figure 30. Daily cycle of water potential and its components; and needle infiltration pressures (N.I.). 18 and 19 August, 1973.
Ψ = water potential; $\Psi_{\pi+\tau}$ = "combined osmotic and matric potentials."

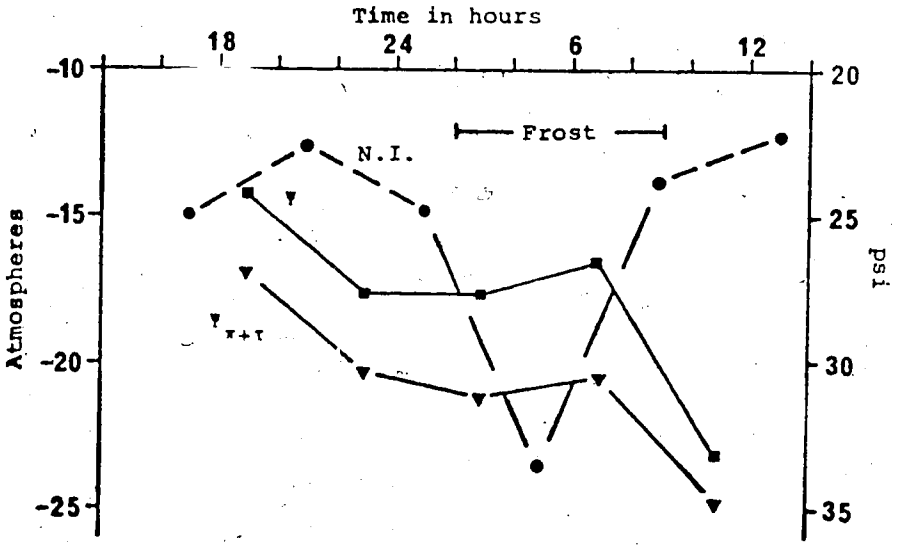


Figure 31. The influence of gibberelic acid (GA_3) on transpiration.

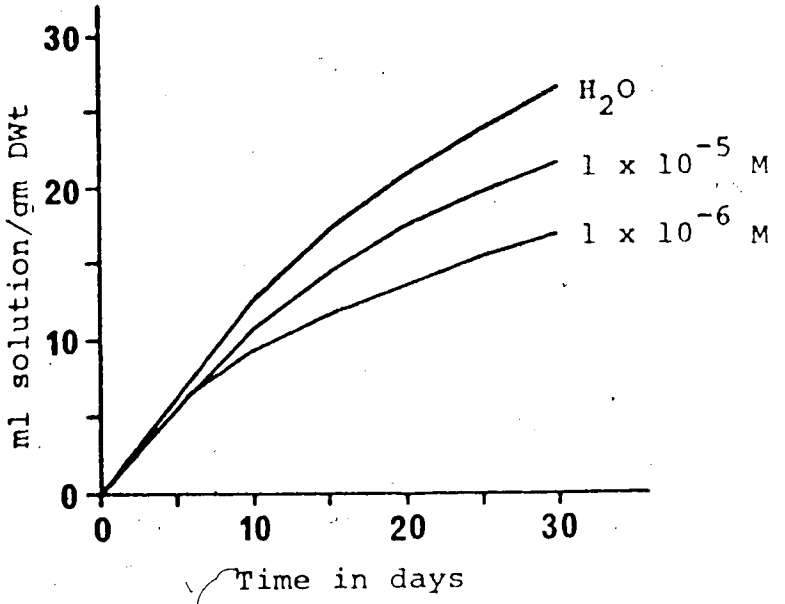


Figure 32. The influence of kinetin on transpiration.

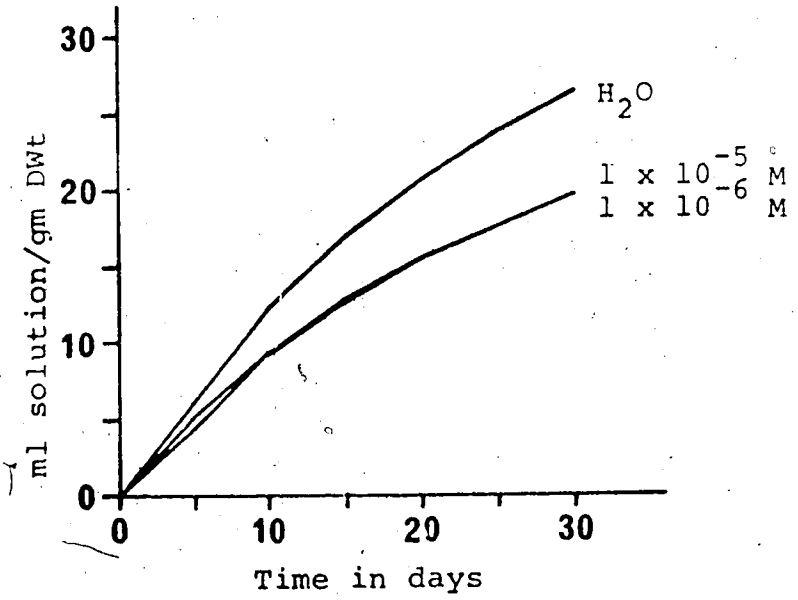


Figure 33. The influen of napthalene acetic acid on transpiration.

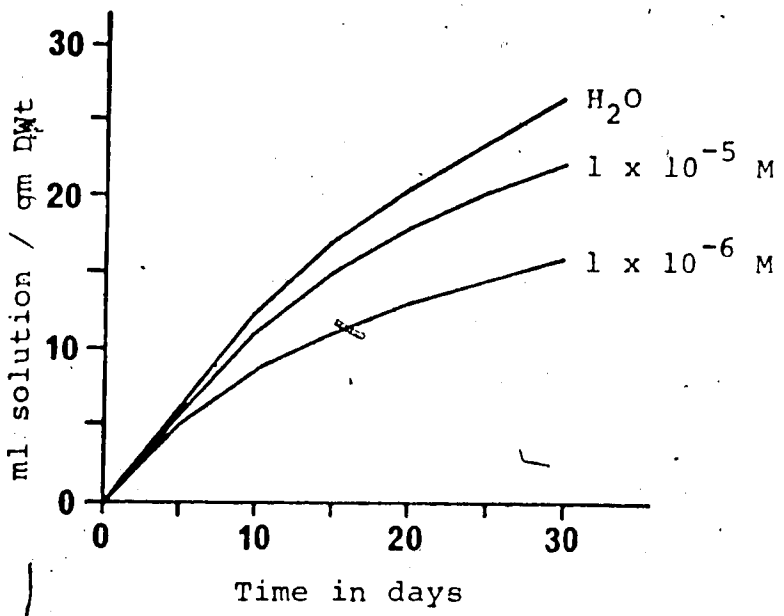


Figure 34. The influence of benzyladenine on transpiration.

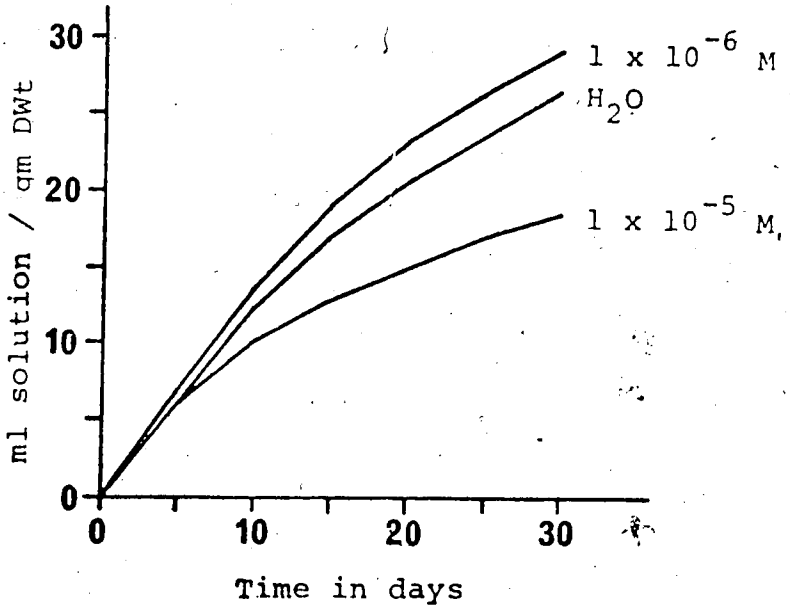


Figure 35. The influence of abscisic acid on transpiration.

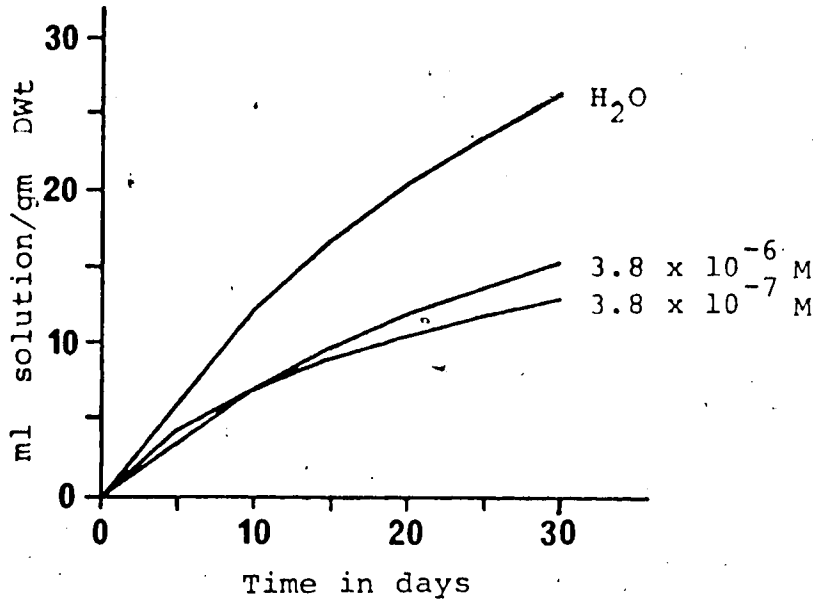


Figure 36. The influence of abscisic acid and benzyladenine on transpiration.

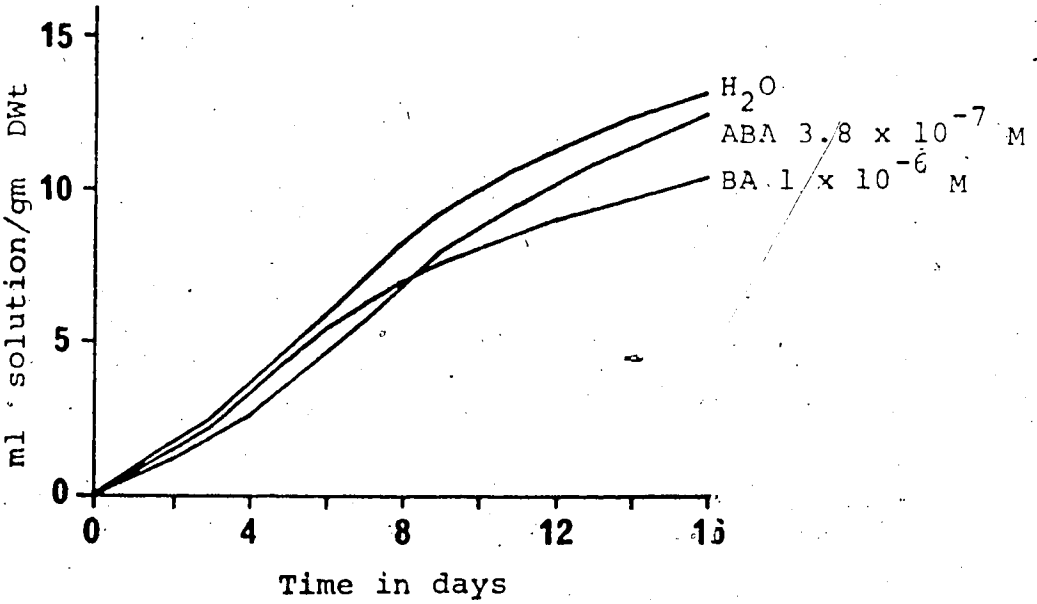


Figure 37. The influence of benzyladenine at various concentrations on transpiration.

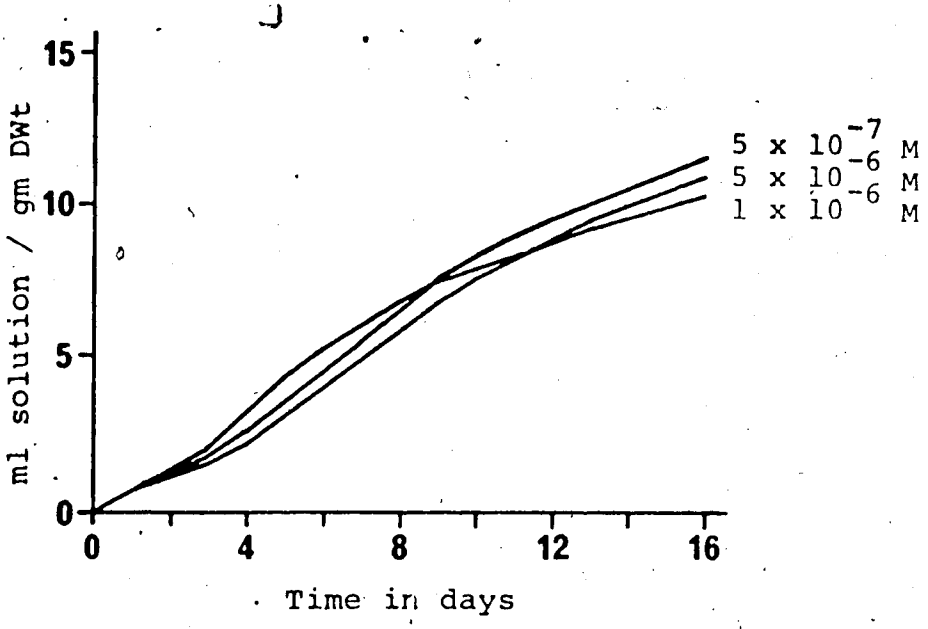


Figure 38. The influence of abscisic acid and various concentrations of benzyladenine on transpiration.

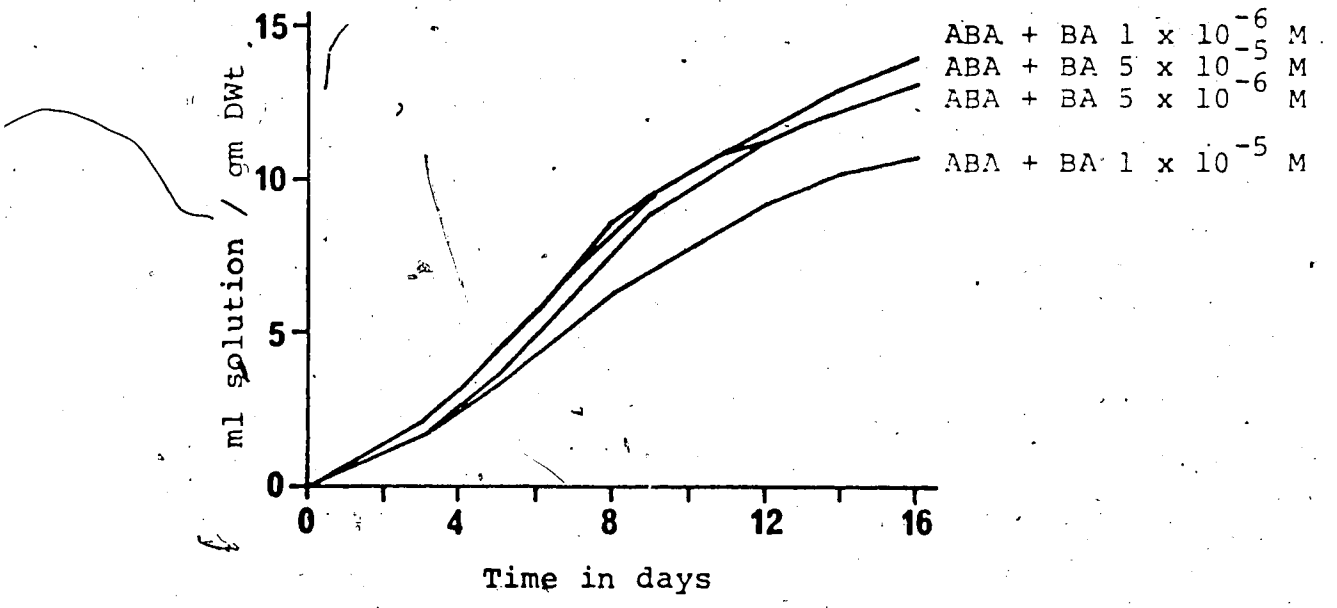


Figure 39. The influence of abscisic acid (ABA), benzyladenine (BA), and water treatments on water potential.

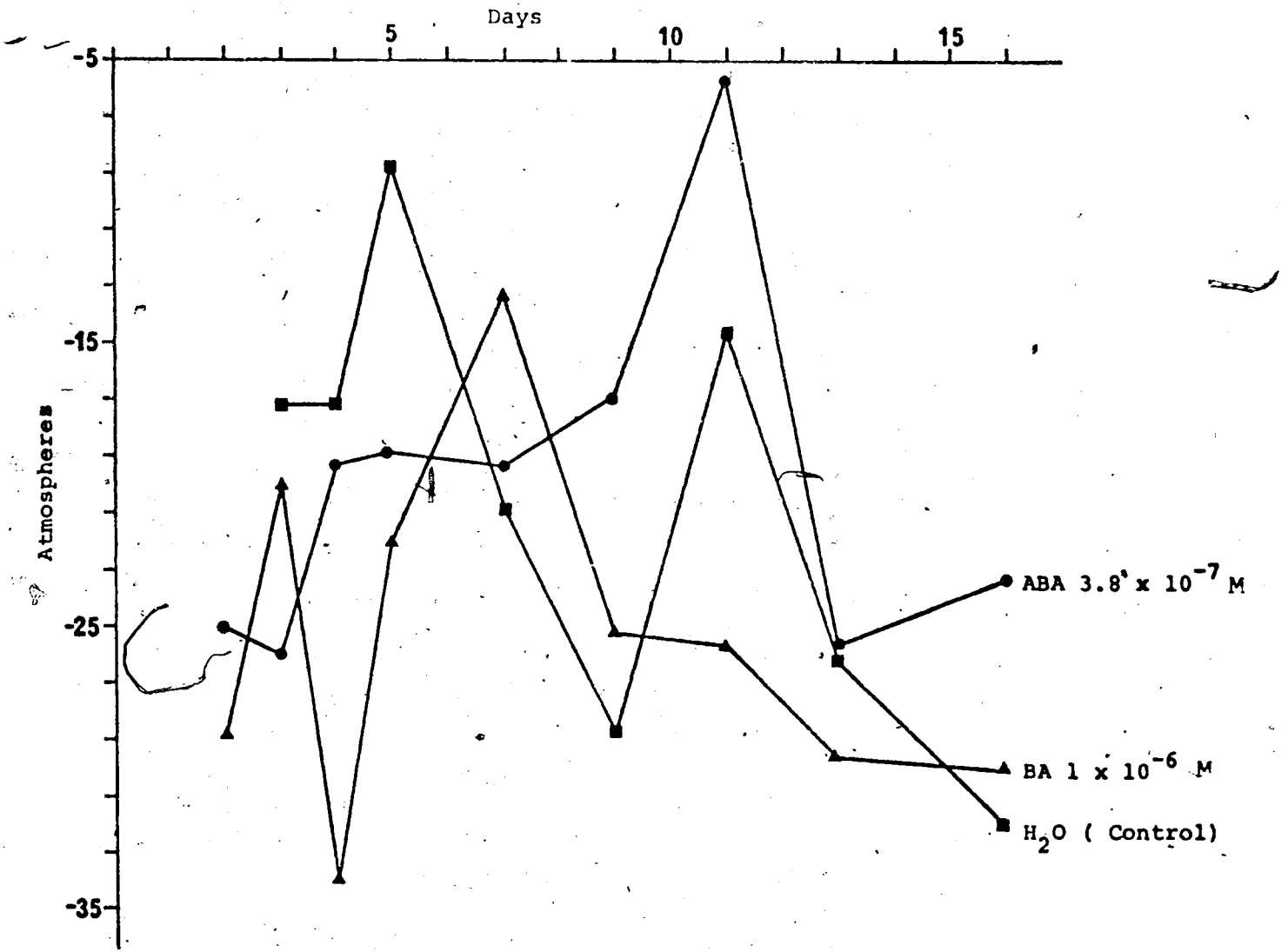


Figure 40. Maximum daily net assimilation rates as influenced by abscisic acid (ABA), and benzyladenine (BA).

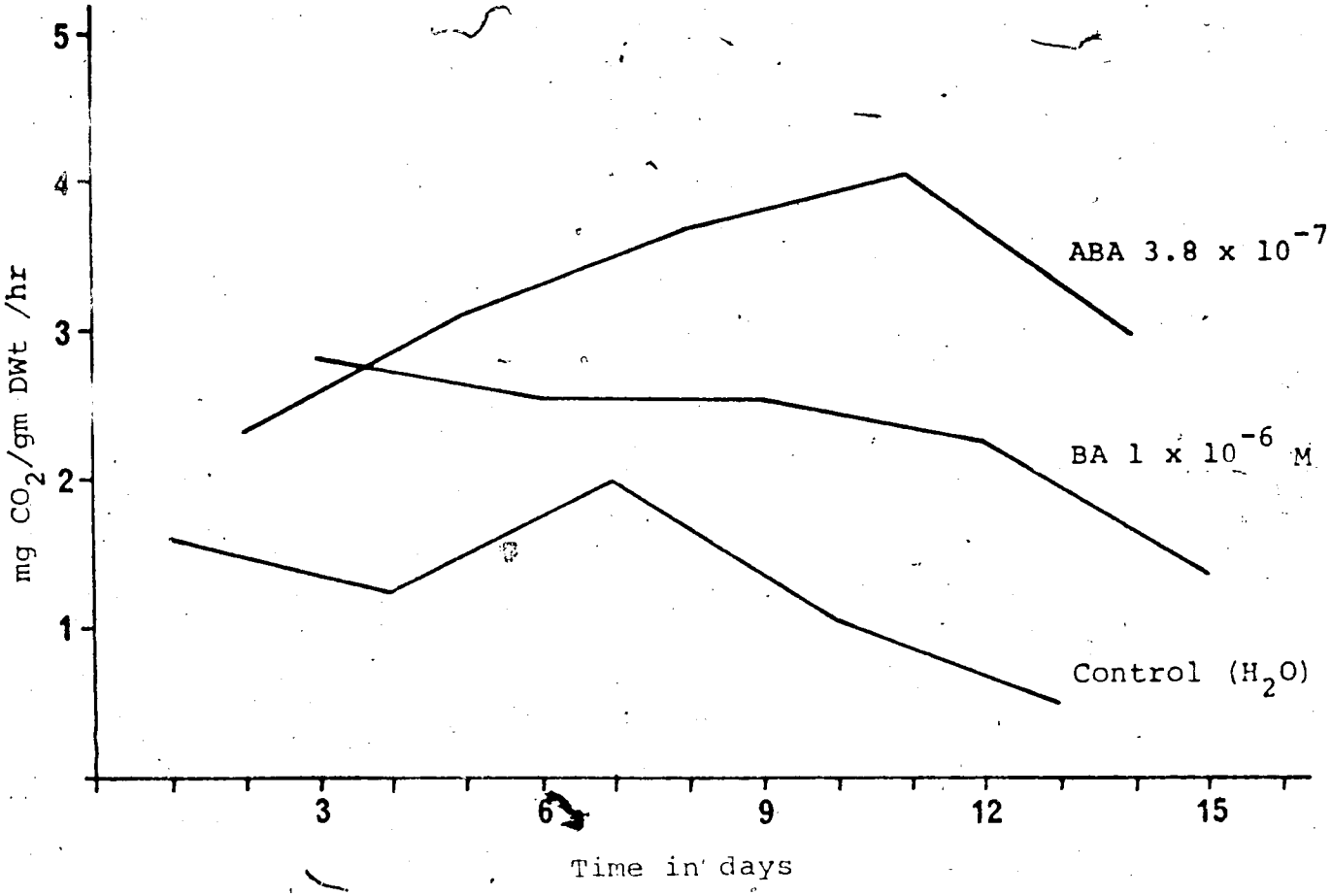


Figure 41. Daily total net assimilation as influenced by abscisic acid (ABA) and benzyladenine (BA).

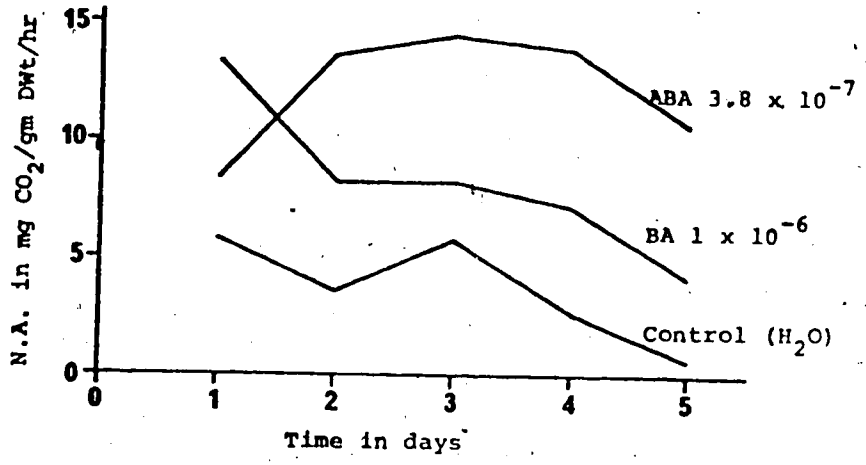


Figure 42. Accumulative increase in CO_2 fixed for the different hormone treatments.

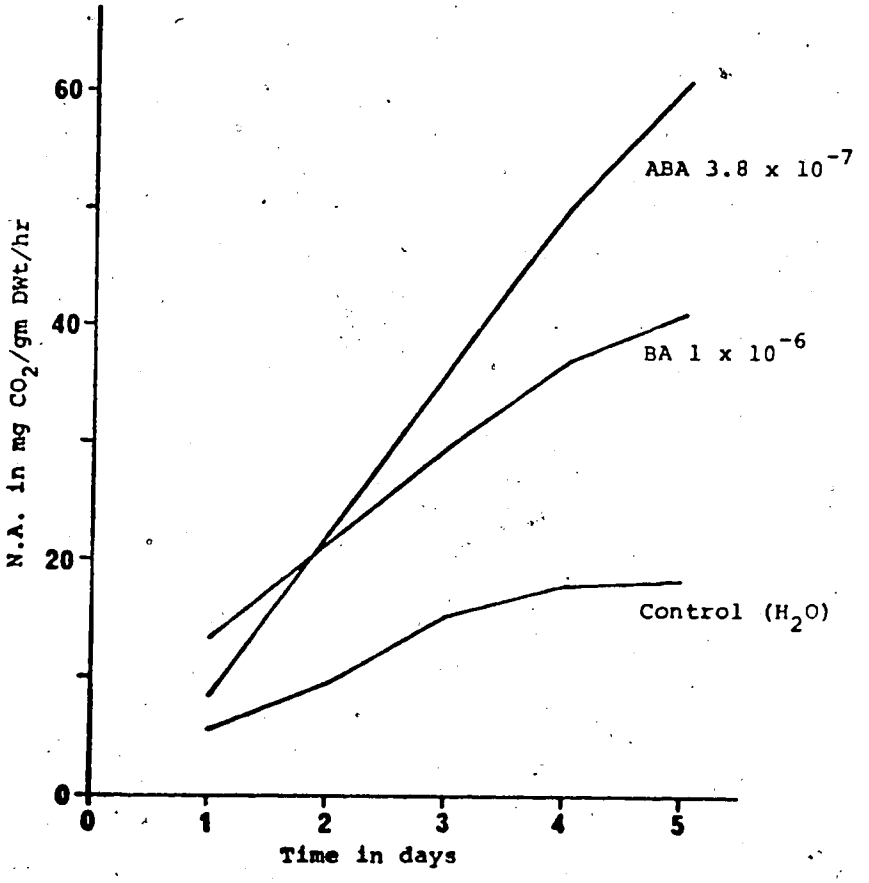


Figure 43. The seasonal trend of net assimilation as found in this investigation. Fixation rates indicated along with needle temperature and water potential at time of reading. Radiation was above 0.2 cal/cm^2/min for all measurements.

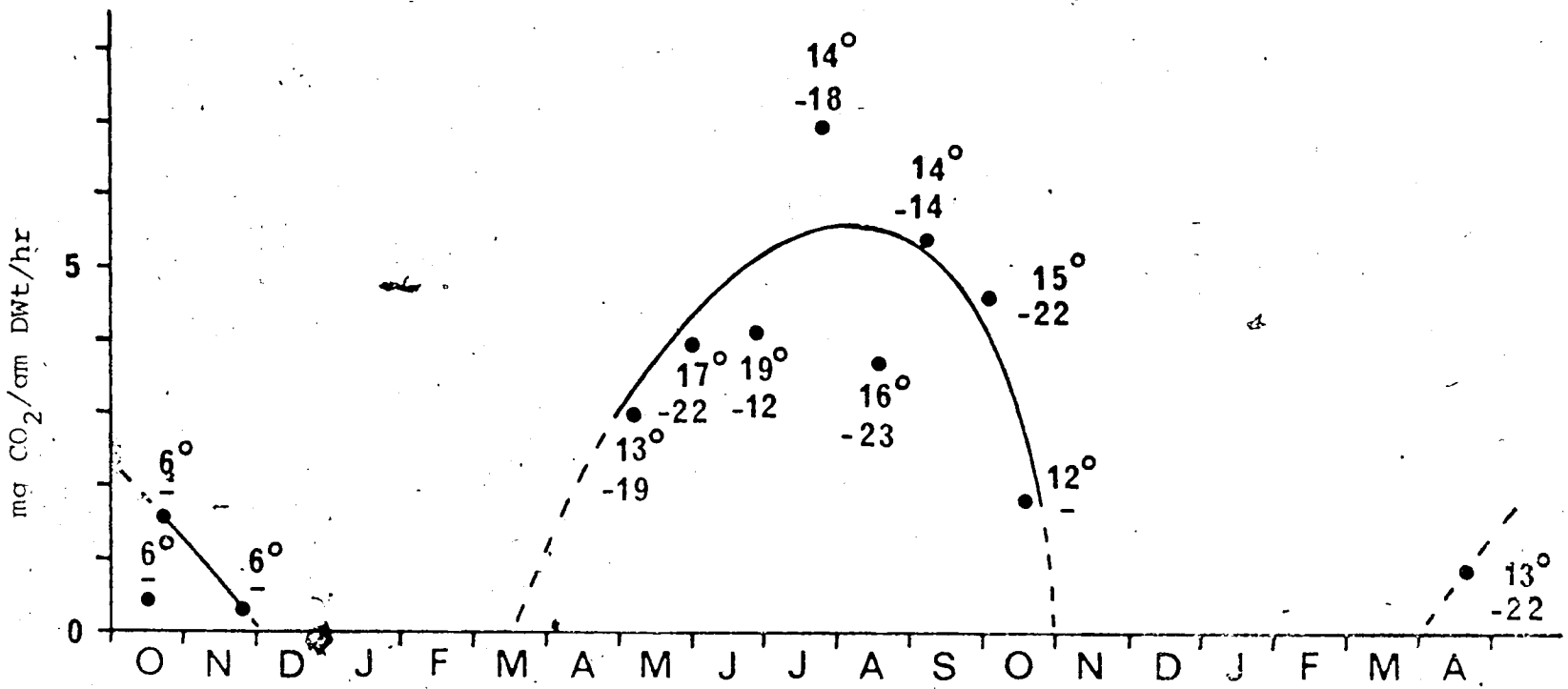
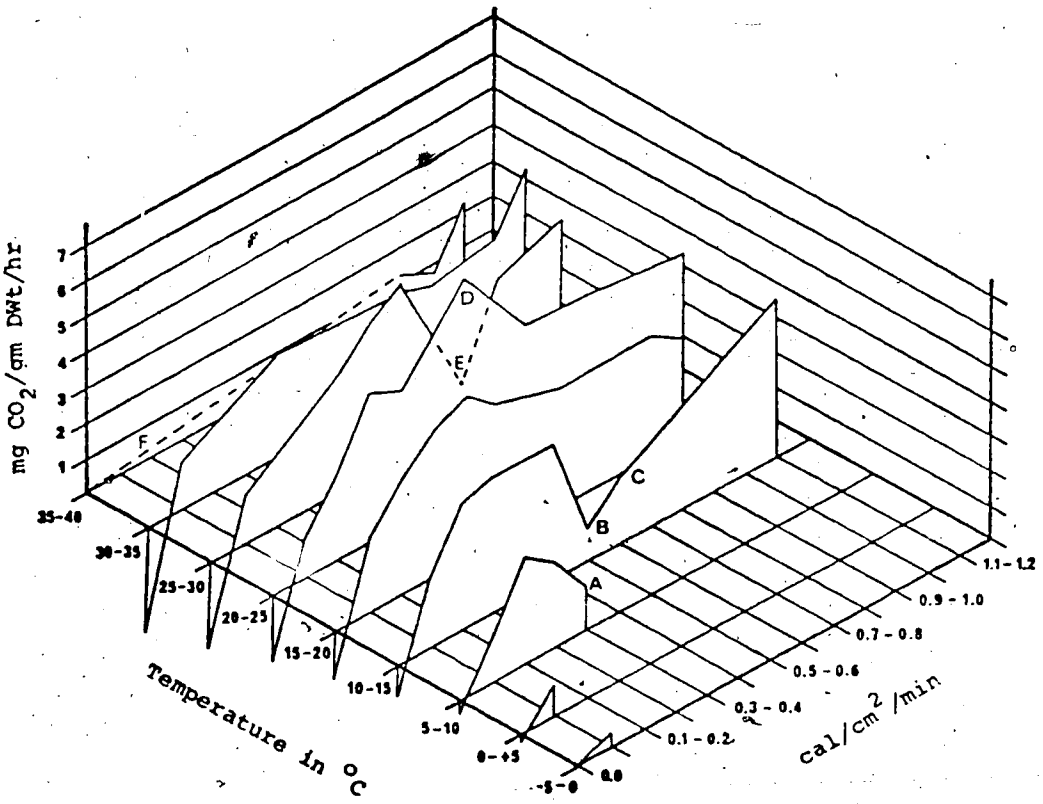


Figure 44. The response of net assimilation to changes in needle temperature and radiation as measured during all the field investigation periods.

A, B, C, and E Single readings with low water potentials.
D. Single reading with high water potential.
F. No respiration data available and no radiation intensities measured below 0.9 cal/cm^2/min.



BIBLIOGRAPHY

Adedipe, N.O., L.A. Hunt, and R.A. Fletcher. 1971. Effects of benzyladenine on photosynthesis, growth and senescence of the bean plant. Physiol. Plant. 25: 151-153.

Ahlgren, C.E., and H.L. Hansen. 1957. Some effects of temporary flooding on coniferous trees. J. Forestry 55: 647-650.

Ashe, J. 1972. Differential temperature basement ventilator. Pop. Electronics 31 - 33. July.

Atmospheric Environment Service. Monthly metereological summary. Department of the Environment, Canada.

Bate, G.C., A. D'Aoust, and D.T. Canvin. 1969. Calibration of infra-red CO_2 gas analyzers. Plant Physiol. 44: 1122-1126.

Belyea, R.M., D.A. Fraser, and A.H. Rose. 1951. Seasonal growth of some trees in Ontario. Forestry Chron. 27 (4): 300-305.

Bowser, W.E., A.A. Kjearsgaard, T.W. Peters, and R.E. Wells. 1962. Soil survey of Edmonton, sheet (83-H). Canada Department of Agriculture, Alberta Soil Survey Report # 21. 66 p.

Boyer, J.S. 1968. Relationship of water potential to growth of leaves. Plant Physiol. 43 (7): 1056-1062.

Christersson, L. 1972. The transpiration rate of unhardened, hardened, and dehardened seedlings of spruce and pine. Physiol. Plant. 26 (2): 258-263.

Clark, J., and J.M. Bonga. 1970. Photosynthesis and respiration in black spruce (*Picea mariana*) parasitized by eastern dwarf mistletoe (*Arceuthobium pusillum*). Can. J. Bot. 48 (11): 2029-2031.

Cleland, R. 1967. A dual role of turgor pressure in auxin induced cell elongation in *Avena* coleoptiles. Planta 77: 182-191.

Courtin, G.M., and J.M. Mayo. 1974. Arctic and alpine plant water relationships. *In* Physiological adaptation to the Environment. *Edited by* F. John Vernberg. Intext Publishers. N.Y. In Press.

D'Aoust, A., G.C. Bate, and D.T. Canvin. 1971. Effect of O_2 concentration and reference cell CO_2 content on the calibration of infra-red CO_2 gas analyzers. Can. J. Bot. 49 (2): 317-320.

Denyer, W.B., and C.G. Riley. 1964. Drought effects on young spruce stands in poor sites. Forestry Chron. 40 (2): 206-208.

Fraser, D.A. 1966. Oxygen and moisture uptake as indices of metabolic activity in white spruce shoot tips. Bi-monthly Res. Notes, Can. Dept. Forestry 22 (5): 2.

Freeland, R.O. 1944. Apparent photosynthesis in some conifers during winter. Plant Physiol. 19 (2): 179-185.

Fry, K.E. 1965. A study of transpiration and photosynthesis in relation to stomatal resistance and internal water potential in Douglas Fir. Unpublished Ph.D. thesis, University of Washington, Seattle.

Fry, K.E., and R.B. Walker. 1967. A pressure-infiltration method for estimating stomatal opening in conifers. Ecology 48: 155-157.

Garner, W.W., and H.A. Allard. 1920. Effect of length of day on plant growth. J. Agr. Res. 18: 553-606.

Genkel, P.A., and E.I. Barskaya. 1960. Seasonal changes in spruce chloroplasts. Soviet Plant Physiol. 7 (6): 535-542.

Gindel, I. 1973. A new ecophysiological approach to forest-water relationships in arid climates. Dr. W. Junk B.V., The Hague. 142 p.

Heber, U.W., and K.A. Santorius. 1964. Loss of adenosine triphosphate synthesis caused by freezing and its relationship to frost hardiness problems. Plant Physiol. 39: 712-719.

Ivanoff, L. 1924. Uber die Transpiration der Holzgewächse im Winter. Ber. Deutsch. Bot. Ges. 42: 44-49.

Laidlaw, T.F. 1971. The black spruce (*Picea mariana*) vegetation of Jasper and Banff Parks. Unpublished M.Sc. thesis, University of Alberta, Edmonton. 190 p.

Larcher, W. 1969. The effect of environmental and physiological variables on the carbon dioxide gas exchange in trees. Photosynthetica 3 (2): 167-198.

Levitt, J. 1972. Responses of plants to environmental stresses. Academic Press, N.Y. 697 p.

Lindsay, J.H. 1971. Annual cycle of leaf water potential in *Picea engelmannii* and *Abies lasiocarpa* at timberline in Wyoming. Arctic and Alpine Res. 3 (2): 131-138.

Little, C.H.A., and D.C. Eidt. 1968. Effect of abscisic acid on bud break and transpiration in woody species. Nature 220 (5166): 498-499.

Lopushinsky, W. 1969a. A portable apparatus for estimating stomatal apperture in conifers. Pacific N.W. For. and Range Exp. Station, Portland, Oregon. 7 p.

Lopushinsky, W. 1969b. Stomatal closure in conifer seedlings in response to leaf moisture stress. Bot. Gaz. 130 (4): 258-263.

Ludlow, M.M., and P.G. Jarvis. 1971. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). I. General characteristics. J. Appl. Ecol. 8 (3): 925-953.

Mayo, J.M. 1974. A thermocouple psychrometer chamber for field and laboratory use. Can. J. Plant Sci. In press.

Miller, P.C., and D.M. Gates. 1967. Transpiration resistance of leaves. Am. Midland Naturalist 77: 77-85.

Mittelheuser, C.J., and R.F.M. van Steveninck. 1969. Stomatal closure and inhibition of transpiration induced by (RS)-abscisic acid. Nature 221: 281-282.

Pallas, J.E., and J.E. Box. 1970. Explanation of stomatal response of excised leaves to kinetin. Nature 227: 87-88.

Parker, J. 1953. Photosynthesis of *Picea excelsa* in winter. Ecology 34: 605-609.

Parker, J. 1963. Causes of winter decline in transpiration, and photosynthesis in some evergreens. Forest Sci. 9 (2): 158-166.

Pharis, R.P., H. Hellmers, and E. Schuurmans. 1970. Effect of sub-freezing temperatures on photosynthesis of evergreen conifers under controlled environment conditions. Photosynthetica 4 (4): 273-279.

Phillips, I.D.J., and P.F. Wareing. 1959. Studies in dormancy of Sycamore II. The effect of daylength on the natural growth-inhibitor content of the shoot. J. Exp. Bot. 10 (30): 504-514.

Pisek, A. 1950. Frostharte und Zusammensetzung des Zellsaftes bei *Rhododendron ferrugeum*, *Pinus cembra* und *Picea excelsa*. Protoplasma 39: 129-146.

Pisek, A., and W. Tranquillini. 1951. Transpiration und Wasserhaushalt der Fichte (*Picea excelsa*) bei zunehmender Lüft und Bodentrockenheit. Physiol. Plant. 4: 1-27.

Pisek, A., and E. Winkler. 1958. Assimilationsvermögen und Respiration der Fichte (*Picea excelsa*) in verschiedener Höhenlage und der Zirbe (*Pinus cembra*) an der alpinen Waldgrenze. Planta 51 (4): 518-543.

Rowe, J.S. 1959. Forest regions of Canada. Department of Northern Affairs, Forestry Branch Bulletin # 123. Ottawa. 172 p.

Samish, R.M. 1954. Dormancy in woody plants. Ann. Rev. Plant Physiol. 5: 183-204.

Sestak, Z., J. Catsky, and P.G. Jarvis. (Ed). Plant photosynthetic production. Manual of methods. Dr. W. Junk B.V. The Hague. 818 p.

Small, E. 1972a. Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in Peat bog plants. Can. J. Bot. 50 (11): 2227-2233.

Small, E. 1972b. Water relations of plants in Peat bogs. Ecology 53 (4): 726-728.

Tranquillini, W. 1963. Beitrage zur Kausalanalyse des Wettbewerbs ökologisch verschiedener Holzarten. Ber. Deutsch. Bot. Ges. 75: 353-364.

Tranquillini, W., and K. Holzer. 1958. Uber das Gefrieren und Auftauen von Coniferennadeln. Ber. Deutsch. Bot. Ges. 71: 143-156.

Tranquillini, W., and I. Machl-Ebner. 1971. Uber den Einfluss von Wärme auf das Photosyntese vermögen der Zirbe (*Pinus cembra* L) und der Alpenrose (*Rhododendron ferrugeum* L) in winter. Rep. Kevo Subarctic Res. Station 8: 158-166.

Turrell, F.M., and S.W. Austin. 1965. Comparative nocturnal thermal budgets of large and small trees. Ecology 46 (1&2): 25-34.

Ungerson, J., and G. Scherdin. 1965. Untersuchungen über Photosyntese und Atmung unter natürlichen bedingungen während des Winter-halbjahres bei *Pinus silvestris* L., *Picea excelsa* Link und *Juniperus communis* L. Planta (Berl.) 67: 136-167.

Vincent, A.B. 1965. Black spruce; a review of its silvics, ecology and silviculture. Can. Dept. Forestry Publ. #1100. 79 p.

Vowinckel, T., W.C. Oechel, and W.G. Boll. 1974. Photosynthesis of *Picea mariana* at the subarctic treeline. Can. Bot. Ass. Bulletin 7 (2): 22.

Walter, H. 1931. Die Hydratur der Pflanze. Gustav Fischer Verlag, Jena. 174 p.

Walter, H. 1960. Einführung in die Phytologie. III. Grundlagen der Pflanzenverbreitung. Teil I Standortslehre. Verlag Eugen Ulmer, Stuttgart. 566 p.

Walter, H. 1968. Die Vegetation der Erde in öko-physiologischer Betrachtung. Band II Die gemäszigten and arktischen Zonen. Gustav Fischer Verlag, Stuttgart. 1001 p.

Walter H., and H. Lieth, 1967. Klimadiagram-Weltatlas. Lierferung 3. Gustav Fischer Verlag, Jena.

Wareing, P.F., and I.D. J. Phillips. 1970. The control of growth and differentiation in plants. Pergamon Press, Toronto. 303 p.

Wareing, R.F., and P.F. Saunders. 1971. Hormones and dormancy. Ann. Rev. Plant Physiol. 22: 261-288.

Weise, G. 1961. Untersuchungen über den Einflusz von Kältebelastungen auf die physiologische Aktivität von Frostgewächsen. Biol. Zentralbl. 80: 137-166.

Wilner, J. 1952. A study of desiccation in relation to winter injury. Sci. Agr. 32: 651-658.

Zacharowa, T.M. 1929. Uber den Gastoffwechsel der Nadelholzpflanzen im Winter. Planta 8: 68-83.

Zeller, O. 1951. Uber Assimilation und Atmung der Pflanzen im Winter bei tiefen Temperaturen. Planta 39: 500-526.

APPENDIX A

Supplementary Field Net Assimilation Data

The first 24-hour investigation was conducted on October 13 and 14, 1972. The minimum cuvette temperature for the period was -10°C. Tranquillini (1963) has shown that net assimilation is depressed on the day following frost of -4°C or more for *Picea excelsa*. This was clearly the case in this instance. It was not until noon on the 14th that net assimilation went positive although conditions were favourable for some time prior to that (light intensities up to 0.4 cal/cm^2/min and temperatures to +11°C) (Fig. 45). The maximum fixation rate obtained on the 14th was 0.31 mg CO_2/gm DWt/hr at +6°C with 0.72 cal/cm^2/min of light (Table 1). Over the 23 hours from 18.00 on the 13th to 17.00 on the 14th a net loss of 0.83 mg CO_2 was recorded.

Between the 14th and 19th October, 1972 when the next investigation was initiated minimum temperatures were not recorded below -6°C and on the 19th a minimum cuvette temperature of -2.5°C was attained. The effect of the warmer days is very evident in that higher net assimilation rates were observed than a week earlier (1.84 mg CO_2/gm DWt/hr at +5.5°C and 0.18 cal/cm^2/min). Furthermore, no significant lag period between sunrise and positive fixation was observed (Fig. 46). A net gain of 5.80 mg CO_2 was recorded during the investigation period. It took five hours on the 20th to replace the 3.57 mg CO_2 lost by respiration during the night.

By the time the next 24-hour investigation was started on November 22, 1972 (Fig. 47) there had been a period of over two weeks during which maximum temperatures did not reach 0°C while minimum temperatures reached -16°C on November 6, 1972. Although a minimum cuvette temperature of only -3.5°C was recorded during the night, maximum net assimilation rates were very low (0.34 mg CO_2/gm DWt/hr at

6.5°C and 0.11 cal/cm^2/min). This is ascribed to the true onset of dormancy.

Problems with power and cuvette temperature arose during this investigation making it impossible to establish if a net gain or loss in CO_2 occurred during the 24 hours.

After August 19, 1973 temperatures again increased and remained above freezing until September 7 when the next investigation was conducted. Possibly due to the frost earlier, photosynthetic rates did not exceed 5.43 mg CO_2/gm DWt/hr at 14°C and 0.20 cal/cm^2/min although the minimum temperature during the night was 9.5°C (Fig. 48). The loss of CO_2 at night (2.82 mg) was similar to the amount lost on July 22, 1973 (3.07 mg) when a night-time minimum temperature of 9.0°C occurred. Respiration thus seemed to be fully recovered from the short frost period three weeks earlier. Throughout the 24-hour investigation 26.26 mg CO_2 was fixed. The CO_2 lost at night was replaced only after five hours of positive fixation, which is due to low light levels until after noon on September 7.

Minimum temperatures as low as -4°C were recorded between September 14 and 18, 1973. Light frost again occurred on September 26 and October 1 and 2, 1973. A minimum temperature of -0.5°C was registered during the night of October 2 and 3 when measurements were again made. This, however, had no adverse effect on the photosynthetic rates and a maximum of 5.67 mg CO_2/gm DWt/hr was found at 14°C and 0.23 cal/cm^2/min (Fig. 49). Due to the low night time temperatures little respiration took place and the CO_2 lost was replaced within three hours. Again, light intensities were very low for the first few hours after sunrise and low initial photosynthetic rates resulted. Over the 24

hours a net gain of 28.70 mg CO_2 was recorded.

Figure 45. Radiation, needle temperature, and net assimilation (N.A.) as measured in the field on 13 and 14 October, 1972.

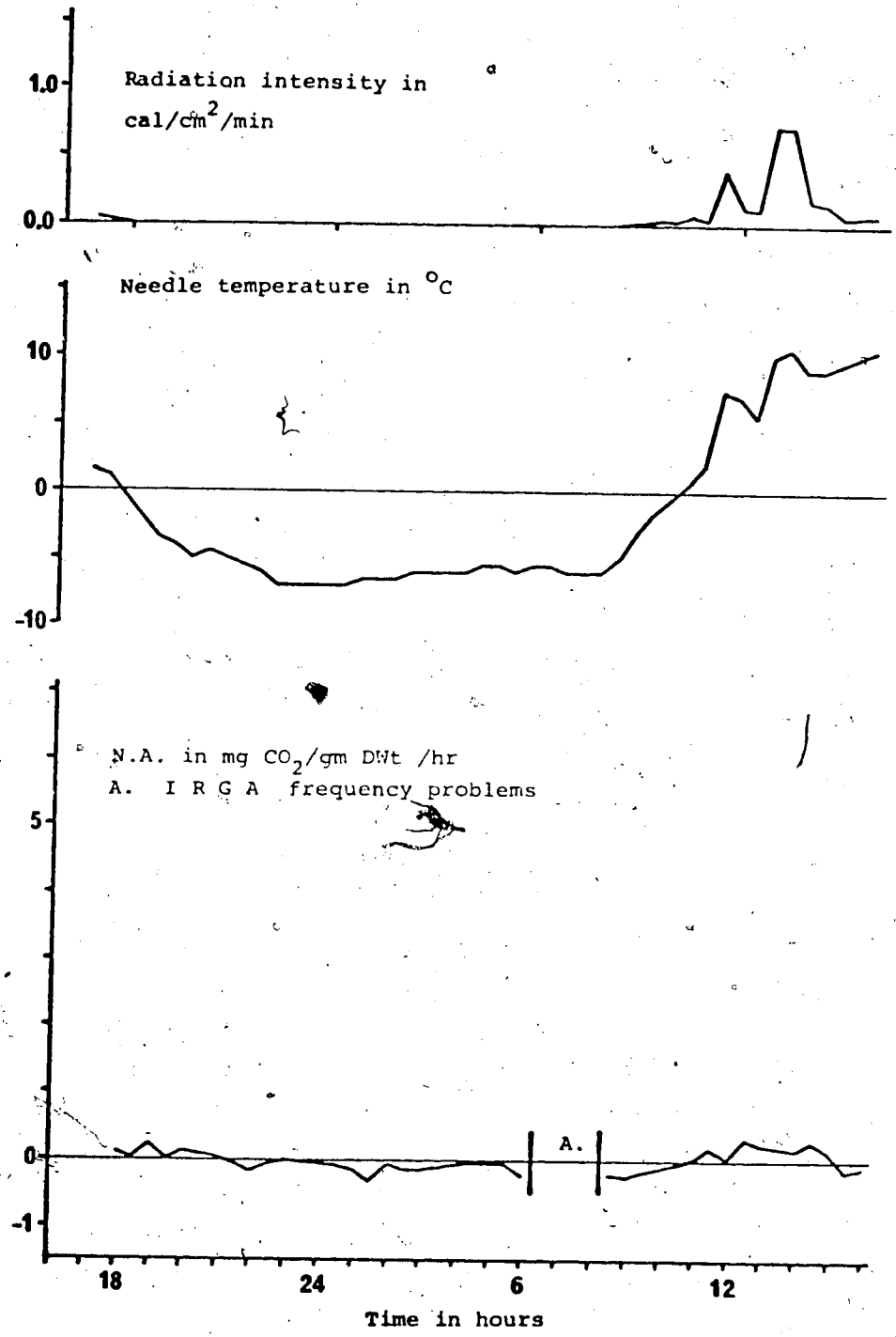


Figure 46. Radiation, needle temperature, and net assimilation (N.A.) as measured in the field on 19 and 20 October, 1972.

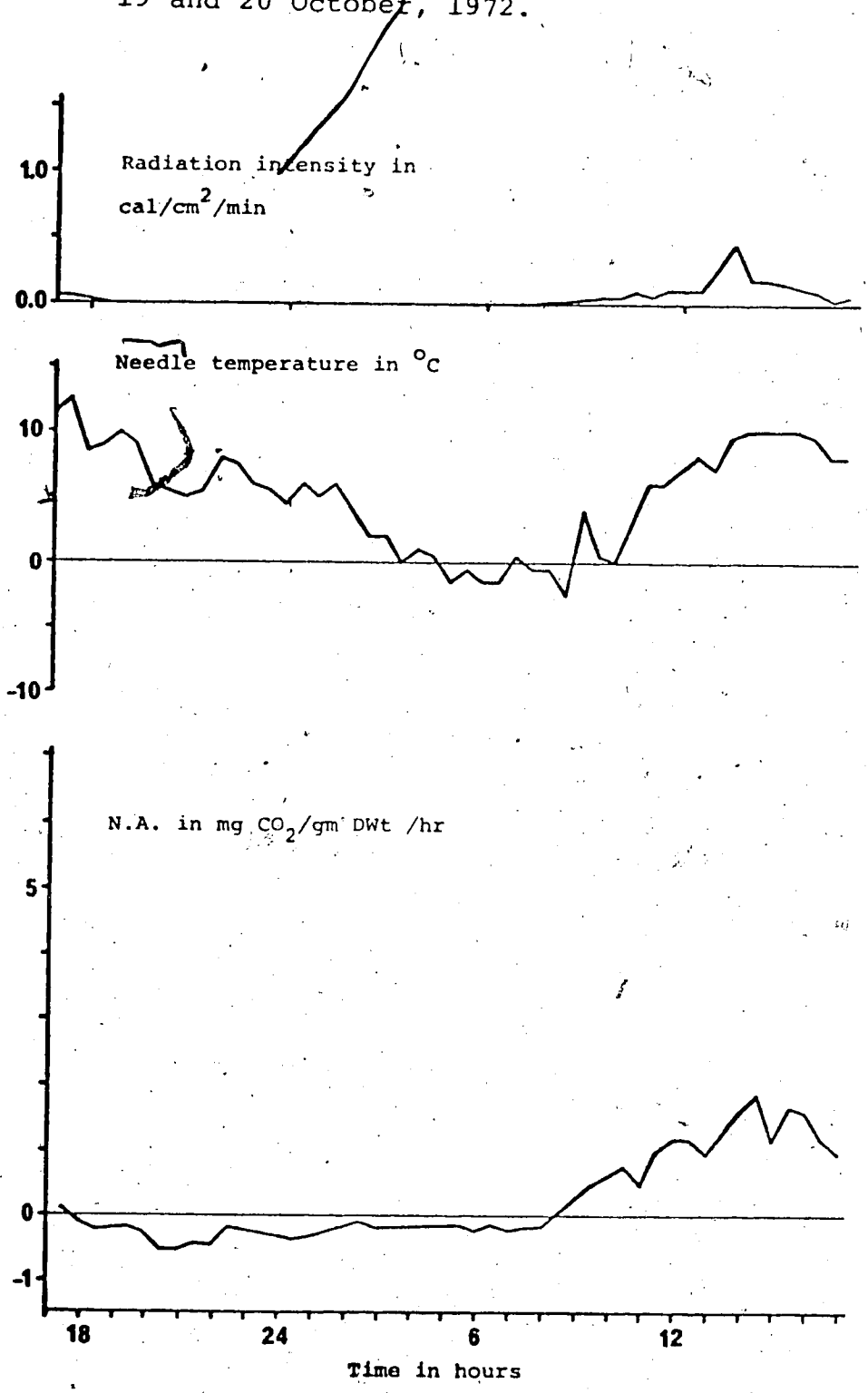


Figure 47. Radiation, needle temperature, and net assimilation (N.A.) as measured in the field on 22 and 23 November, 1972.

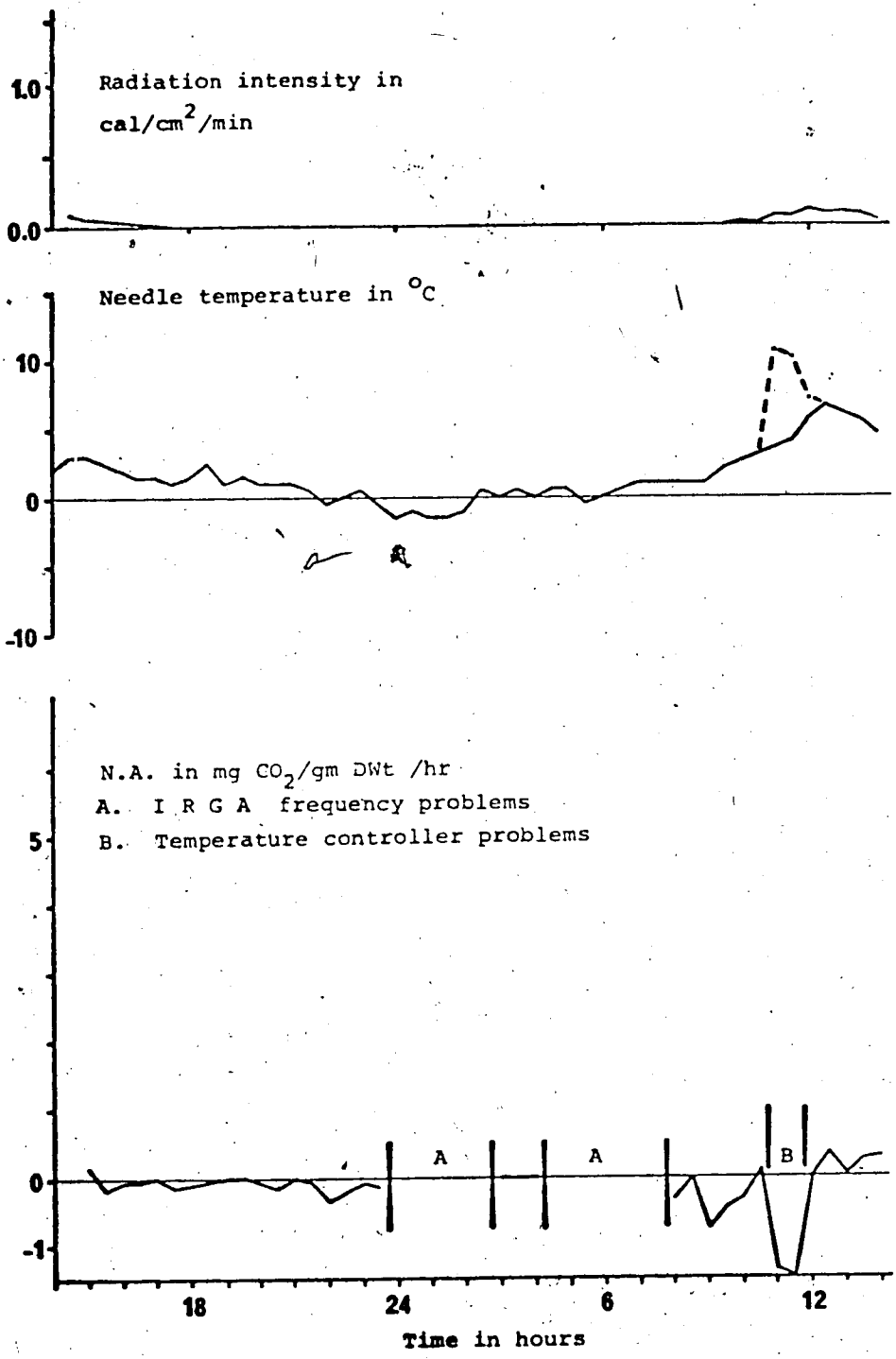


Figure 48. Radiation, needle temperature, and net assimilation (N.A.) as measured in the field on 6 and 7 September, 1973.

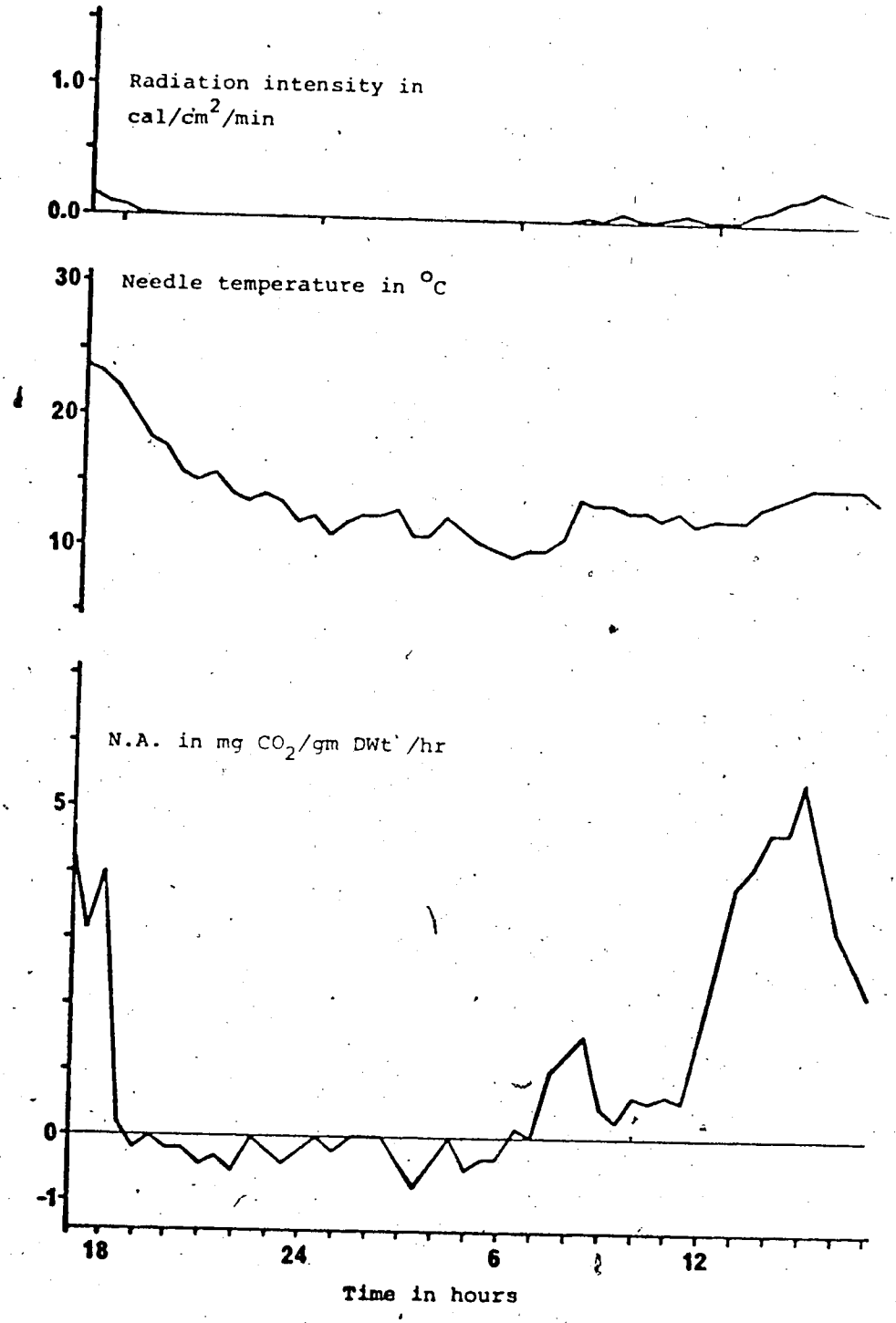
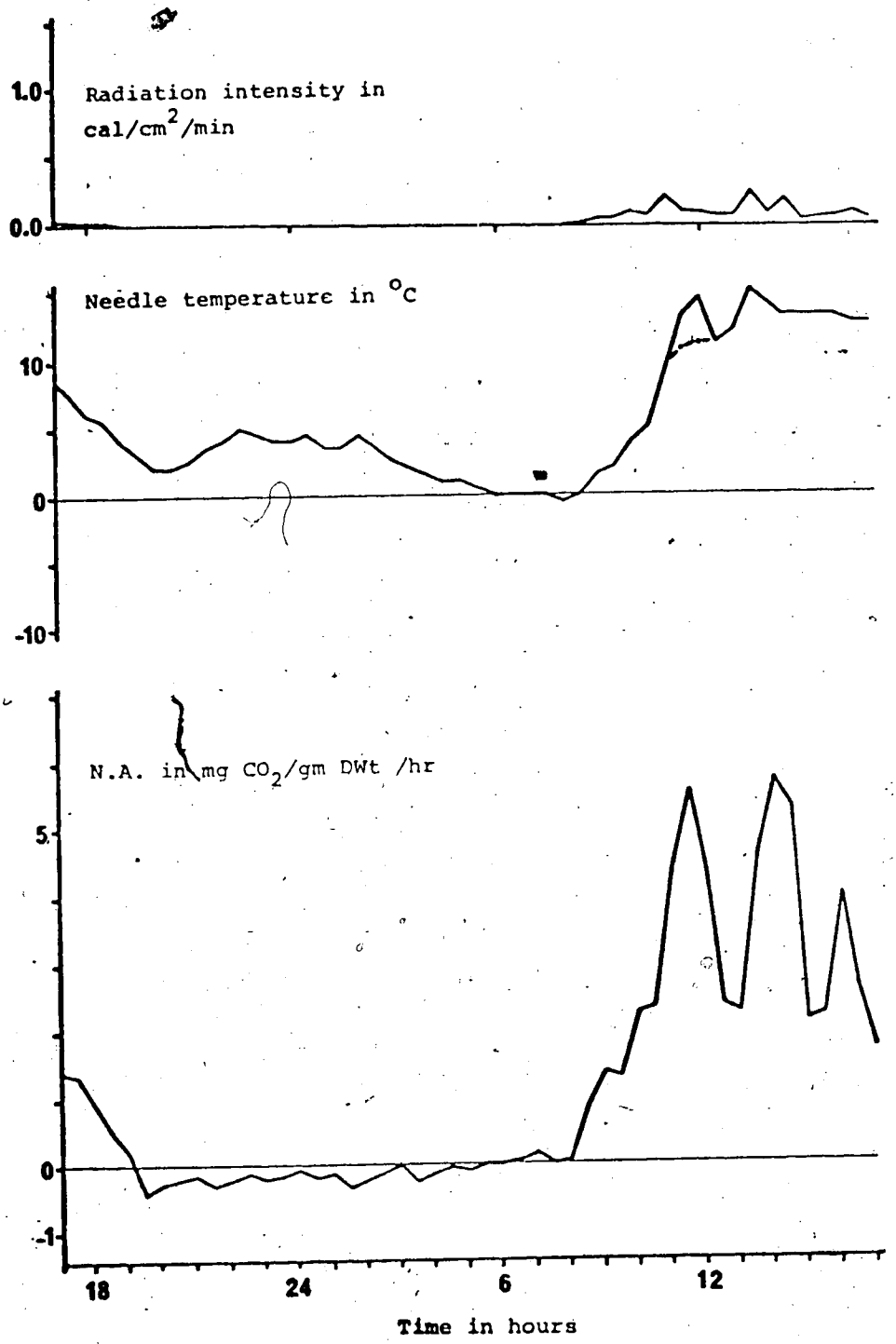


Figure 49. Radiation, needle temperature, and net assimilation (N.A.) as measured in the field on 2 and 3 October, 1973.



APPENDIX B

Daily Net Assimilation During the Termination of Dormancy

TABLE 8. Radiation intensity and duration and photosynthetically active radiation (PAR, 400-700 nm) in growth chamber from February 18 to 21, 1973.

Time	Incandescent	Fluorescent	Radiation cal/cm^2/min	PAR µE/m^2/sec
00.00 - 06.00	--	--	--	--
06.00 - 08.00	1/3	--	0.03	10
08.00 - 10.00	1/3	1/3	0.08	160
10.00 - 14.00	3/3	1/3	0.14	190
14.00 - 16.00	1/3	1/3	0.08	160
16.00 - 18.00	1/3	--	0.03	10
18.00 - 24.00	--	--	--	--

TABLE 9. Radiation intensity and duration, and photosynthetically active radiation (PAR, 400-700 nm) in growth chamber from February 22 to March 4, 1973.

Time	Incandescent	Fluorescent	Radiation cal/cm^2/min	PAR µE/m^2/sec
00.00 - 06.00	--	--	--	--
06.00 - 08.00	1/3	--	0.03	10
08.00 - 10.00	1/3	1/3	0.08	160
10.00 - 14.00	3/3	3/3	0.21	420
14.00 - 16.00	1/3	1/3	0.08	160
16.00 - 18.00	1/3	--	0.03	10
18.00 - 24.00	--	--	--	--

Figure 50. Radiation, needle temperature, and net assimilation (N.A.) with emergence from dormancy on 22 February, 1973.

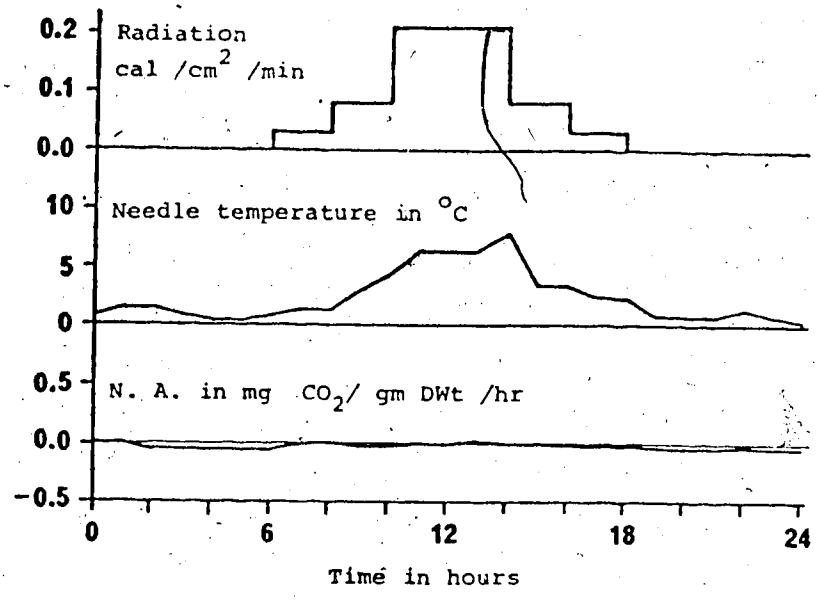


Figure 51. Radiation, needle temperature, and net assimilation (N.A,) with emergence fron dormancy on 23 February, 1973.

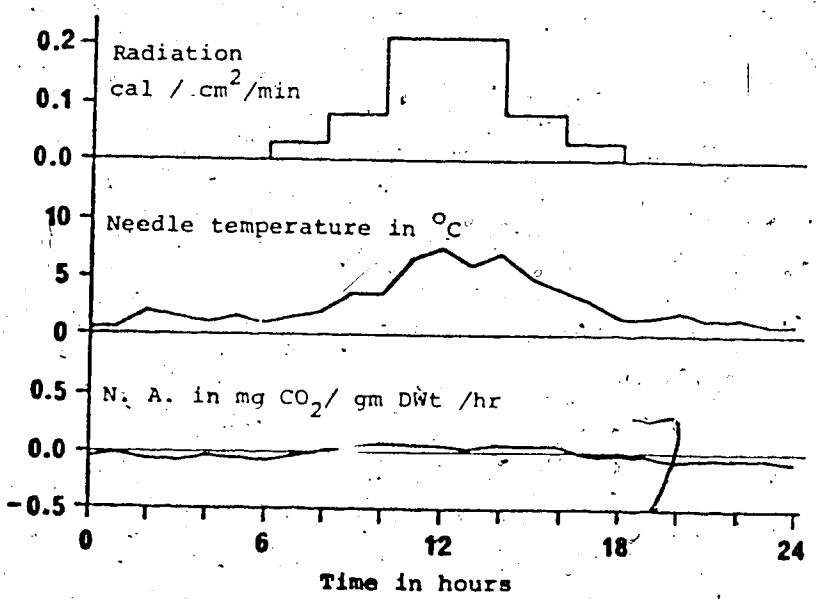


Figure 52. Radiation, needle temperature, and net assimilation (N.A.) with emergence from dormancy on 24 February, 1973.

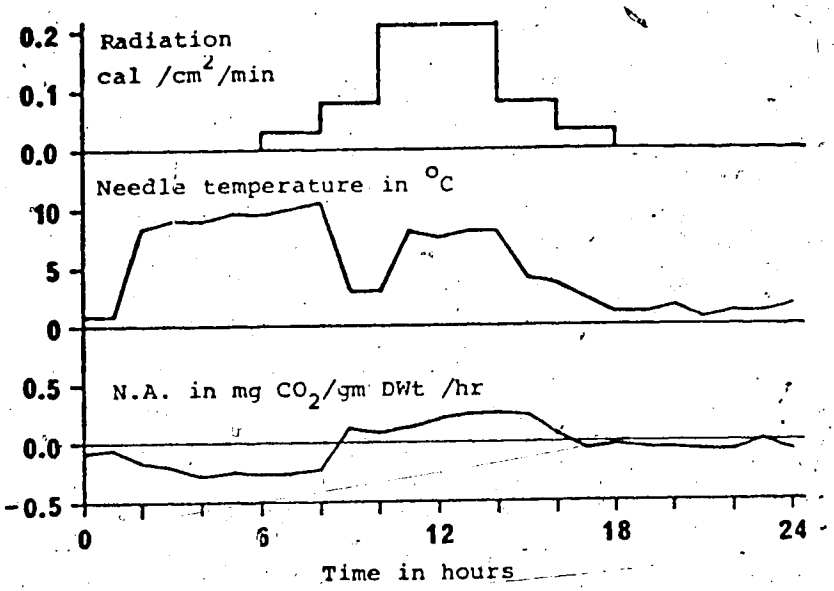


Figure 53. Radiation, needle temperature, and net assimilation (N.A.) with emergence from dormancy on 25 February, 1973.

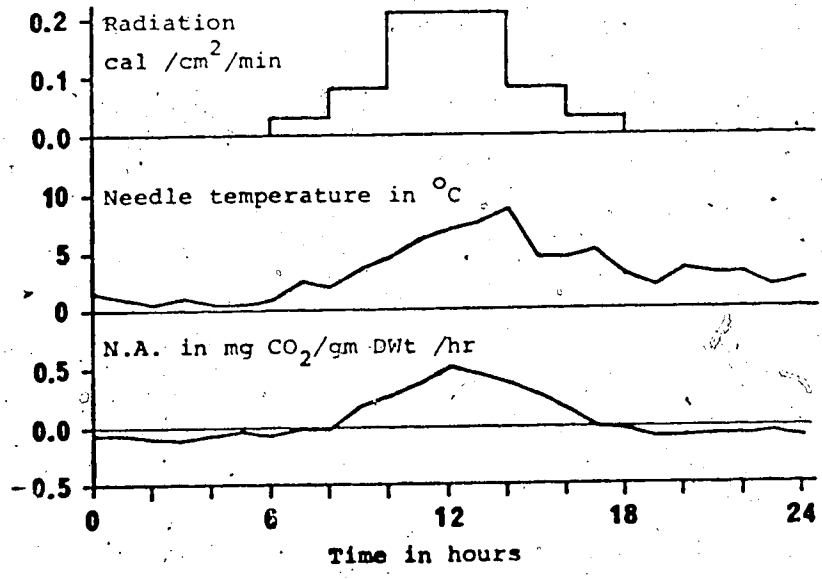


Figure 54. Radiation, needle temperature, and net assimilation (N.A.) with emergence from dormancy on 26 February, 1973.

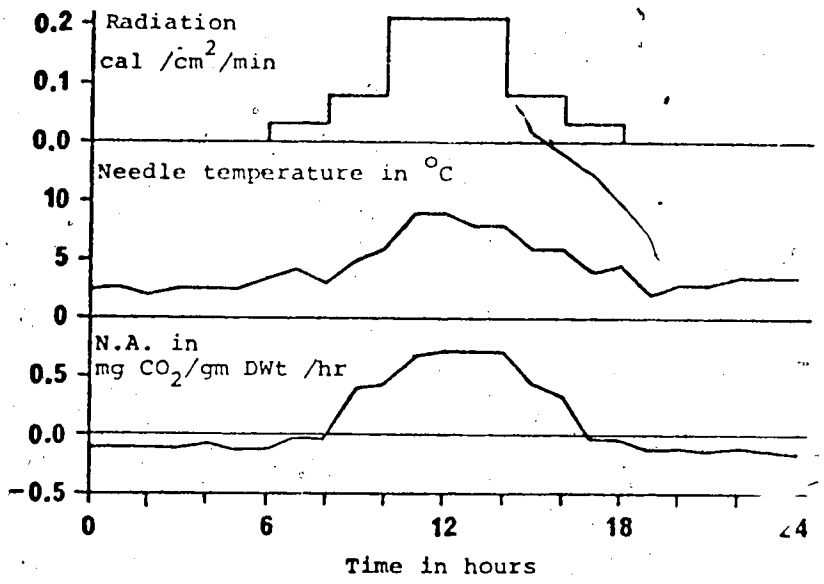


Figure 55. Radiation, needle temperature, and net assimilation (N.A.) with emergence from dormancy on 27 February, 1973.

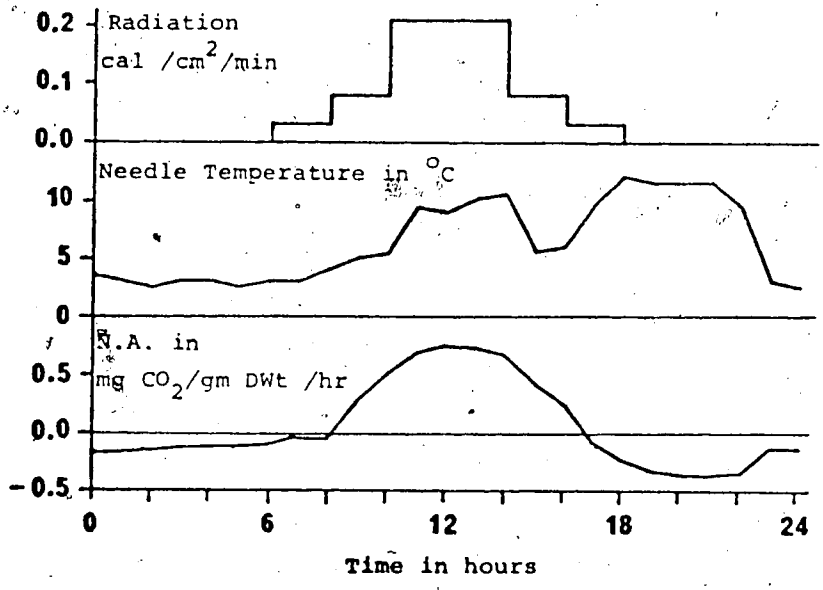


Figure 56. Radiation, needle temperature, and net assimilation (N.A.) with emergence from dormancy on 28 February, 1973.

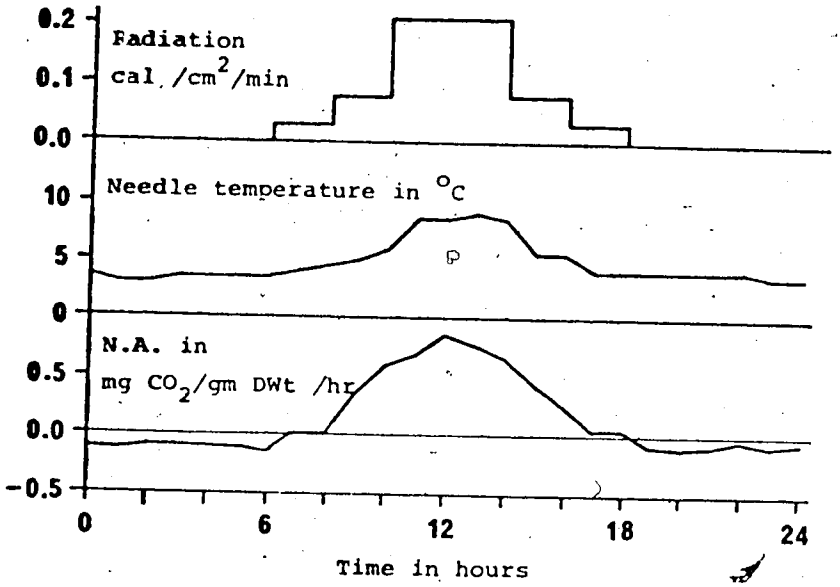


Figure 57. Radiation, needle temperature, and net assimilation (N.A.) with emergence from dormancy on 1 March, 1973.

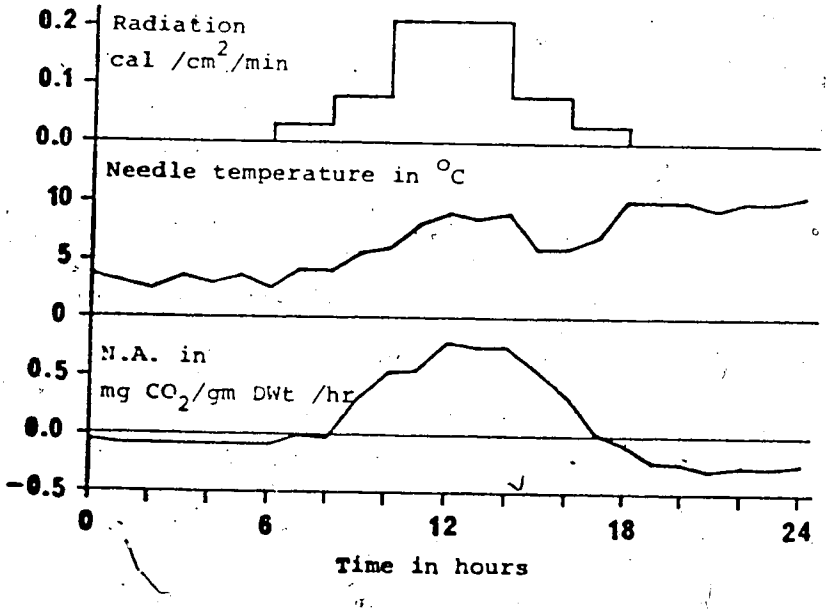


Figure 58. Radiation, needle temperature, and net assimilation (N.A.) with emergence from dormancy on 2 March, 1973.

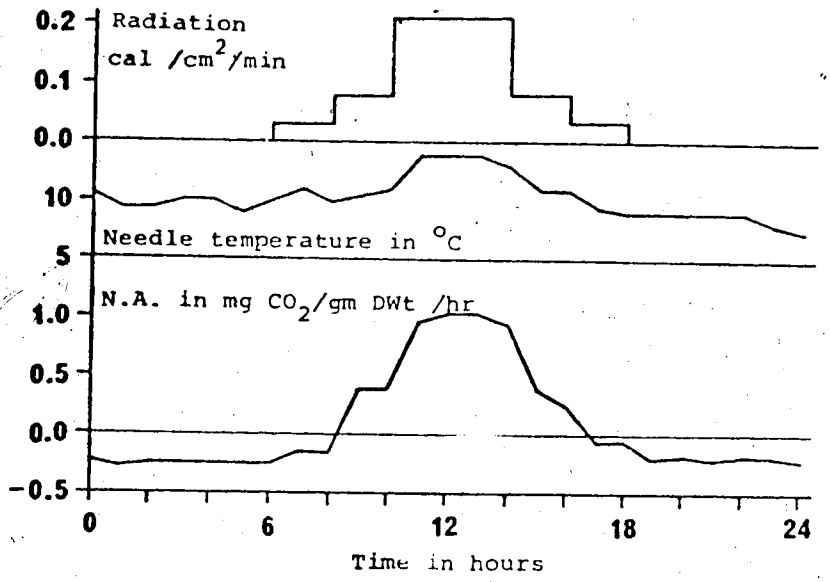
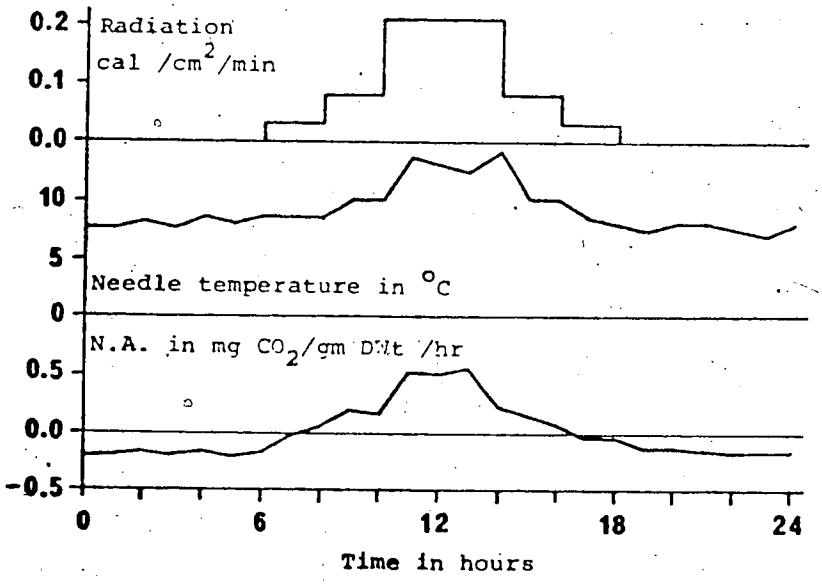


Figure 59. Radiation, needle temperature, and net assimilation (N.A.) with emergence from dormancy on 3 March, 1973.



APPENDIX C

Supplementary Field Water Relations Data

Intermittent rain on July 21 and 22, 1973, along with problems with the pressure chamber caused the data for this 24-hour period to be incomplete. Water potentials changed dramatically over the day as did the "combined osmotic and matric" potentials (Fig. 60). As a result these data are considered doubtful. To some extent this may have been because the needles were not completely dry when placed in the sample chamber.

Air temperatures were well above freezing on September 6 and 7, 1973 when the next 24-hour investigation was conducted. Needle infiltration pressure indicated that the stomata fluctuated between fully open and slightly closed (Fig. 61). Due to rain during the morning of September 7 the relative humidity of the air was high and little water was lost through transpiration. Water potentials thus increased gradually during the day to a maximum value (-14.3 atm) at 15.00 on September 7 from a minimum of -22.8 atm at 13.00 on September 6.

Mild frost occurred during the night of October 2 and 3, 1973 (a minimum temperature of -0.5°C was reached). Again needle infiltration pressures indicated that the stomata were between fully open and partially closed (Fig. 62). Water potentials gradually increased during the first half of the night and then showed a sharp decrease. During the period of light frost the water potential decreased sharply and did not recover afterward. The stomata showed a tendency to close after the frost and had not reversed this trend by 17.00 on October 3.

Needle infiltration pressures indicated that the stomata were closing during the late afternoon of October 17, 1973 (Fig. 63) and were shut by 01.00 on October 18. Thereafter, they opened gradually

and were fully open by noon only to start closing again during the afternoon.

The final 24-hour investigation for which data are available was on April 18 and 19, 1974 (Fig. 64). The stomata varied between half closed in the early evening of April 18 to fully open at noon on April 19. Water potentials over the 24 hours changed little while "combined osmotic and matric" potentials decreased considerably during the night and then increased again next day to end at about the same value 24 hours later.

Figure 60. Summer daily cycle of water potential and its components. 21 and 22 July, 1973.
Ψ = water potential; $\Psi_{\pi+\tau}$ = "combined osmotic and martic potentials."

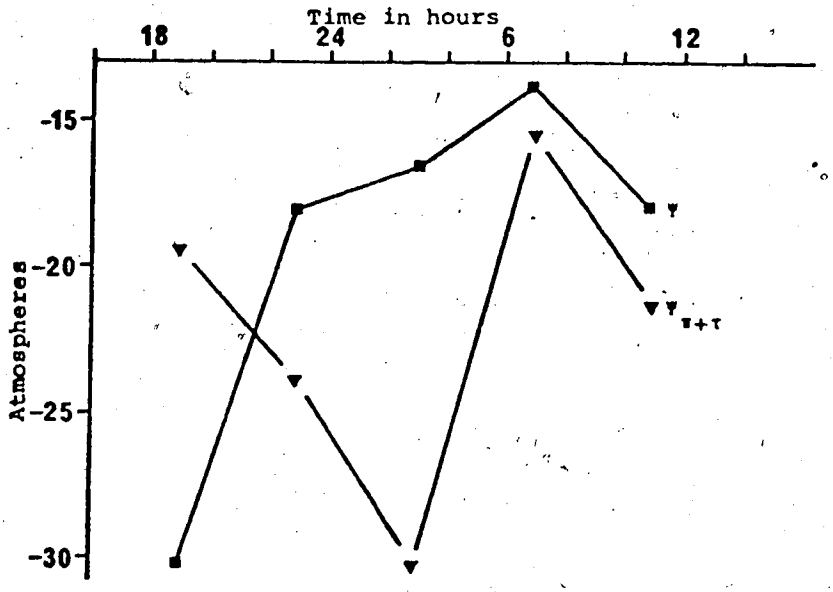


Figure 61. Autumn daily cycle of water potential and its components. 6 and 7 September, 1973.
Ψ = water potential; $\Psi_{\pi+\tau}$ = "combined osmotic and matric potentials."

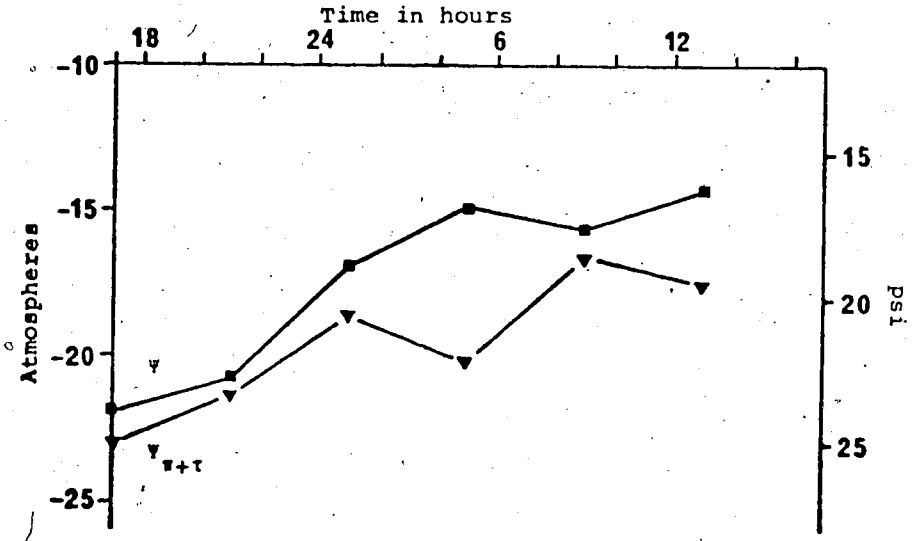


Figure 62. Fall daily cycle of water potential and its components; and needle infiltration pressures (N.I.). 2 and 3 October, 1973.
Ψ = water potential; $\Psi_{\pi+\tau}$ = "combined osmotic and matric potentials."

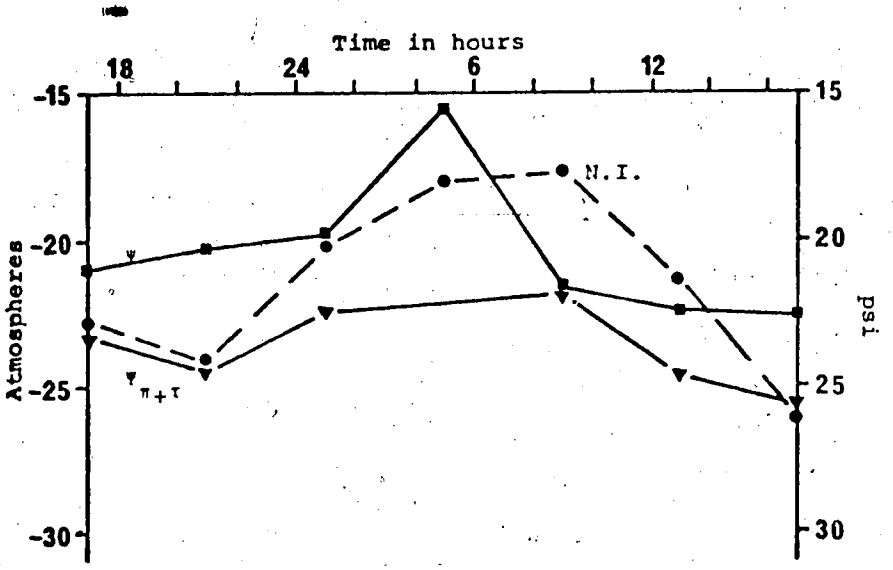


Figure 63. Fall daily cycle of needle infiltration pressures (N.I.) on 17 and 18 October, 1973.

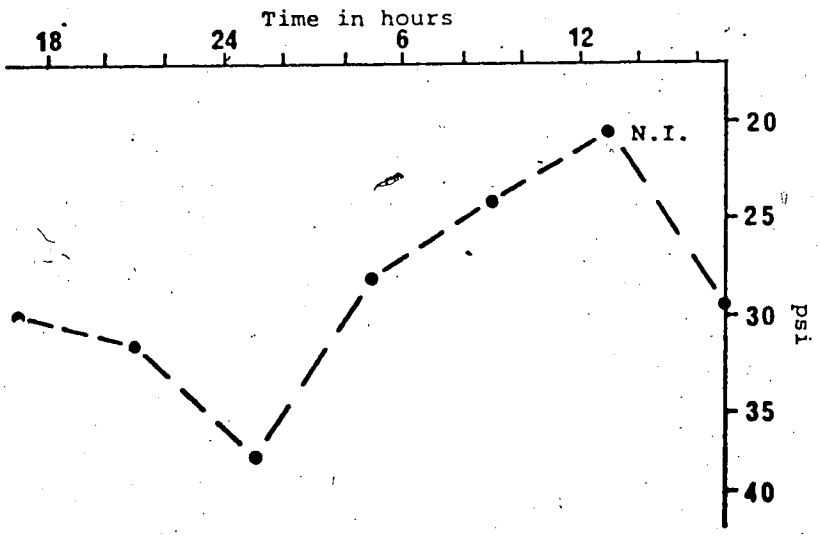
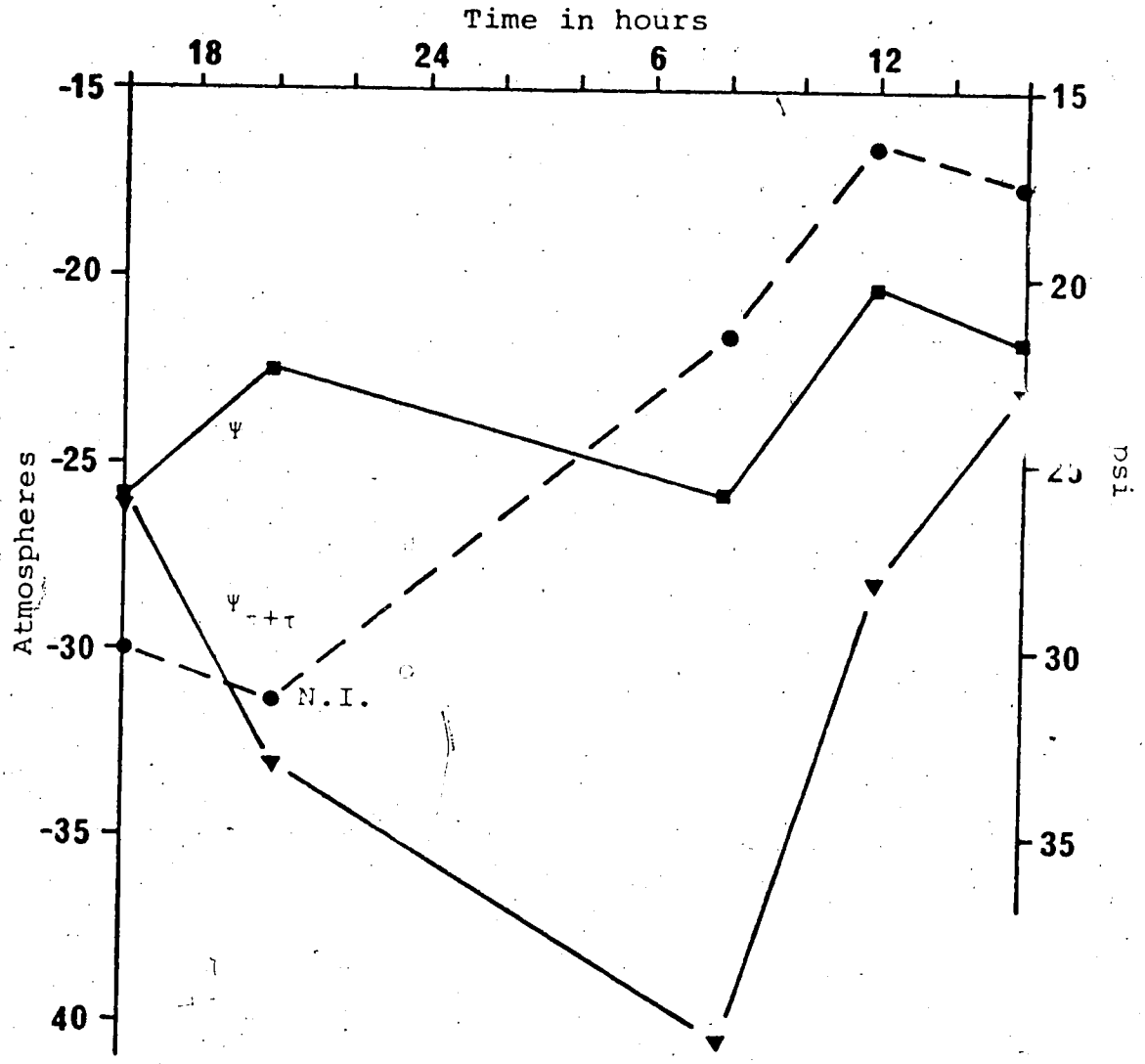


Figure 64. Spring daily cycle of water potential and its components; and needle infiltration pressures (N.I.). 18 and 19 April, 1974.
Ψ = water potential; $\Psi_{\pi+\tau}$ = "combined osmotic and matric potentials."



APPENDIX D

Daily Net Assimilation Data for the Different Hormone Treatments

Figure 65. Net assimilation (N.A.) data for hormone treatments from day 1 to 3 at a constant temperature of 10 ± 1°C.

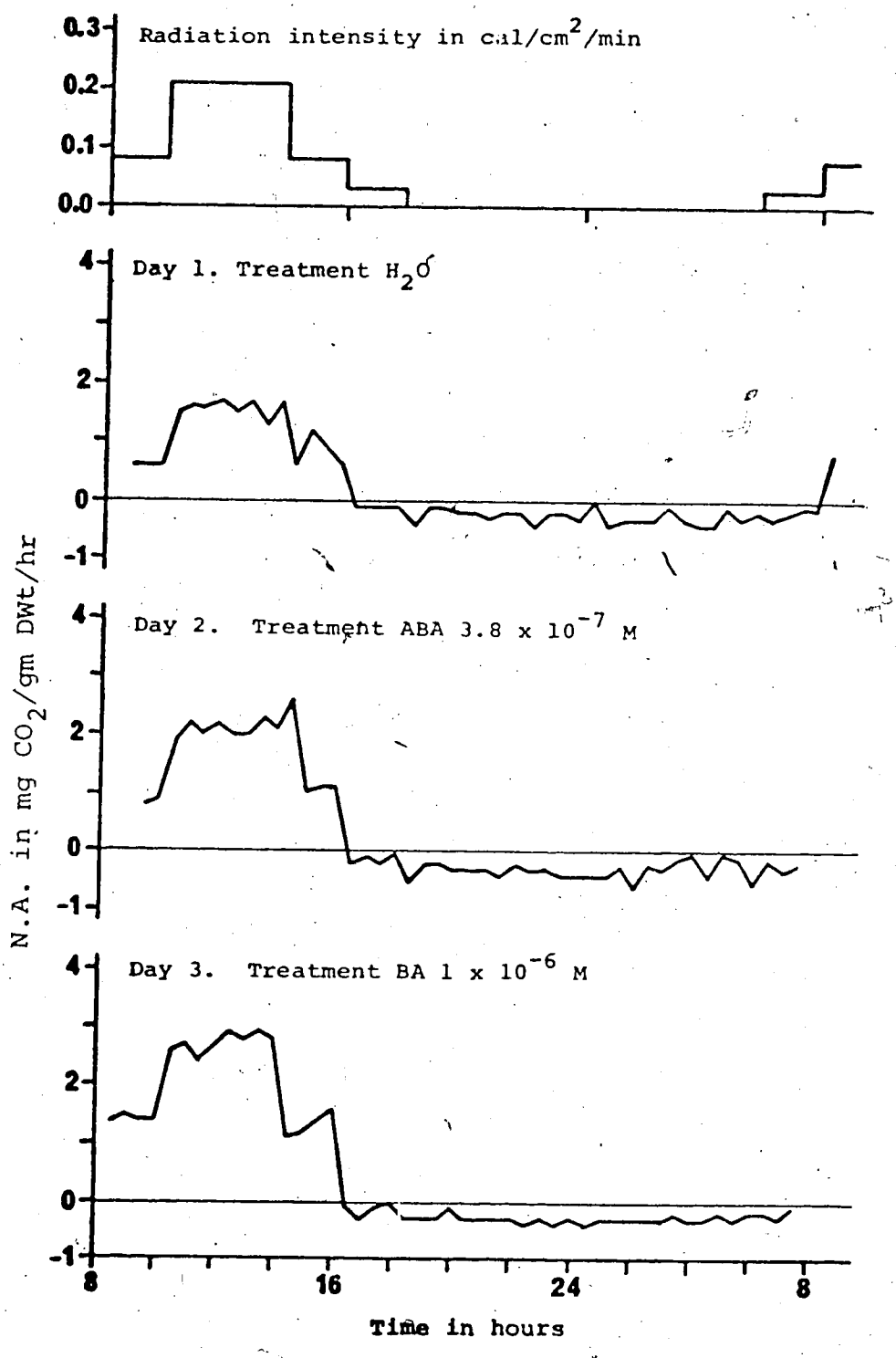


Figure 66. Net assimilation (N.A.) data for hormone treatments from day 4 to 6 at a constant temperature of 10 ± 1°C.

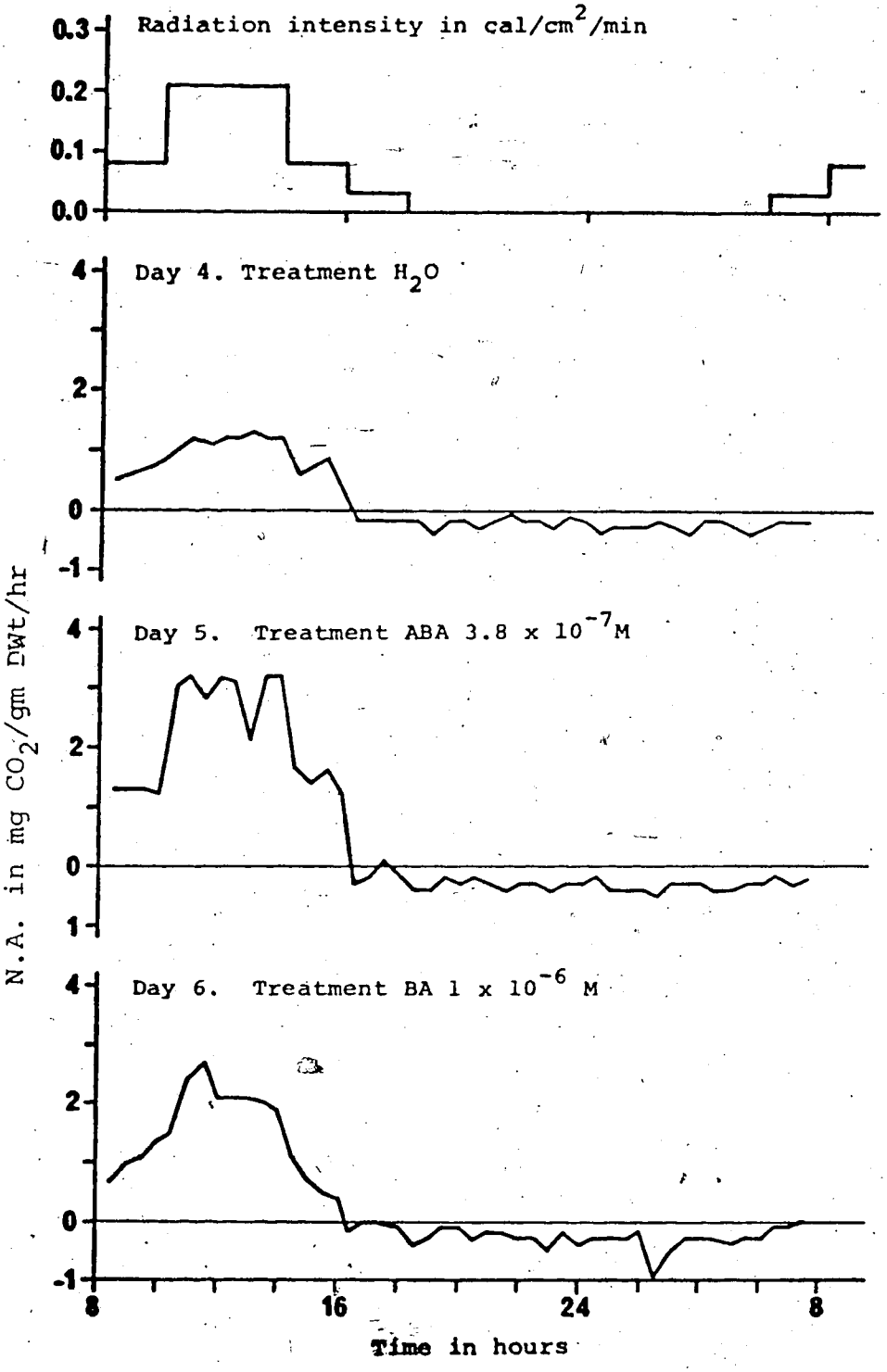


Figure 67. Net assimilation (N.A.) data for hormone treatments from day 7 to 9 at a constant temperature of 10 ± 1°C.

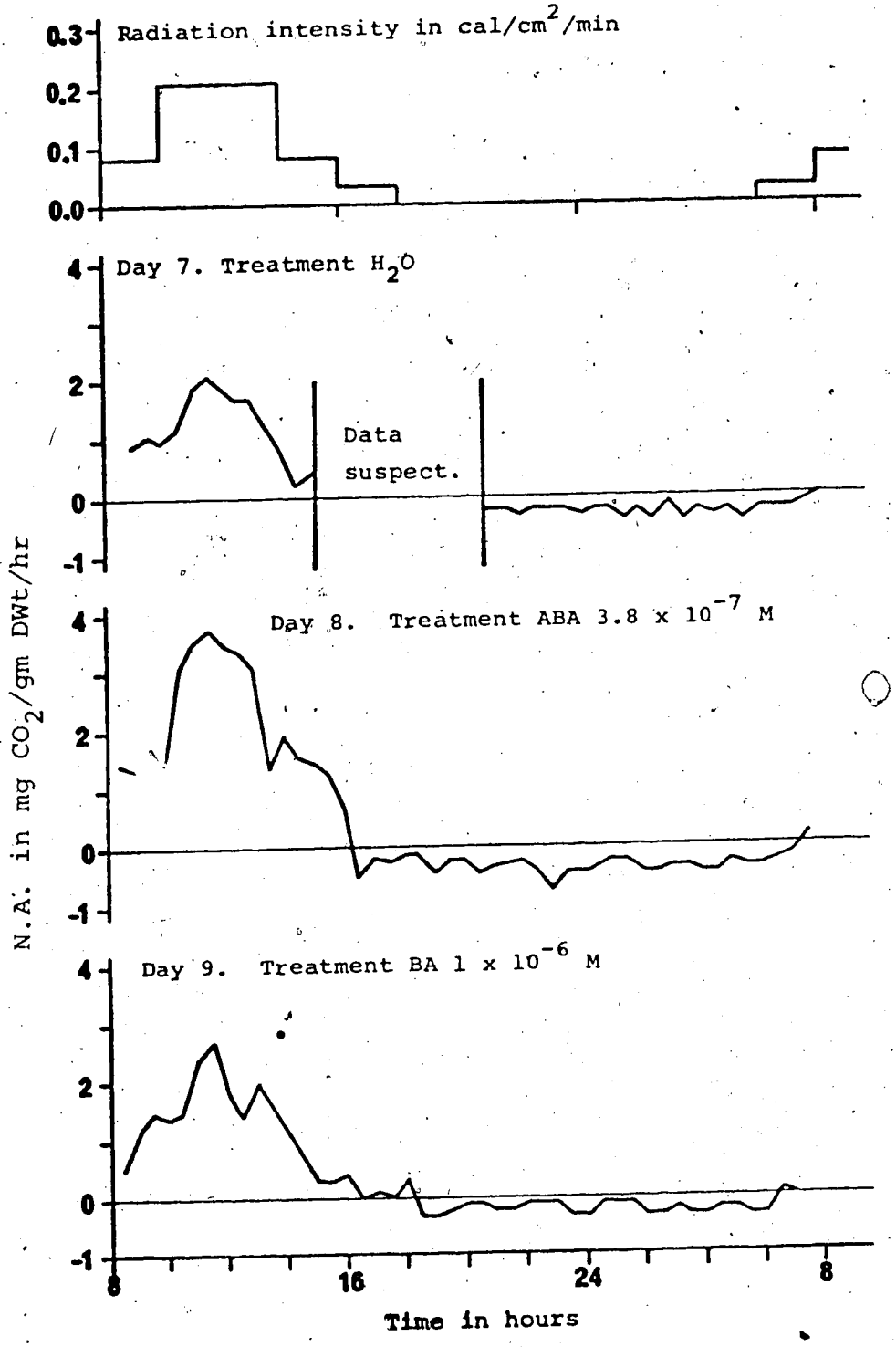


Figure 68. Net assimilation (N.A.) data for hormone treatments from day 10 to 12 at a constant temperature of 10 ± 1°C.

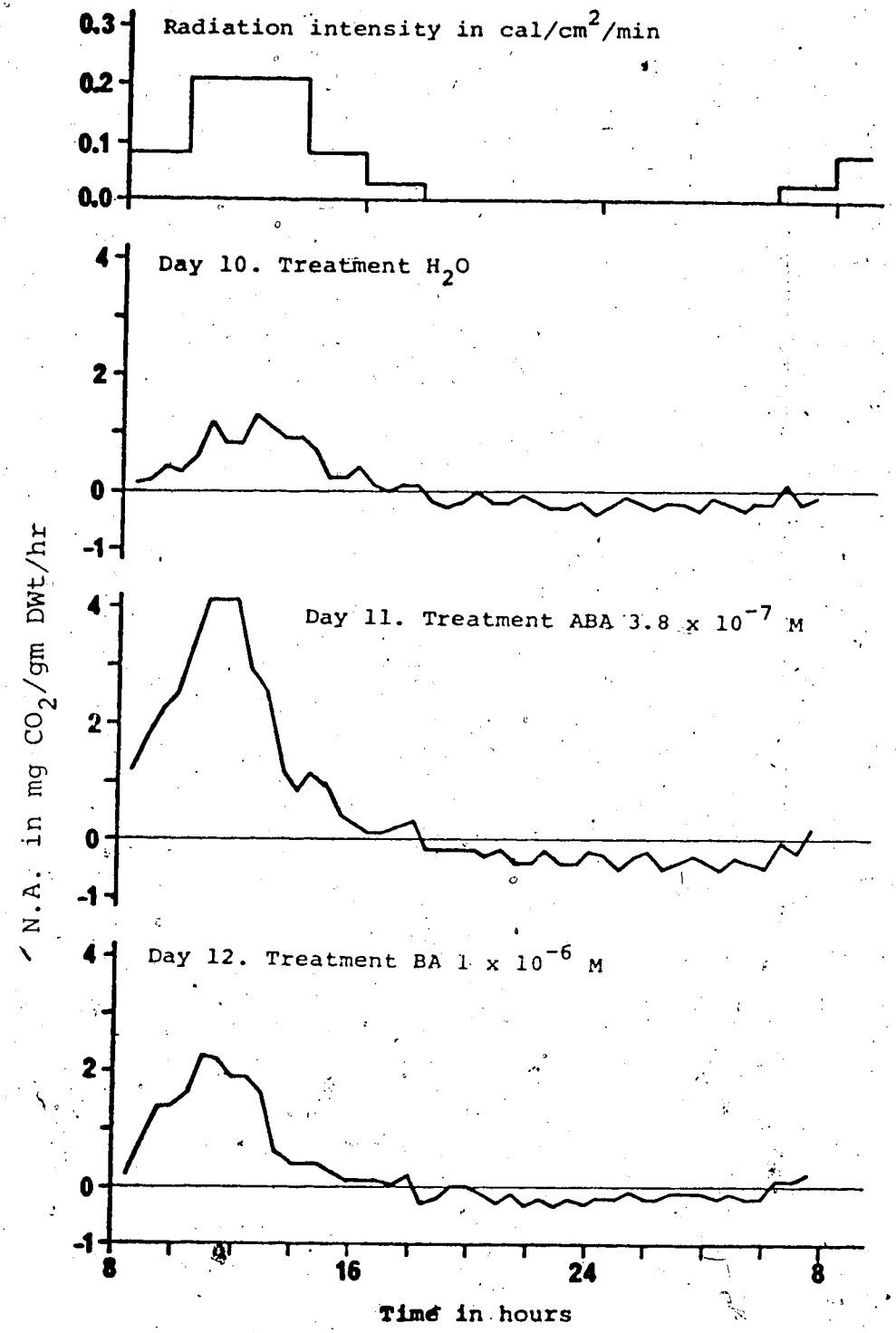
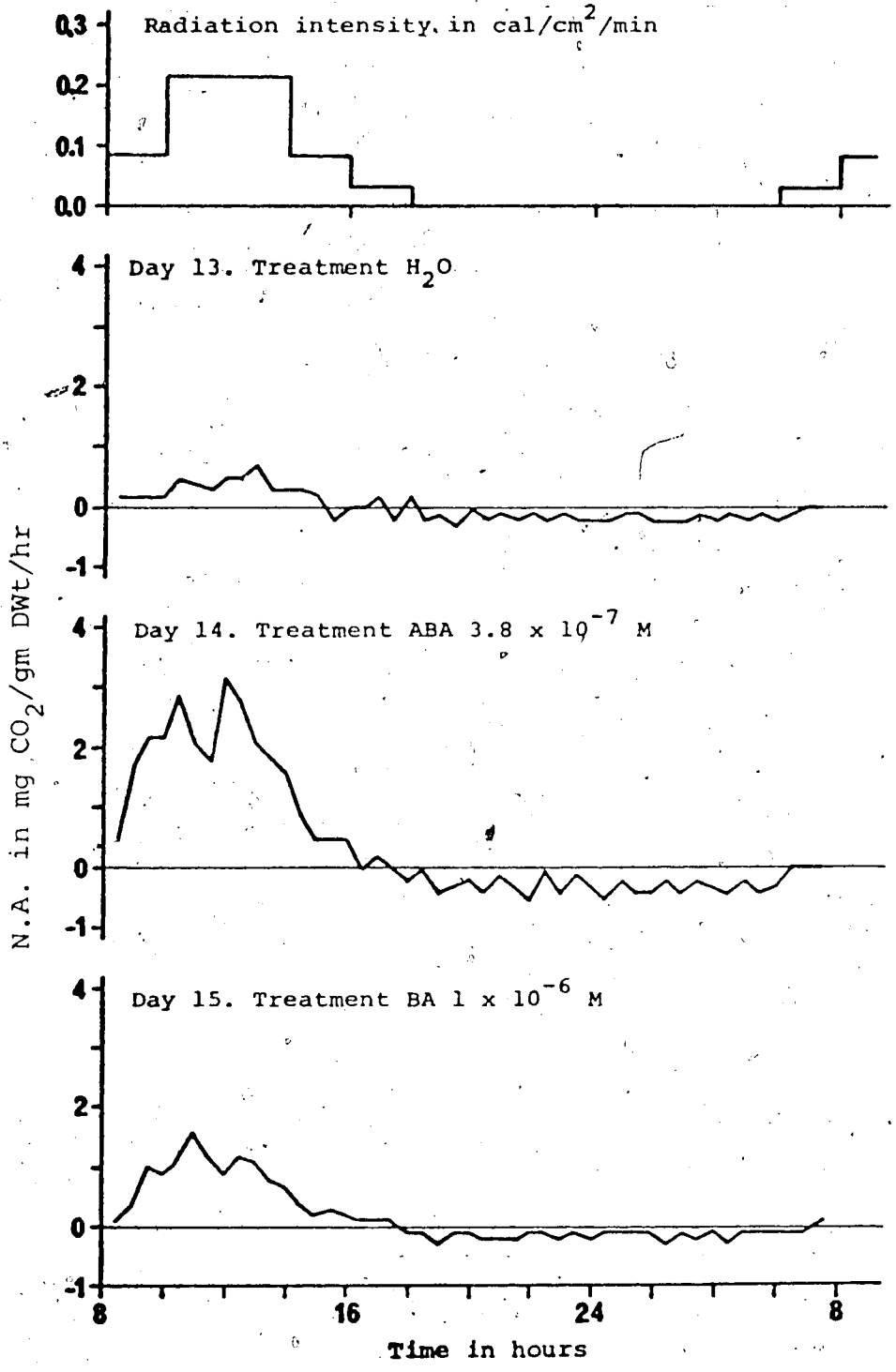


Figure 69. Net assimilation (N.A.) data for hormone treatments from day 13 to 15 at a constant temperature of 10 ± 1°C.



APPENDIX E

Growth Chamber Transpiration Data

Transpiration Measurement - Methods

A few transpiration measurements were made on small trees with a specially constructed transpiration balance. A general diagram of the system is given in Fig. 70. The balance used was an Ohaus model 1119 heavy duty type with a sensitivity of 1 gm and a maximum capacity of 20 kg. The plant with the soil in the pot covered by aluminum foil was placed on the pan. Two electrodes made of thick copper wire were connected to the arm of the balance. One electrode was longer than the other and was immersed in a mercury bath. The other was adjusted so that when the system was in balance it would be just above the surface of the mercury. The electrodes were connected to the gates of two S.C.R.'s that were capable of switching 110 V AC. As the tree transpired it would lose weight and the arm of the balance move down. The two electrodes made contact with the mercury. This caused the S.C.R. to turn on and a solenoid valve to open. When this happened water was slowly added to the pot by gravity feed until the balance was returned to the original position with one electrode just above the mercury. The solenoid valve was manufactured by Valcor Engineering (model 51C 19N34-6) and the tubing used was Intramedic polyethylene tubing (Clay Adams type 160 with an I.D. of 0.02 cm). Connections were made using size 18 g syringe needles.

The S.C.R.'s not only activated the solenoid valve but were also connected to a Hurst model SM 1 rpm motor. This motor was connected to the shaft of a 1K ten turn potentiometer with a flexible joint.

A Heath model EUA 20-27 Zener Reference supply was used to provide a constant voltage. This was connected to a 1 meg ohm resistor and the

1K ten-turn potentiometer in series as shown in Fig. 70. When the potentiometer was turned fully from one end to the other, an output of 0 to 9.6 mV was obtained. This output was connected to a 0 to 10 mV recorder making it possible for continuous recording of the transpiration rate.

The system was calibrated by flowing known volumes of water through it and observing the output difference for the different volumes. Calibrations gave 1.2 and 1.8 ml per recorder division depending on the recorder in use and the set-up of the system. Since average transpiration rates were 5 ml/hr and the chart paper could be read off in 1/4 divisions, i.e., 0.3 and 0.45 ml, respectively, it was considered accurate enough for this study. Throughout the transpiration experiments air, needle and soil temperatures were also recorded as described previously.

Transpiration Measurements - Results

Gindel (1973) reported that transpiration is too small to be measured during the physiological "resting phase" of trees even though wind and evaporation might be at a maximum. Coniferous trees in mesic climates transpire only 1/55 to 1/250 as much in winter as in summer, whereas *Picea excelsa, Picea obovata, Pinus sylvestris* and *Pinus cembra* have a rate equal to 1/300 of that of summer even though soil water is abundant (Gindel, p. 82). Christersson (1972) working with *Pinus silvestris* and *Picea excelsa* found the transpiration rate of frost-hardened seedlings to be half that of dehardened seedlings. The hardened plants exhibited a very slight reaction to light, indicating that the stomata did not respond greatly to light at that stage.

Transpiration balance experiments in the growth chamber on dormant black spruce trees showed a loss of less than 0.3 ml/24 hr. No real change could be measured with the balance. Most of this work was conducted on small trees collected at Inuvik, N.W.T. These trees were needed later for other experiments therefore the transpiration rates were not expressed on a gram dry weight basis. The data presented are not completely comparable since they were not obtained on the same tree.

Several experiments were conducted to investigate the influence of temperature on the transpiration rate of dormant trees. At 5°C needle temperature the transpiration rate varied between 0.0 and 0.45 ml/hr (Fig. 71). Needle infiltration pressures measured at 14.00 on November 30 indicated that the stomata were closed. The transpiration rate of the same tree at a needle temperature of 15°C also varied between 0.0 and 0.45 ml/hr (Fig. 71). Again needle infiltration pressures indicated that the stomata were closed. The stomata were, however, found to be partially open at a needle temperature of 28°C when a reading of 28 psi was obtained. Transpiration rates were, however, unaltered (Fig. 71). On the three occasions above, low transpiration rates were recorded during the dark period and generally higher rates during the light period. The overall conclusion that can be drawn from this is that while the trees are dormant the stomata are closed and any transpiration which takes place is cuticular.

The tree used in the above experiments was brought out of dormancy and its transpiration rate monitored during the bud swelling stage. Figure 72 gives the data obtained at that stage and shows slightly higher transpiration rates during full light than during the twilight period. A needle infiltration pressure of 23 psi indicated that the stomata were

open and giving rise to much higher transpiration rates (1.8 to 6.3 ml/hr). The temperature of the growth chamber was maintained at a constant 10 ± 1°C during this investigation.

A tree of similar dimensions was brought out of dormancy and its transpiration rate measured for an eight-hour period at 15°C and for 12 hours at 5°C. A two-hour change over occurred between the temperatures. The transpiration rates, depicted in Fig. 73, exhibited a distinct diurnal pattern. Little transpiration took place during the period of low temperature and low light intensity, but reasonable rates were recorded during the warm period with high light intensity. The maximum rate, however, may have occurred because a different tree with a different biomass was used in this experiment. On March 7, a distinct mid-day lag period, as has also been found in the field studies of net assimilation, was present.

A final experiment was conducted in which the influence of cold soil was investigated. One of the trees used in the preceding experiments was placed in a styrofoam container with an open bottom. It was then placed on a cold-plate and the soil temperature was gradually decreased to below freezing while above ground parts remained on the 5 - 15°C cycle. The result was an immediate cessation of transpiration. After a few days in this condition the tree gave the appearance of having gone into dormancy. Upon heating of the soil to ambient air temperature the tree resumed growth after bud break.

Figure 70. Diagram of the automatic transpiration measuring device.

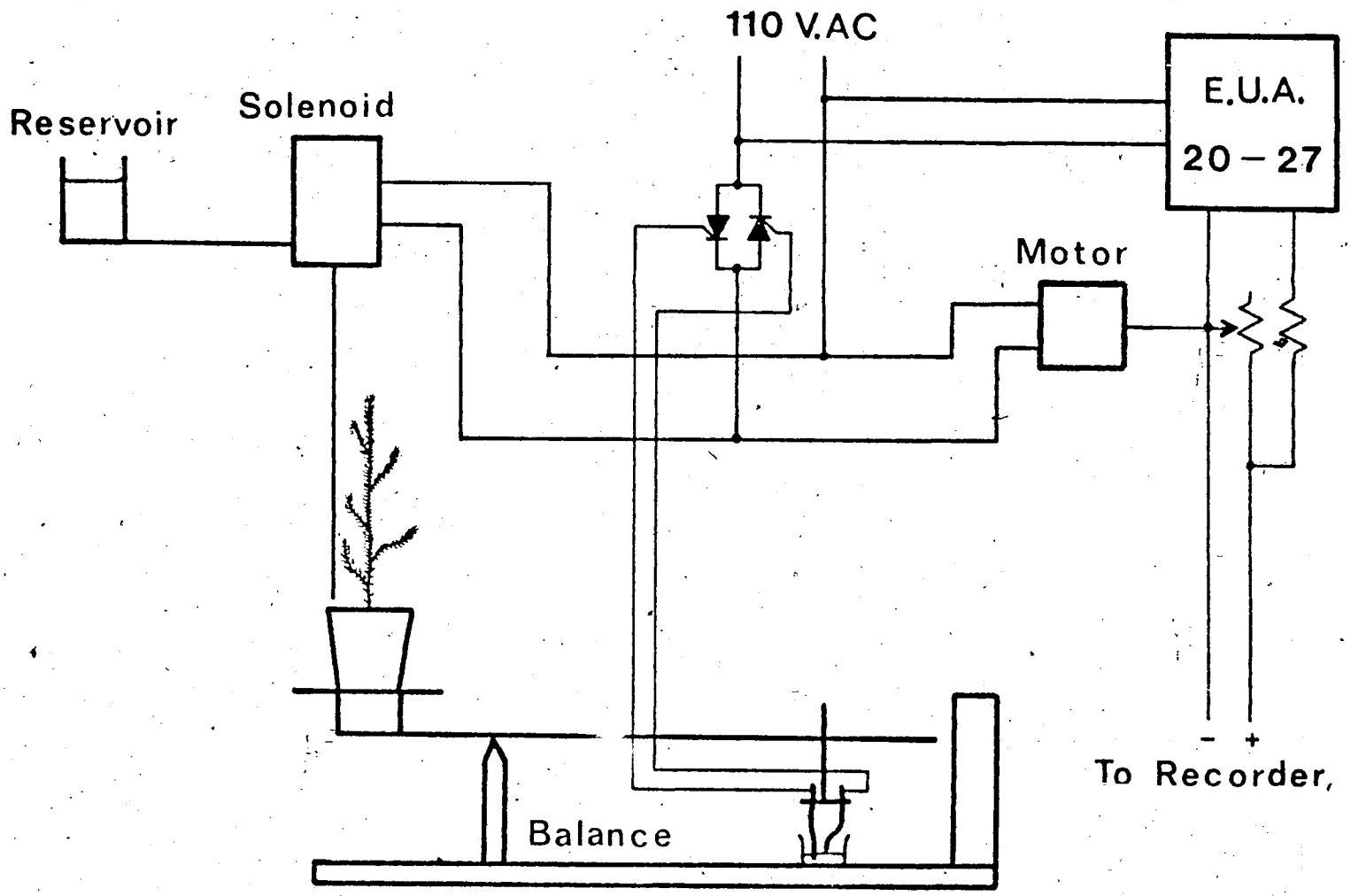


Figure 71 Transpiration (Tps.) rate of a dormant tree at various remperatures.

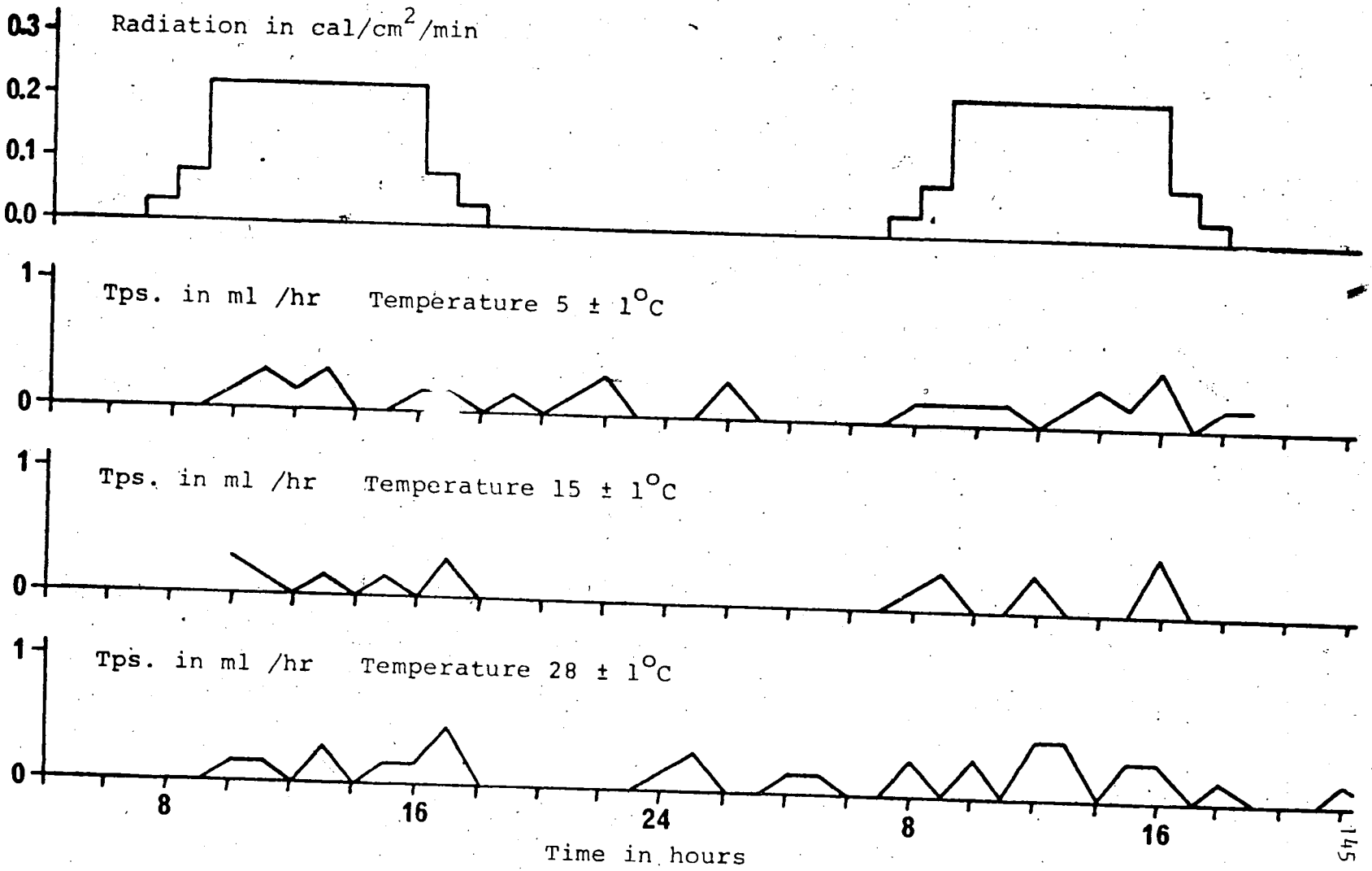


Figure 72. Transpiration (Tps.) rate of a non-dormant tree at 10 ± 1°C with varying radiation.

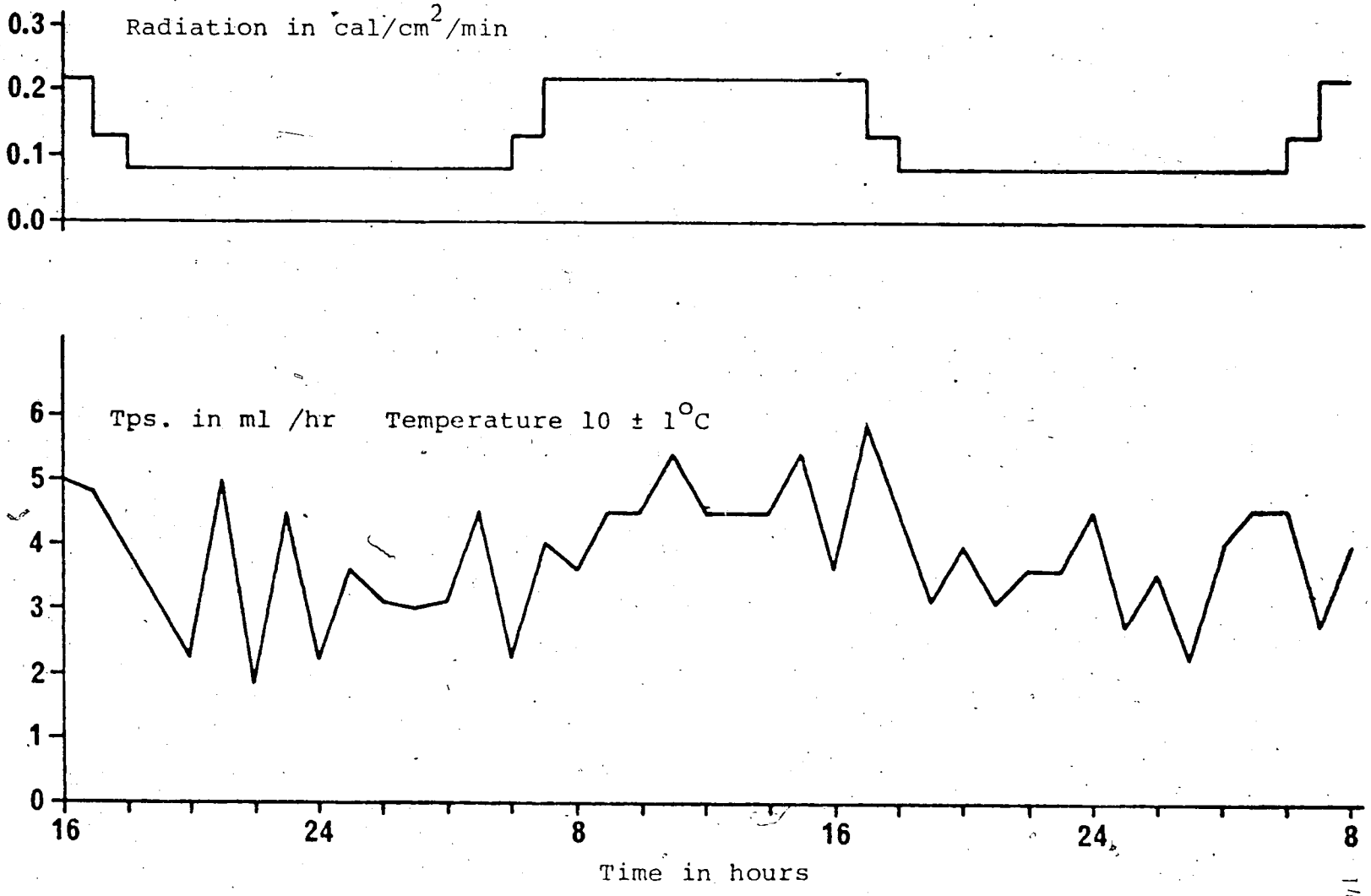
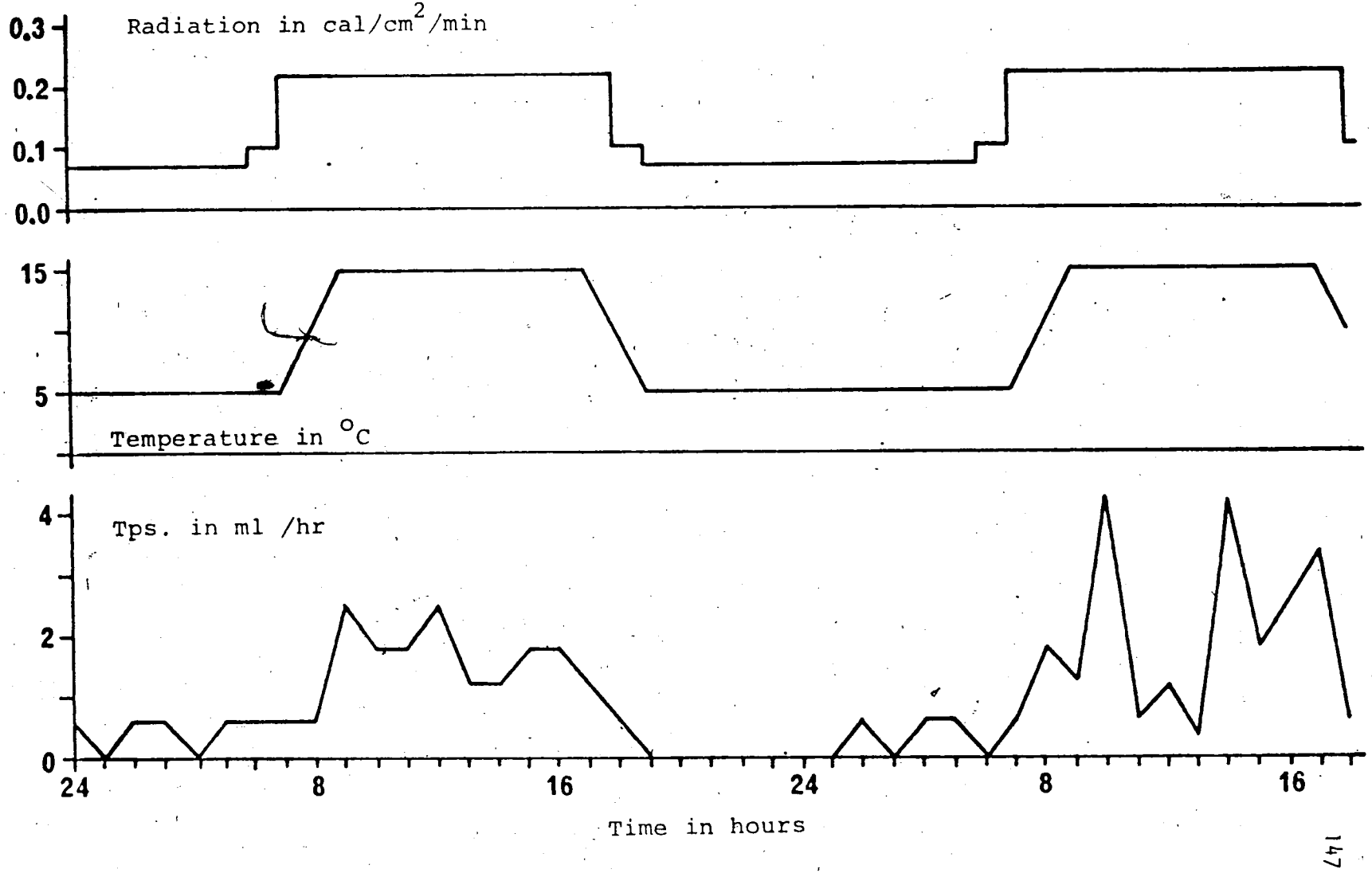


Figure 73. Transpiration (Tps.) rate of a non-dormant tree under ideal growing conditions.



APPENDIX F

ISCO Spectroradiometer data taken in the field during the investigation periods. All results given as μ W/cm^2/nm.

Legend for sky co[illegible]

clear - no clo[illegible]

clear S[illegible]t readings taken in the shade.

H. cloud - thin high altitude clouds present.

cloudy - clouds in sky, could lead to the results being taken in full sunlight and shade during the period of measurement.

overcast - no blue sky visible.

Photosynthetically active radiation (PAR) measured in μ E/m^2/sec.

Total radiation measured in cal/cm^2/min.

Radiant (luminous) flux measured in Lux.

6 & 7 May, 1973

Wavelength	Time	20.00 clear	08.00 clear	12.00 cloudy	16.00 cloudy
380		0.32	0.00	3.93	2.79
400		1.63	1.68	14.62	10.88
425		3.32	3.32	29.03	24.07
450		4.62	4.33	61.20	31.55
475		4.74	4.14	65.80	35.72
500		4.45	3.85	68.62	35.77
525		3.85	3.95	49.35	32.43
550		3.58	4.10	61.09	32.04
575		3.09	4.09	63.24	31.62
600		2.84	4.05	58.32	29.97
625		2.74	4.09	60.59	29.93
650		2.64	3.97	56.32	28.16
675		2.67	3.90	42.88	28.80
700		2.43	3.72	40.32	50.40
725		2.37	4.08	40.80	64.80
650		2.51	4.60	38.94	67.85
800		2.27	3.36	34.16	70.76
850		1.96	2.81	29.82	63.90
900		1.53	2.17	23.78	49.20
950		0.76	1.05	14.70	27.72
1000		0.93	1.25	17.94	27.30
1050		0.77	1.07	14.03	14.95
1100		0.50	0.72	10.43	7.48
1150		0.20	0.29	4.63	4.22
1200		0.26	0.30	5.12	3.63
1250		0.22	0.25	4.60	3.22
1300		0.16	0.19	3.30	2.43
1350		0.06	0.18	1.24	1.50
1400		0.02	0.01	0.35	0.38
1450		0.01	0.00	0.36	0.27
1500		0.03	0.01	0.80	0.73
1550		0.03	0.02	1.08	0.90
PAR		46.0	49.5	1200	1500
cal/cm^2/min		--	--	--	--
Lux		2260	2470	50000	70000

29 & 30 May, 1973

Wavelength \ Time	20.00 H. cloud	08.00 H. cloud	12.00 Overcast	16.00 clear	20.00 clear
380	0.41	0.75	3.93	9.25	0.32
400	1.42	2.75	10.03	25.67	1.66
425	2.87	5.27	20.24	53.48	3.21
450	4.08	7.48	28.56	81.60	4.08
475	3.95	7.33	30.08	90.24	3.93
500	3.72	7.15	30.66	93.44	3.43
525	3.31	6.48	28.76	90.24	2.82
550	3.13	6.41	29.06	93.13	2.47
575	2.88	6.19	28.37	93.00	2.12
600	2.63	5.83	26.32	89.10	1.82
625	2.52	5.69	25.55	88.33	1.64
650	2.43	5.25	23.68	83.20	1.44
675	2.40	5.18	23.04	83.20	1.34
700	2.21	4.73	20.99	74.34	1.19
725	2.22	4.71	20.10	66.00	1.23
750	2.42	5.43	22.13	67.85	1.44
800	2.56	10.07	21.35	71.98	1.34
850	2.20	8.52	19.17	63.19	1.14
900	1.80	7.01	14.51	50.02	0.89
950	1.01	3.28	7.69	25.20	0.45
1000	1.13	4.21	9.91	31.2	0.57
1050	0.92	3.57	8.54	26.84	0.48
1100	0.64	2.31	5.94	17.16	0.31
1150	0.29	0.87	2.64	7.55	0.15
1200	0.33	1.16	3.43	9.41	0.16
1250	0.28	1.04	3.11	8.05	0.13
1300	0.20	0.80	2.33	5.93	0.10
1350	0.07	0.23	0.86	1.87	0.05
1400	0.03	0.07	0.27	0.74	0.04
1450	0.02	0.05	0.20	0.51	0.02
1500	0.03	0.08	0.32	1.31	0.03
1550	0.04	0.15	0.39	1.76	0.03
PAR	50.0	200	470	1540	43.0
cal/cm^2/min	0.04	0.14	0.34	1.05	0.21
Lux	2630	10040	30500	80000	1900

27 & 28 June, 1973

Time	17.00	21.00	05.00	09.00	12.45	17.00
Wavelength	clear S	H. cloud	Overcast	clear S	cloudy	cloudy
380	0.73	0.30	0.00	0.52	10.00	2.00
400	3.06	1.05	0.07	2.64	25.50	5.51
425	5.50	2.14	0.17	4.55	80.22	10.89
450	7.40	3.26	0.26	6.09	130.56	15.78
475	6.71	3.50	0.27	5.45	142.88	16.92
500	5.87	3.42	0.25	4.82	146.00	16.79
525	5.15	3.05	0.20	4.23	135.36	15.79
550	4.99	2.89	0.16	3.99	134.10	16.09
575	4.37	2.60	0.13	3.44	134.85	16.74
600	3.66	2.41	0.12	2.89	127.17	15.71
625	3.21	2.37	0.12	2.61	105.85	15.26
650	2.72	2.32	0.15	2.21	108.80	14.08
675	2.43	2.38	0.17	2.04	105.60	13.76
700	2.46	2.21	0.17	2.03	100.80	12.47
725	3.54	2.19	0.17	2.94	99.60	12.24
750	5.10	2.45	0.19	4.51	106.20	14.75
800	5.55	2.35	0.18	4.54	91.50	12.69
850	4.83	2.04	0.15	3.92	79.52	10.65
900	3.90	1.69	0.12	3.26	53.30	9.27
950	1.97	0.80	0.05	1.34	25.20	4.03
1000	2.31	1.02	0.07	1.83	27.30	5.11
1050	1.95	0.89	0.07	1.57	28.67	4.45
1100	1.30	0.57	0.04	0.99	19.36	2.82
1150	0.47	0.22	0.01	0.29	7.03	1.04
1200	0.50	0.29	0.02	0.36	10.89	1.35
1250	0.44	0.25	0.02	0.36	10.12	1.27
1300	0.32	0.18	0.02	0.27	7.80	0.99
1350	0.08	0.07	0.01	0.07	2.52	0.34
1400	0.02	0.02	0.00	0.02	0.86	0.11
1450	0.01	0.01	0.00	0.01	0.60	0.08
1500	0.02	0.04	0.00	0.02	1.62	0.25
1550	0.03	0.04	0.01	0.04	2.30	0.39
PAR	74.2	29.0	4.95	66.0	1980	310
cal/cm^2/min	0.06	0.02	0.003	0.07	1.43	0.22
Lux	3550	1400	219	3600	10000	15600

21 & 22 July, 1973

Wavelength	Time	20.00 Overcast	08.00 Overcast	12.00 Overcast
380		0.43	0.25	
400		1.12	0.95	
425		2.33	2.10	
450		3.37	3.13	
475		3.48	3.27	N
500		3.36	3.30	O
525		3.10	3.07	
550		3.03	3.04	R
575		2.84	2.84	E
600		2.59	2.51	A
625		2.56	2.59	D
650		2.40	2.34	I
675		2.43	2.37	N
700		2.14	1.95	G
725		2.10	1.74	S
750		2.54	2.42	
800		2.44	2.20	D
850		2.13	1.81	U
900		1.72	1.43	E
950		0.71	0.30	
1000		1.14	0.75	T
1050		1.00	0.77	O
1100		0.62	0.44	
1150		0.17	0.06	R
1200		0.28	0.11	A
1250		0.28	0.12	I
1300		0.20	0.08	N
1350		0.05	0.01	
1400		0.02	0.01	
1450		0.01	0.00	
1500		0.01	0.00	
1550		0.02	0.00	
PAR		42.0	31.0	
cal/cm^2/min		0.04	0.02	
Lux		2240	1690	

18 & 19 August, 1973

Time	16.00	20.00	08.00	12.00	16.00
Wavelength	cloudy	cloudy	clear S	clear	cloudy
380	3.82	0.27	0.52	10.89	69.62
400	11.22	0.88	1.62	26.01	142.80
425	27.50	1.79	2.99	57.30	86.33
450	42.70	2.41	4.05	89.76	8.84
475	47.00	2.23	3.70	94.00	50.76
500	48.18	1.96	3.24	91.98	41.46
525	41.60	1.54	2.69	86.01	25.38
550	44.70	1.30	2.47	82.25	29.06
575	41.39	1.07	2.13	91.14	22.60
600	45.12	0.90	1.81	91.53	21.95
625	39.42	0.81	1.59	89.06	1.90
650	24.48	0.74	1.36	83.84	1.60
675	24.48	0.70	1.22	83.20	0.19
700	20.16	0.59	1.24	72.45	0.72
725	19.20	0.54	1.74	66.00	1.24
750	20.65	0.56	2.51	66.08	0.00
800	59.17	0.60	2.75	65.88	70.15
850	51.12	0.49	2.38	57.51	60.35
900	38.95	0.35	2.04	42.64	6.36
950	20.58	0.15	0.96	24.36	3.36
1000	24.18	0.20	1.21	26.52	3.90
1050	20.74	0.16	1.06	20.13	23.18
1100	13.20	0.09	0.69	13.11	6.16
1150	5.03	0.03	0.25	5.88	5.55
1200	6.24	0.03	0.28	6.63	6.93
1250	4.72	0.03	0.25	5.34	5.75
1300	2.85	0.02	0.18	3.90	4.95
1350	0.62	0.01	0.06	1.43	1.46
1400	0.19	0.01	0.01	0.67	0.17
1450	0.14	0.00	0.01	0.47	0.07
1500	0.33	0.00	0.01	0.99	0.15
1550	0.48	0.00	0.01	1.17	0.19
PAR	780	18.0	38.0	1340	1360
cal/cm^2/min	0.62	0.01	0.03	0.93	1.00
Lux	3200	900	1980	6500	14500

6 & 7 September, 1973

Wavelength	Time 14.00 cloudy	18.00 clear S	10.00 Overcast	15.00 Overcast
380		11.07		2.79
400	8.36	5.10		12.5
425	16.62	10.93		25.02
450	24.75	15.56		39.17
475	25.19	15.74		39.10
500	24.73	14.60		38.40
525	22.14	12.55	N	35.52
550	21.90	11.95	O	35.02
575	22.04	10.79		33.95
600	20.49	9.40		30.78
625	20.00	8.83	R	30.15
650	18.56	7.74	E	27.20
675	18.50	7.42		26.88
700	16.95	6.36	A	23.94
725	15.72	5.76	D	21.60
750	17.35	6.49	I	24.49
800	10.13	2.50	N	10.13
850	8.80	2.06	G	8.80
900	7.50	1.80	S	7.59
950	3.49	0.73		3.26
1000	4.95	1.05		5.05
1050	4.27	0.96		4.58
1100	2.79	0.60	D	2.88
1150	1.00	0.18	U	0.97
1200	1.40	0.29	E	1.50
1250	1.31	0.27		1.45
1300	0.98	0.20		1.12
1350	0.33	0.05	T	0.29
1400	0.08	0.02	O	0.09
1450	0.06	0.01		0.04
1500	0.14	0.03		0.12
1550	0.22	0.05	R	0.20
PAR	318.0	78.0	A	312.0
cal/cm^2/min	0.26	0.05	I	0.24
Lux	18700	4200	N	17600

2 & 3 October, 1973

Time	18.00	10.00	14.00
Wavelength	clear S	clear	clear S
380	0.17	0.79	5.96
400	1.32	4.15	18.84
425	1.58	4.41	75.11
450	2.82	8.46	127.84
475	2.82	8.69	138.00
500	2.42	8.11	116.60
525	2.08	7.63	113.36
550	1.80	7.37	108.81
575	1.46	6.72	91.80
600	1.30	6.30	49.28
625	1.14	5.71	45.60
650	1.03	5.22	36.40
675	0.94	5.11	30.60
700	0.80	4.75	29.00
725	0.76	4.80	25.48
750	0.77	4.84	24.96
800	0.68	5.21	15.68
850	0.53	4.52	10.32
900	0.39	3.92	5.92
950	0.20	2.28	3.73
1000	0.25	3.09	4.86
1050	0.23	3.05	4.58
1100	0.16	2.40	2.34
1150	0.06	1.10	1.05
1200	0.08	1.52	1.56
1250	0.08	1.50	1.20
1300	0.06	1.19	0.87
1350	0.02	0.41	0.34
1400	0.02	0.11	0.06
1450	0.00	0.10	0.07
1500	0.01	0.19	0.14
1550	0.01	0.26	0.20
PAR	23.5	92.5	130.0
cal/cm^2/min	0.01	0.07	0.10
Lux	1230	5200	6600

17 & 18 October, 1973

Time	18.00	10.00	14,30
Wavelength	Overcast	clear S	clear S
380	0.08	0.63	0.63
400	0.53	2.32	3.14
425	0.65	2.42	3.25
450	1.18	4.06	5.32
475	1.20	3.96	4.83
500	1.01	3.18	3.98
525	0.81	2.73	3.38
550	0.78	2.49	3.04
575	0.65	2.07	2.52
600	0.60	1.79	2.14
625	0.57	1.55	1.80
650	0.59	1.37	1.51
675	0.61	1.21	1.33
700	0.58	1.20	1.30
725	0.56	1.59	1.76
750	0.59	2.06	2.35
800	0.47	2.09	2.31
850	0.43	1.88	2.06
900	0.36	1.58	1.69
950	0.20	0.87	1.00
1000	0.28	1.15	1.28
1050	0.27	1.19	1.28
1100	0.22	0.94	1.02
1150	0.10	0.35	4.36
1200	0.15	0.48	0.54
1250	0.14	0.47	0.54
1300	0.12	0.38	0.44
1350	0.04	0.14	0.16
1400	0.01	0.00	0.03
1450	0.01	0.00	0.01
1500	0.02	0.00	0.03
1550	0.04	0.04	0.05
PAR	7.0	34.5	22.0
cal/cm^2/min	0.01	0.03	0.03
Lux	4.5	1830	2250

18 & 19 April, 1974

Time	17.00	09.00	13.00	17.00
Wavelength	Overcast	Overcast	Cloudy	clear S
380	2.21	1.19	3.98	1.11
400	7.31	4.08	14.62	5.24
425	14.41	7.74	26.80	8.78
450	17.67	9.02	27.26	10.15
475	18.91	9.73	31.74	9.94
500	18.90	9.72	32.40	9.02
525	20.90	9.08	33.00	8.03
550	21.18	8.83	23.40	7.49
575	14.13	0.09	18.46	6.67
600	13.57	7.55	19.20	6.02
625	13.57	7.54	20.30	5.51
650	13.01	7.34	19.98	5.24
675	12.79	7.12	16.12	4.78
700	12.24	6.12	15.30	4.08
725	11.81	5.54	15.68	3.92
750	12.25	6.13	16.66	3.97
800	13.91	5.47	13.68	2.85
850	13.10	4.52	11.79	2.62
900	12.32	3.70	11.55	2.16
950	5.64	1.48	5.64	1.21
1000	7.29	2.03	6.48	1.46
1050	6.91	1.81	5.90	1.44
1100	5.34	1.51	4.18	1.10
1150	2.73	0.46	2.06	0.47
1200	3.35	0.50	2.80	0.62
1250	3.08	0.27	2.66	0.61
1300	2.39	0.19	2.15	0.48
1350	1.01	0.07	0.53	0.18
1400	0.26	0.05	0.21	0.05
1450	0.16	0.00	0.19	0.05
1500	0.19	0.00	0.42	0.13
1550	0.24	0.00	0.40	0.20
PAR	242	99.0	300	91.0
cal/cm^2/min	0.20	0.07	0.19	0.06
Lux	10230	4900	15000	4500