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WINTER PLANT - WATER RELATIONS
WITH SPECIAL REFERENCE TO ALPINE
TREELINE

PETER J. MARCHAND

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WINTER PLANT-WATER RELATIONS WITH SPECIAL REFERENCE
TO ALPINE TREELINE

by

PETER J. MARCHAND

M.S., University of New Hampshire, 1972

A THESIS

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ABSTRACT

WINTER PLANT-WATER RELATIONS WITH SPECIAL REFERENCE
TO ALPINE TREELINE

by

PETER J. MARCHAND

The purpose of this study was to examine the interactions of environmental and biotic factors, especially the role of leaf resistances, affecting the rate of water loss from conifers during the winter. Results are related to the influence of winter conditions on the success of the dominant tree species in the subalpine zone of the White Mountains in New Hampshire.

Transpiration rates from excised branches of black spruce were measured, using potometers, under low temperature, controlled environment conditions. Leaf resistance to transpiration in dormant branches was sensitive to changes in light intensity at temperatures above 5° C. Diffusive resistance decreased from approximately 300 sec cm⁻¹ in the dark to 120 sec cm⁻¹ at a radiation intensity of 1.1 ly min⁻¹. At temperatures below 2° C, however, response of leaf resistance to changing light intensity was inhibited.

Maximum transpiration rates were observed when the leaf tissue was heated above 5° C in nearly still air. Transpiration was reduced by approximately 50% when wind

speed was increased to 200 cm sec^{-1} . Increasing wind speed to 700 cm sec^{-1} caused no further decrease in transpiration rate. These results are explained in terms of reduced leaf-air temperature differences at low wind speeds and consequent reduction in the vapor concentration gradient between the leaf and bulk air.

Field studies throughout two winter seasons showed no significant decline in relative water content of leaf tissue exposed above the snowpack near treeline on Mt. Washington. Fluctuations in relative water content of balsam fir at a low elevation site, 160 kilometers south of Mt. Washington, roughly paralleled those observed during the winter at the Mt. Washington site. It is concluded that winter desiccation cannot be considered a primary cause of the low treeline on Mt. Washington, and that continual exposure to high winds during the winter affects the tree adversely only in relation to its susceptibility to sustaining physical damage.

INTRODUCTION

Treeline - Definitions and Ecological Significance

Treeline may be variously defined as (1) the limit of the forest itself, in the physiognomic sense, regardless of its reproductive capacity, (2) the limit of arborescent trees regardless of their spacing, or (3) the limit of a tree species regardless of its growth form. Hustich (1966) refers to each of these, in order, as the physiognomic forest-line, tree-line, and species line. Young (1971) defines the northern or arctic treeline as the poleward limit of arborescent conifers, this further restriction indicating an important floristic as well as vegetational boundary.

Each of these definitions is somewhat problematical however. The forest at its poleward or altitudinal limit may vary in species composition as well as in morphological character. Trees which may develop normally at their furthest outpost may become so widely spaced as to lose any connection with the physiognomic "forest". They may take on growth forms scarcely fitting any reasonable definition of "tree", and may even become reproductively isolated from the "species" through infrequent cone production (see for example, Griggs, 1946; Clausen, 1965; Teeri, 1968; Holtmeier, 1973; Plesnik, 1973a, 1973b).

In an ecological context, a good working definition of treeline is one which denotes a significant change in vertical structure of the plant community as the closed

canopy of the forest gives way to the "open" tundra vegetation. Treeline in this sense is seldom a clear physiognomic boundary. It is instead a mosaic of "trees" and tree-less patches of herb-shrub vegetation best described as an ecotone, a complex of vegetational and microclimatic gradients of varying abruptness, a transition zone encompassing all of the above definitions of treeline.

It is primarily with the change in canopy structure at the forest limit that treeline assumes ecological significance, for it is this change which is most important to organisms which have adapted to the modifications of habitat imposed by the forest dominants. Within and beneath the forest canopy the physical environment is as much influenced by the presence of the dominants as by the local macroclimate itself. Light is greatly attenuated as it filters to the lower strata (Kinerson, 1973). Reduced insolation, coupled with long wave radiative exchanges between the ground and canopy, influences both diurnal and nocturnal temperatures in the lower strata (Reifsnyder and Lull, 1965). Wind is greatly reduced in the canopy and therefore has little effect on heat and gas exchange processes in the understory (Kinerson, 1971). Precipitation is intercepted and redistributed, the effects of which may be particularly important with regard to snowcover and its influence on soil temperatures, soil- and plant-water balance, and length of growing season.

Beyond the forest limits, in the arctic and alpine tundras, there is little but local relief to modify the

climate. Wind becomes a particularly important factor in terms of its role in heat dissipation and gas exchange, mechanical injury, and snow removal. In the absence of an overhead canopy, nocturnal long-wave radiative loss to the atmosphere (clear sky) is unimpeded. Life in the alpine tundra in particular is therefore subject to more pronounced fluctuations in temperature as well as light, variability itself becoming an important environmental factor (Billings et al., 1971).

Causes of Treeline

It is not likely that the phenomenon of treeline will ever be explained in terms of a single, universally operating factor. There are several possible causes, each of which may vary in importance from one area to another. Out of the vast body of literature on the subject, however, there emerge two hypotheses for the cause of treeline which have gained considerable favor.

Foremost of these is the idea that forest advance is limited, in one developmental stage or another, by critically low summer temperatures. While a universal, temperature-related physiological control is not yet evident, highly significant correlations between growth season temperatures and radial growth, shoot and needle elongation, and cone yield have been demonstrated in conifers at northern treeline in Scandinavia (Hustich, 1948; Mikola, 1962; Eklund, 1957). Correlations between the position of northern treeline and the 10° C mean July isotherm are well known, though troubled by considerable deviation in some areas

(see for example, Hustich, 1966; Young, 1971). In North America there appears also, a close correspondence between northern treeline and the mean summer position of the Polar front (Bryson, 1966).

The above relationships have not been established for alpine treelines however. There may be significant differences in the assimilation/respiration balance between trees at high latitudes and their counterparts in high mountains further south (Holtmeier, 1973). Wardle (1971) nonetheless has demonstrated seedling mortality above alpine treeline in New Zealand due to failure of the plant to mature and harden properly in a short, cold growing season, thus rendering it susceptible to winter damage. Failure of plants at treeline to harden sufficiently is also considered important by LaMarche and Mooney (1972), who suggest, however, that late summer precipitation may be as important as the length of growing season, since drought may induce early hardening.

A second frequently encountered hypothesis, particularly with reference to alpine treeline, is that tree-line position is significantly influenced by adverse plant water balance during the winter. Very low plant-water potentials have been observed in winter by Lindsay (1971), Hansen and Klikoff (1972), and Tranquillini (1963), and this is believed to influence treeline position primarily through desiccation and death of tissue exposed above the snowpack (Klikoff, 1965; Wardle, 1968; Sakai, 1970; Tiffney, 1972). Lowering of plant-water potential in winter is usually

attributed to a combination of factors including a cold or frozen substrate, low atmospheric humidity, and persistent high winter winds. It is generally assumed in this regard, that (1) plant stomates, in the case of evergreens, remain closed throughout the winter but cuticular transpiration is significant and enhanced by exposure of plants to high radiation loads and high wind speeds, and (2) that absorption or replacement of water lost is greatly restricted.

In the final analysis, both low summer temperatures and damaging winter desiccation may be important in controlling alpine treeline. Growth during favorable periods and survival during unfavorable periods are singularly important. It is with the desiccation hypothesis, however, that this paper is concerned.

Winter Plant-Water Relations in Review

Plants have been reported to occur in snowless locations in which, for a period of five months, they were unable to absorb water from the frozen substrate while they continually lost water from exposed tissue (Tranquillini, 1963). Hygen (1963) has calculated that under conditions of no replenishment, the total water loss from Norway spruce during the winter would amount to nearly ten times the sublethal water deficit, the critical amount of water needed for survival. Since in both cases plants survive such conditions, however, one has to suspect that either the amount of water loss is overestimated, the plant finds some way to meet the water loss, or the degree to which such water loss stresses the plant in winter is overestimated.

There is, in fact, little quantitative evidence that lethal winter desiccation is of widespread occurrence at treeline and even less experimental evidence as to what factor or combination of factors most influence the winter plant-water balance. In a study of the development of Picea engelmannii krummholz in Colorado, Wardle (1968) reported what he considered to be only a normal winter decrease in water content, on the order of 20% (dry weight basis) in needles on the leeward sides of shoots. He found much greater reductions in the water content of needles on the windward sides, however, and concluded that "dry winter winds were the immediate, though probably not the ultimate, cause of the krummholz growth forms in the forest-tundra ecotone."

Tranquillini (1963) reported that seedlings of Pinus cembra wintering in snowless locations above treeline, had osmotic values approaching -42 atm. with the water content of needles lowering to 52% to 78% of their dry weight, half their autumn water content. He cites as the primary cause though, the heating of branches under high radiation loads rather than exposure to high winds. He notes too, that the critical level of water deficit for this species is depressed during the winter and that sub-lethal water contents are seldom reached. Increased tolerance to dehydration during the winter has been reported for other species as well (Larcher, 1972; Khlebnikova et al., 1963), indicating that some caution is necessary in interpreting the physiological significance of low winter plant-water potentials.

In a detailed study of seasonal changes in the water status of flagged Picea engelmannii and Abies lasiocarpa at treeline in the Medicine Bow Mountains of Wyoming, Lindsay (1971) reported a decline in leaf water potential from a summer maximum of -15 bars to a winter minimum of approximately -33 bars. He concluded that constant exposure to high winds was instrumental in causing severe water stress during the winter. Lindsay's data show however, that the greatest decline in leaf water potential at treeline occurred in early autumn, perhaps the result of low soil-water supply. From the end of October through the remainder of the winter period, the leaf water potential of exposed Picea engelmannii remained essentially unchanged, fluctuating about a value of -29 bars except for a single dip to approximately -33 bars in mid-January. Similarly, the water potential of Abies lasiocarpa had already dropped to -30 bars by the end of October and further declined only 4 bars through the winter. Thus it is not entirely clear that the conditions which prevailed at treeline throughout the winter in his study area were any more significant, in terms of the water balance of exposed plants, than those conditions which caused the sharp decline in leaf water potential during the autumn.

The Transpiration Process

In view of the general confusion as to which factors most affect the winter plant-water balance, a review of the biophysical process of transpiration is in order.

Transpiration from a leaf surface may be described

by the equation $T = \frac{c_l - c_a}{r_l + r_a}$ where T is the transpiration rate, $c_l - c_a$ is the water vapor concentration difference between the intercellular spaces of the leaf and the bulk air outside the leaf boundary layer, and r_l and r_a are respectively the leaf and boundary layer resistances to gaseous transfer (see Gates, 1965, or Ehrlner and van Bavel, 1968). The driving force for transpiration is then, $c_l - c_a$, a gradient strongly influenced by the temperature difference between the leaf and air. Since the saturation vapor concentration of the leaf interstices will be a function of leaf temperature, the greater the elevation of leaf temperature above air temperature, the greater the vapor concentration gradient between the leaf and air.

Leaf resistances to the diffusion of water vapor are provided by the stomates and cuticle, the relative magnitude of these being somewhat species dependent. The minimum stomatal resistance of the alpine species Ledum groenlandicum is, for example, less than 2 sec cm^{-1} , as determined for plants growing in both a northern bog (Small, 1972) and above timberline on Mt. Washington, New Hampshire (Marchand, unpublished data). The stomatal resistance of conifers may be somewhat higher, perhaps near 20 sec cm^{-1} (Waggoner and Turner, 1971). In contrast, cuticular resistance is usually several times greater in magnitude, having been reported (Holmgren et al., 1965) as high as 460 sec cm^{-1} for the European species Quercus robur. In addition, cuticular resistance has been found to increase sharply with decreasing temperature (Holmgren et al., 1965).

Boundary layer resistance is provided by a transfer zone of air in contact with (and influenced by) the leaf. The thinner this surrounding layer, the more rapid will be the heat convection of vapor transfer through this zone, since heat and vapor concentration gradients between the leaf and bulk air will be steeper. Single leaf boundary layer resistances have been found to be generally less than 0.9 sec cm^{-1} for several deciduous woodland species (Holmgren et al., 1965), although this will vary directly with leaf size and shape and inversely with windspeed (Gates, 1965).

It is through reduction of boundary layer resistance that the influence of wind currents is important. The effect of wind is two-fold; (1) it facilitates removal of moist air from the leaf surface, thereby increasing the rate of transpiration, and (2) it increases the rate of heat transfer from the leaf, through forced convection, thus tending to maintain temperature equilibrium between the leaf and air. In the latter case, $c_l - c_a$ is reduced and consequently transpiration is decreased. The relative importance of these two processes will depend on other microenvironmental factors as well as on the physiological behavior of the plant.

During the summer growth period, the most significant leaf resistance to loss of water (under non-stress conditions) is that of the open stomates. Cuticular transpiration is negligible as long as the stomates remain open. At this time of year then, the boundary layer resistance is closer in magnitude to the leaf resistance and any reduction of r_a by turbulent exchange becomes significant

in terms of increasing transpiration.

In the wintertime, the relative importance of the diffusive resistances is changed significantly. Stomatal opening has not been reported to occur during the winter (Tranquillini, 1961; Schulze et al., 1967), as apparently it is prevented by low temperatures (Stalfelt, 1962). As a result, vapor diffusion is largely via cuticular pathways and the leaf resistance may thus be expected to increase several-fold. When the leaf resistance is very high, say on the order of 200 sec cm^{-1} , any reduction of the boundary layer resistance, which in the case of conifers may be much less than 1.0 sec cm^{-1} , by high winds would seem unimportant in terms of increasing vapor transfer. The dominant effect of wind in the wintertime may therefore be related to the consequences of forced convection which are (1) maintenance of leaf temperatures below the freezing point of cell water when air temperatures are very low, and (2) reduction of temperature differences between the leaf and air with consequent reduction of $c_l - c_a$. In both cases, the net effect of wind would be to reduce, rather than increase water loss.

From the foregoing analysis it is evident that the effects of atmospheric factors on the water-balance of winter-exposed plants is in need of experimental review, as the conclusions reached above are not in harmony with widely-held beliefs. The relationships between wind, radiation load, and the leaf resistances to transpiration have not been systematically investigated at low temperatures

under controlled conditions, though it is clearly important that they be understood before any inferences are made with respect to the occurrence of winter desiccation in the alpine and subalpine zones. This study therefore focuses on the interaction of environmental and biotic factors, especially the role of leaf resistances, affecting the rate of water loss from conifers during the winter. Particular reference is made to the influence of winter conditions on the success of the dominant tree species in the subalpine zone of the Presidential Range in the White Mountains of New Hampshire.

METHODS

Field Studies - Winter

For purposes of assessing the extent of, and circumstances accompanying water loss from winter-exposed trees at treeline, a semi-permanent sampling station was maintained at an elevation of 1372 m on the Chandler Ridge of Mount Washington, N.H. (Fig. 1). This ridge lies to the northeast of the summit of Mt. Washington (elevation 1917.8 m) with its axis running approximately north-south, normal to the direction of prevailing winds. The subalpine zone of matted "krummholz" trees extends in this area from about 1220 m to 1400 m, placing it among the lowest treelines in the Presidential Range, a fact which suggests particularly severe environmental conditions.

The station was equipped with recording soil and air thermographs, fitted with eight-day spring-driven charts. However, the instruments were subject to occasional failure at extremely low winter temperatures and the shelters occasionally packed with wind-blown snow. Therefore, the record served mainly to improve extrapolation of weather records from the continuously maintained Mt. Washington Observatory located on the summit. These records are summarized for the study period in Table 1. For a low elevation "control", a similarly equipped station was maintained during the second winter of the study at a Christmas tree plantation in Marlbury, N.H. (elevation ca. 100 m).

Winter transpiration losses at both field sites

Figure 1. Chandler Ridge field site, Mount Washington, N.H.

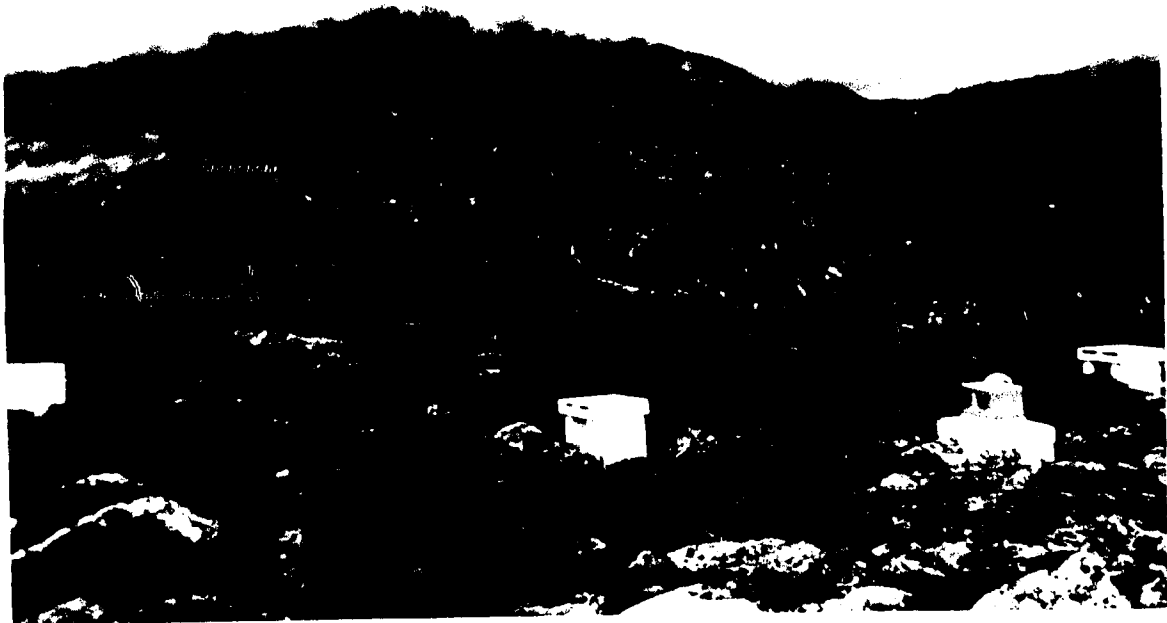


Table 1. Summary of weather observations on Mt. Washington throughout the study period. Data, except for soil temperatures, are taken from the records of the Mt. Washington Observatory. Records obtained at the study site indicate that air temperatures (ground level) average approximately 4° C warmer than the summit observations.

<u>1972-73</u>		Ave. Daily Max. (C)	No. Days Max 0° C	Ave. Daily Min. (C)	No. Days Soil 0° C	Precip. as Snow or Ice (cm)	Total Precip.- Water Equiv.(cm)	Ave. Hourly Wind (m sec ⁻¹)	Ave. Hourly Wind (mph)	% of Possible Sunshine
Oct	+0.5	16	-6.9	-	31.7	21.28	12.96	29.0	39	
Nov	-3.9	6	-11.1	30*	204.9	38.81	14.66	32.8	33	
Dec	-6.9	3	-16.7	7	232.7	40.79	19.62	43.9	17	
Jan	-9.6	5	-19.3	6	179.1	28.96	23.91	53.5	34	
Feb	-10.9	2	-18.8	1	89.4	14.53	17.21	38.5	41	
Mar	-1.7	10	-8.8	15*	117.1	22.89	14.08	31.5	40	
Apr	-1.3	13	-8.2	-	182.6	33.85	17.97	40.2	35	
May	+3.2	24	-2.0	-	64.3	29.44	10.77	24.1	19	

<u>1973-74</u>		Ave. Daily Max. (C)	No. Days Max 0° C	Ave. Daily Min. (C)	No. Days Soil 0° C	Precip. as Snow or Ice (cm)	Total Precip.- Water Equiv.(cm)	Ave. Hourly Wind (m sec ⁻¹)	Ave. Hourly Wind (mph)	% of Possible Sunshine
Oct	+3.4	23	-2.8	-	26.6	19.58	12.69	28.4	48	
Nov	-4.7	7	-11.2	9*	117.6	30.15	20.96	46.9	21	
Dec	-3.6	8	-13.4	0	140.7	45.59	16.85	37.7	31	
Jan	-9.6	1	-18.7	0	125.7	20.98	22.44	50.2	16	
Feb	-11.3	1	-21.1	-	136.4	23.95			45	
Mar	-8.1	3	-18.1	-	196.34	40.54			26	
Apr	-0.6	14	-8.5	-	162.6	37.08			29	
May	2.1	18	-4.9	-	26.9	19.30	14.34	32.1	23	

! Early snow cover
 * Data missing some days

were related qualitatively to fluctuations in tissue relative water content (RWC). It was assumed that conditions resulting in high transpiration rates and/or reduced absorption would be accompanied by decreasing water contents, while conditions favoring reduced transpiration and/or improved absorption would be reflected in increasing water contents. For relative water content determinations, branch tips exposed above the snowpack were collected, usually in a frozen state, and sealed immediately in plastic bags. These were kept in the dark and transported in a cooler to minimize water loss. In the laboratory, fresh weights were measured to the nearest ten-thousandth of a gram. The samples were then floated on distilled water in petri dishes at a constant 5° C for 24 hours, a time period found sufficient to allow recovery of full turgor. Error in RWC determinations resulting from differences in the temperature of the leaf tissue when collected and the temperature at which water uptake was allowed (Millar, 1966) was thought to be minimized by standardizing temperature at 5° C during the absorption step. After 24 hours, the samples were blotted dry and reweighed. They were then placed in a drying oven at 70° C and after three days were weighed a final time. Tissue water content under field conditions was then expressed as a percentage of the turgid water content of the samples and related to plant-water potential by a previously established curve of RWC vs. water potential as determined by thermocouple psychrometer and pressure bomb (see Fig. 6). Fluctuations in tissue RWC were

then related, by stepwise multiple regression, to variations of air temperatures, wind speed, and radiation load, based on the records of the Mt. Washington Observatory. Since attempts at maintaining a recording pyrliometer at the Mt. Washington field station failed, daily insolation was determined by the method of Hason et. al. (1954) using the Observatory records of daily sunshine duration.

Field Studies - Summer

As a basis for evaluating winter transpiration rates observed later under controlled conditions, growth season transpiration rates for potted seedlings of paper birch (Betula papyrifera var. cordifolia), balsam fir (Abies balsamea), and black spruce (Picea mariana), transplanted from Mt. Washington, were determined gravimetrically. Three seedlings of each species, along with three control pots to account for soil evaporation, were placed out-of-doors with the pots insulated to prevent excessive soil heating (Fig. 2). Transpiration rates were determined by weighing the pots to the nearest tenth of a gram at mid-morning and again in late afternoon. Soil-water was maintained at or near field capacity for these studies. Environmental variables monitored were wind speed, total solar radiation, air temperature, and relative humidity. Additionally, evaporation was monitored with both a black, flat-surfaced Livingston Atmometer and a Piche evaporimeter. Leaf area for paper birch was determined by establishing a relationship between leaf length and area as measured with a dot grid, and thereafter measuring the leaf lengths for

Figure 2. Experimental set-up for growth-season transpiration study.



each of the seedlings. For the two conifers, the surface area of a large sample of needles was determined by measurement with a micrometer and then related to the dry weight of the needles. Total surface area for the seedlings was then determined by needle count or by needle weight, the latter method being used also for later controlled environment experiments. The seasonal course of transpiration was then correlated, by species, with atmospheric variables by a stepwise multiple regression analysis for the period June to October, 1973.

Controlled Environment Studies

With the onset of dormancy the gravimetric technique became too insensitive for transpiration studies. Sealing the pots with parafin and lanolin to eliminate soil evaporation did little to improve the technique, as the weight loss by transpiration was simply too small in relation to the mass of potted seedlings. Therefore, a system of six potometers mounted side by side was used to measure water movement through cut stems under carefully controlled conditions. These were constructed with graduated one-tenth ml pipettes which allowed measurement of water loss to an accuracy of 0.001 ml. Plant stems, which were collected in the field and handled in such a way as to prevent an air embolism in the transpiration stream, were sealed into the potometers with silicone rubber (G.E. RTV 21). The xylem water column was thus continuous through the potometer to a reservoir which was maintained at the same level as the stem so that no net hydrostatic

pressure or tension was exerted on the plant.

The potometer system was then positioned in a wind tunnel such that only the plants protruded into the air stream. Wind velocities up to 715 cm sec^{-1} (16 mph) were controlled by changing fan speed with a variac transformer. Wind speed was measured with a hot-wire thermistor type anemometer (Hastings B-27 Precision Air-Meter). The tunnel itself was situated inside a walk-in, low temperature growth chamber which allowed air temperature manipulation down to 0° C with an accuracy of $\pm 0.5^{\circ} \text{ C}$. Relative humidity was not controlled but was stable ($\pm 5\%$) throughout any given experiment. Incandescent flood lamps were used as a light source giving a maximum intensity at the plant level of 1.1 ly min^{-1} . Light intensity was regulated by placing screens over the clear plastic cover of the wind tunnel so that the heat load from the lamps remained constant, therefore contributing to the stability of the relative humidity. Radiant load on the plants was measured with a Lintronics Solarimeter. Very fine copper-constantan thermocouples were embedded in the leaf tissue to allow monitoring of leaf-air temperature differentials throughout the environmental manipulations. Finally, a Piche evaporimeter with an enlarged filter disk for increased sensitivity was placed inside the tunnel to monitor evaporation simultaneously with transpiration.

RESULTS

Summer Field Study

The time of maximum transpiration for paper birch occurred in late June. Bud burst and needle elongation was delayed in the two conifers so that their maximum transpiration occurred fully one month later. At their maxima, transpiration rates were 1.10, 0.40, and 0.42 ml/dm²/hr for paper birch, black spruce, and balsam fir, respectively. Transpiration for all species declined throughout the summer, the rate for paper birch dropping off more rapidly as leaf senescence approached (Fig. 3). Use of the same gravimetric procedure in mid-winter (in the greenhouse) showed no significant difference at the 95% confidence level between the water loss from the spruce and fir seedlings and that from the soil controls.

Correlations of summer transpiration rates with the four measured atmospheric variables by stepwise multiple regression analysis are shown in Table 2. Listed are the variables in the order in which they account for the variation in transpiration rate, the sums of squares reduced in each step of the regression, and the adjusted correlation coefficient as each variable is entered into the regression. For the spruce and fir seedlings, summer transpiration was most closely correlated with the maximum air temperature ($R=.80$ and $.73$ respectively). Mean relative humidity, wind speed, and radiation load accounted for very little of the variation in transpiration.

Figure 3. Seasonal course of transpiration for potted seedlings of paper birch (— —), black spruce (——), and balsam fir (----).

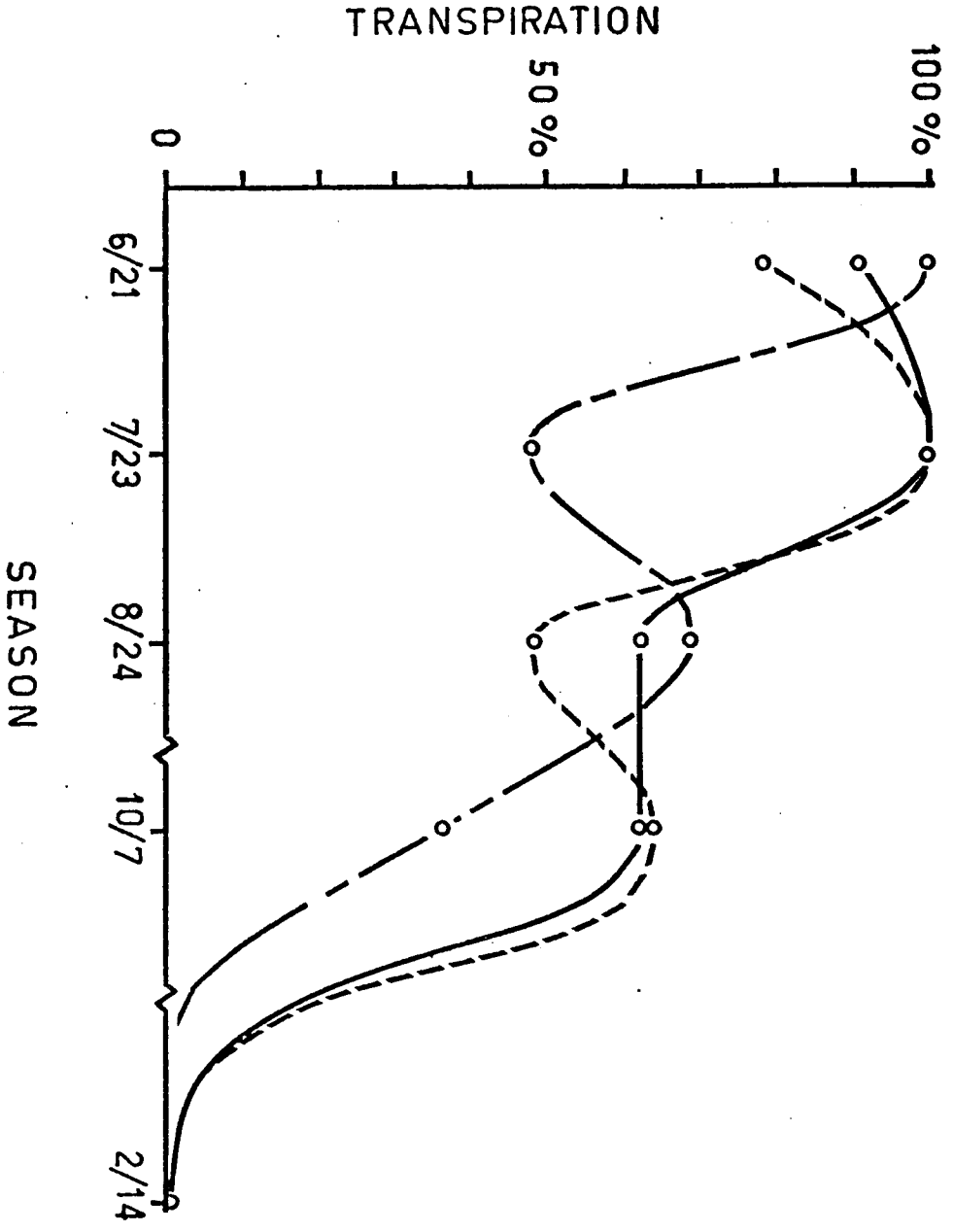


Table 2. Results of stepwise multiple regression analysis for summer transpiration study. Atmospheric variables are listed in the order in which they account for the observed transpiration rates.

	<u>Variable</u>	<u>S.S. Reduced</u>	<u>Adjusted R[*]</u>	<u>Reg. Coef.</u>
Fir	Max.Temp.	37.283	0.726	0.579
	Mean RH	5.854	0.765	-0.121
	Wind	4.161	.790	-1.068
	Radiation	1.854	.787	-0.038
			(Y intercept = 1.306)	
Spruce	Max.Temp.	27.340	0.797	0.499
	Mean RH	2.285	.816	-0.064
	Wind	1.119	.816	0.586
	Radiation	0.220	.795	-0.013
			(Y intercept = -4.250)	
Birch	Mean RH	0.237	0.156	0.045
	Radiation	1.019	.687	0.027
	Wind	0.155	.711	0.219
	Max.Temp.	0.032	.682	0.017
			(Y intercept = -4.258)	
Control	Radiation	122.837	0.807	0.139
	Wind	24.460	.883	2.836
	Mean RH	14.997	.930	-0.186
	Max.Temp.	9.696	.964	0.293
			(Y intercept = 3.204)	

* Adjusted R = $\sqrt{1 - (1 - R^2) \frac{(n-1)}{(n-m)}}$ where n is the number of observations and m is the number of independent variables.

For paper birch, mean relative humidity appeared to account for most of the variation but with an insignificant correlation coefficient of .16. When combined with radiation however, the correlation coefficient was improved considerably. The two variables taken together were many times more significant ($R=.69$) than either one alone. Evaporation from the bare soil was most sensitive to radiation ($R=.81$) but with each added variable improving the regression equation considerably. All four variables taken together accounted for 93% of the variation in soil-water loss.

Winter Field Study

At the Mt. Washington field site, the relative water content of exposed but undamaged tissue fluctuated about a mean of 90.0% for black spruce and 91.4% for balsam fir during each of the 1972-73 and 1973-74 winter periods (November through April), i.e., the mean RWC of each species was the same for both winters (Figs. 4 and 5). These means differ little from the relative water contents observed during September and October. A mean RWC of 90% corresponds to a plant-water potential of approximately -11 bars in each species (Fig. 6). The lowest RWC recorded over the two winters for undamaged samples was 82.4% for spruce and 84.7% for fir, corresponding to water potentials of approximately -17.5 bars and -28.0 bars respectively. The fluctuation in RWC for balsam fir at the Madbury site during the second winter roughly paralleled that of the Mt. Washington site with a nearly identical mean over

Figure 4. 1972-1973 seasonal course of relative water content in exposed branches of paper birch (Δ), black spruce (\bullet), and balsam fir (\circ) from treeline, Mt Washington, N.H. Dashed line represents damaged samples.

Figure 5. 1973-1974 seasonal course of relative water content in exposed branches from the subalpine zone, Mt. Washington. Details as in figure 4. Periodic RWC determinations for balsam fir (\times) from the Madbury, N.H. plantation are shown for comparison.

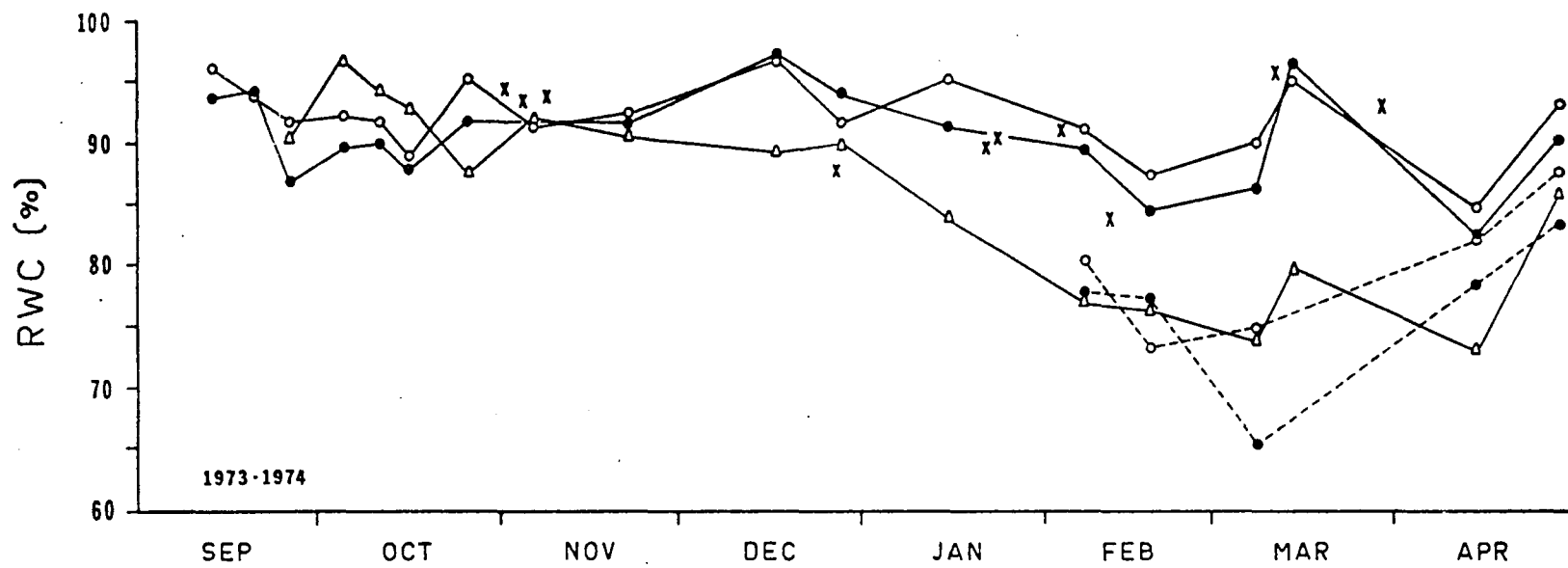
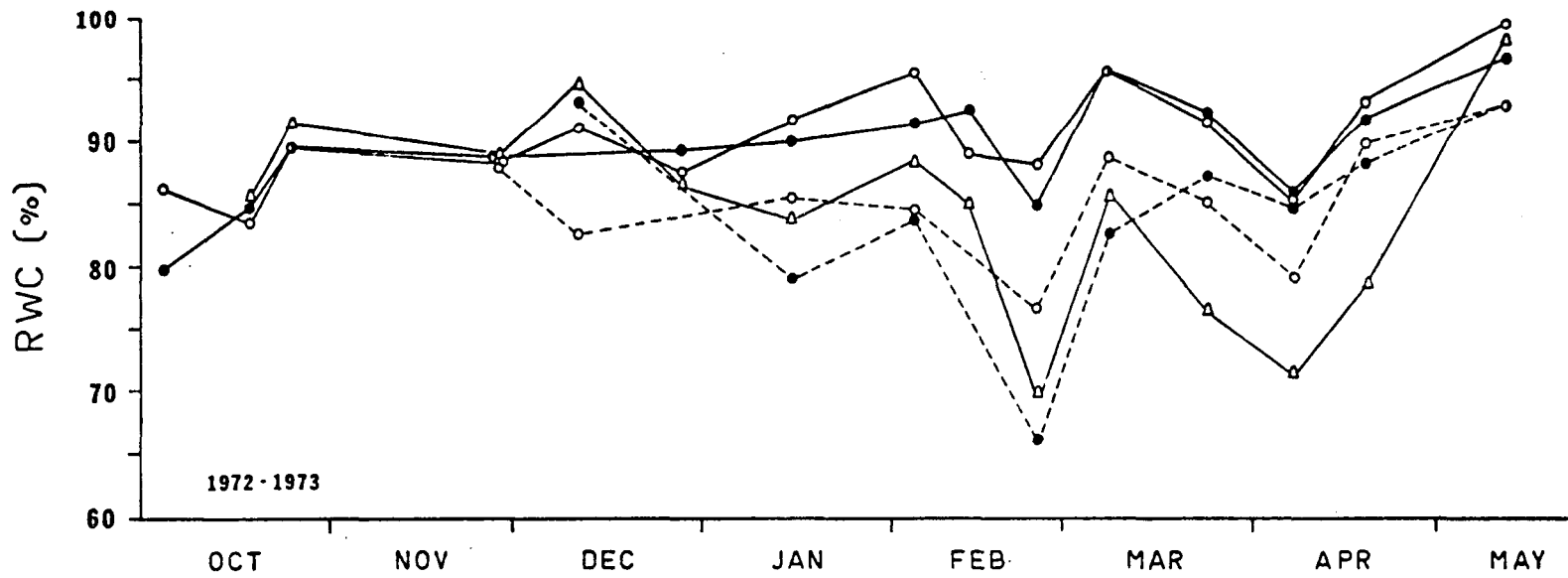
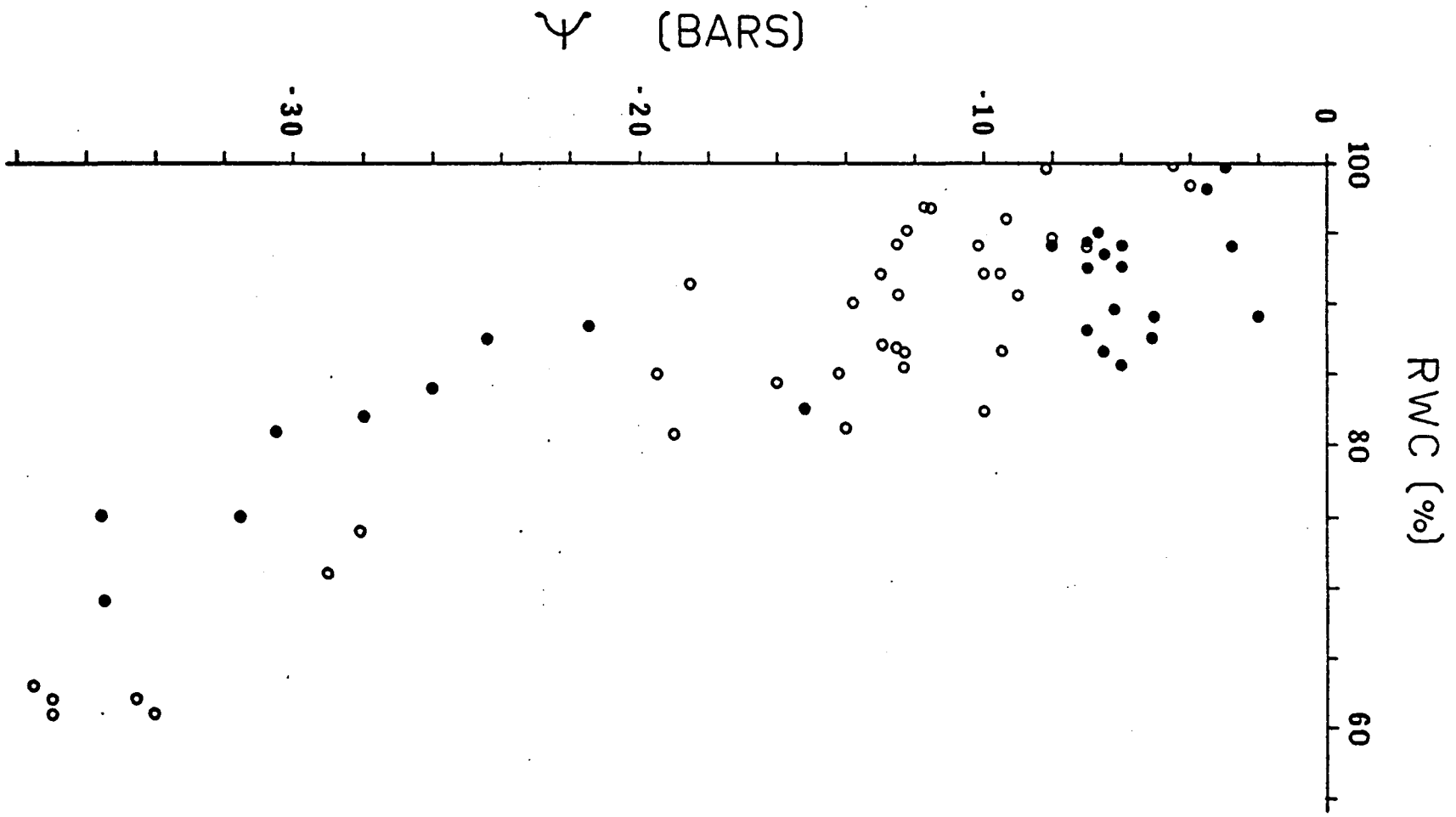


Figure 6. Plant-water potential (Ψ), determined by thermocouple psychrometer and pressure bomb, as a function of relative water content (RWC) for balsam fir (○) and black spruce (●).



10 sampling dates of 91.3% (Fig. 5).

Throughout the season, damaged branch tips showed similar fluctuations but had consistently lower relative water contents than the undamaged samples (figs. 4 and 5). During the 1972-73 winter the RWC of damaged spruce and fir averaged 88.3% and 84.4%, respectively. Over 5 sampling dates late in the 1973-74 winter their respective RWC averages were 76.4% and 79.6%. Water content variation was also considerably greater within damaged samples. For example, a sample of 9 exposed but undamaged spruce branches on April 20, 1973 gave a mean RWC of 91.4% with a standard deviation of 3.3%, while on the same day, 9 damaged branches had a mean RWC of 83.4% with a standard deviation of 6.2%. Differences in RWC of the same magnitude were often found between damaged and similarly exposed but undamaged portions of the same plant.

There were no significant differences in RWC found among the different needle age classes. In the undamaged portion of a fir sample collected Nov. 30, 1973, the RWC of old needles (85.2%) was comparable to that of the new needles (84.5%), while the damaged portion of the same sample treated intact, i.e., all remaining needles and stem considered together, showed only a slightly lower RWC of 82.7%. A sampling of damaged spruce showed similar results—essentially no difference between the RWC of old needles, usually remaining on the leeward side of the stem (90.0%) and that of new needles (89.5%). An additional sampling, on February 14, 1973, of old vs. new needles on

exposed but undamaged branch tips gave the following results: fir, 89.9% (old) vs. 93.5% (new); spruce, 90.7% (old) vs. 91.9% (new).

The seasonal trend of RWC in leafless birch stems somewhat paralleled that of the two conifers except that the RWC in birch became progressively lower with time. Variation within samples also tended to be much greater, giving, for example, standard deviations of 7.1, 4.1, and 12.1 for samples of 6 stems on each of three different days. The RWC of exposed birch trees reached lows of 70.0% and 73.1% in two successive winters but in both years recovery was very rapid starting around mid-April (figs. 4 and 5).

Fluctuations of tissue RWC in the field did not correspond to changes in temperature, wind speed, and radiation with the same sensitivity indicated later in the controlled environment studies. Results of a stepwise multiple regression analysis are given in Table 3. The average maximum air temperature of the two days prior to sampling accounted for the greatest amount of variation in the RWC of the conifers but showed a correlation coefficient of only .21 for spruce and .32 for fir. Adding wind speed and radiation data into the regression reduced the correlation (table 3). Using data only for the months of February through April when the RWC fluctuations were more pronounced did not improve the correlation. For birch, the total radiation for the three days prior to sampling accounted by itself for most of the sample variation, but again the correlation coefficient was a low

Table 2. Results of stepwise multiple regression analysis for winter RWC determinations. Atmospheric variables are listed in the order in which they account for the observed RWC values.

	<u>Variable</u>	<u>S.S. Reduced</u>	<u>Adjusted R</u> [*]	<u>Reg. Coef.</u>
Fir	2-day Max T ^o	33.550	0.322	0.144
	4-day \bar{m} Wind	3.974	.272	0.036
	3-day tot.Rad.	1.941	.172	0.001
			(Y intercept = 87.189)	
Spruce	2-day Max.T ^o	28.218	0.208	0.122
	3-day tot.Rad.	1.429	0	-0.001
	2-day \bar{m} Wind	0.309	0	0.015
			(Y intercept = 87.471)	
Birch	3-day tot.Rad.	181.726	0.349	-0.009
	3-day \bar{m} Temp.	154.488	.479	0.291
	4-day \bar{m} Wind	22.912	.457	0.085
			(Y intercept = 80.343)	

* Adjusted R = $\sqrt{1 - (1 - R^2) \frac{(n-1)}{(n-m)}}$ where n is the number of observations and m is the number of independent variables.

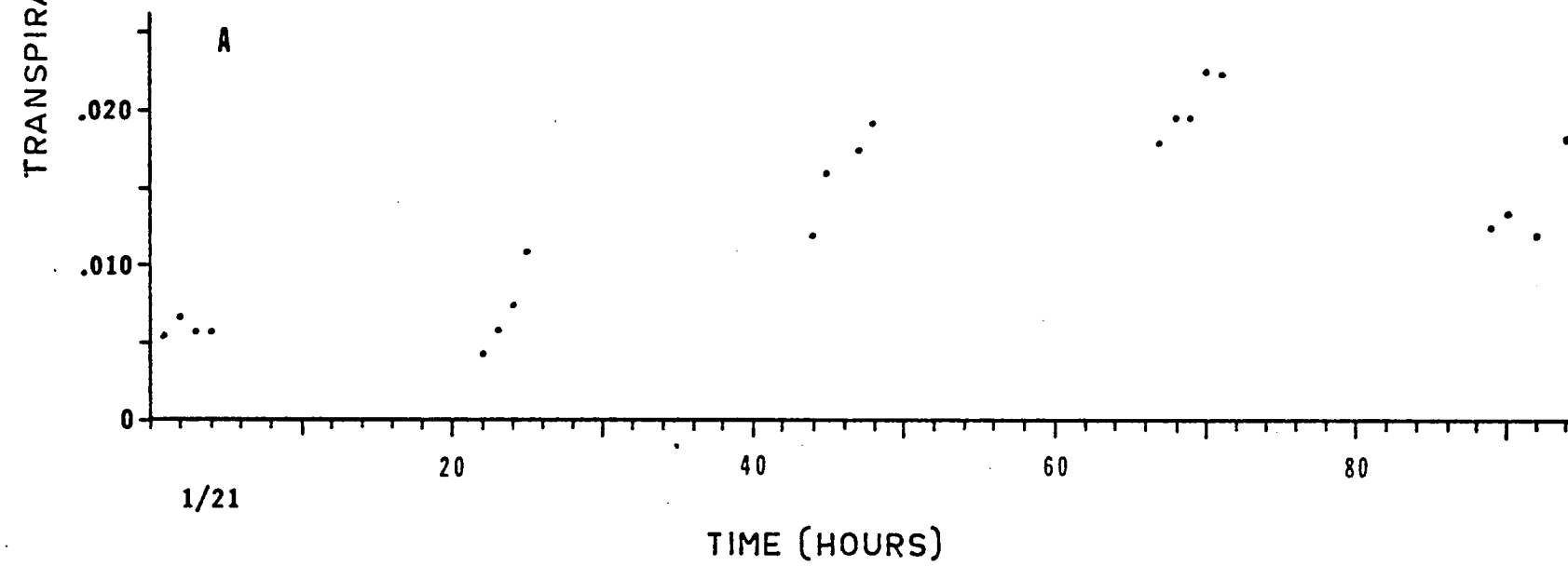
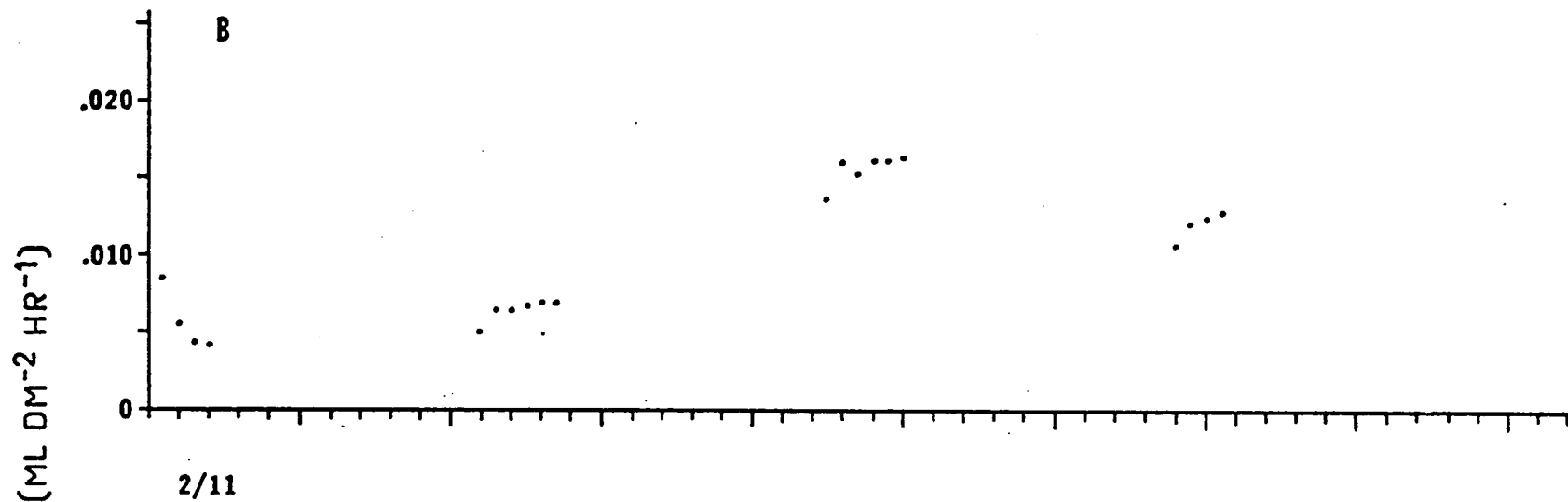
.35. Adding temperature and wind speed data into the regression improved the correlation only slightly (Table 3).

Controlled Environment Studies

During the course of the controlled environment experiments, several factors were found to affect the plant water balance of dormant black spruce. Results indicate that freezing causes some disruption of the water column so that water conduction is inhibited for some time after thawing. When frozen stems were brought in from the field, re-cut under water and sealed in the potometers, it was found to take 3 to 4 days at an air temperature of 5°C and radiation load of 0.5 ly min^{-1} (6 hrs/day) for transpiration to approach a steady state (Fig. 7). Initially the transpiration rate (averaged for 4 branches over the first 4 hours) was just under $0.006\text{ ml/dm}^2/\text{hr}$ in each of two trials. On successive days the initial hourly transpiration rate after the lights were turned on nearly equalled or exceeded the highest hourly transpiration rate of the proceeding day. Hour to hour increases were dampened when wind speed was increased from near zero to 200 cm sec^{-1} , but the daily trend of increasing transpiration was otherwise the same (fig. 7b).

Once transpiration had reached a nearly steady state the rate was found to be strongly light dependent. With relative humidity ranging from 35% to 41% at a constant temperature of $5^{\circ}\text{C} \pm 0.5^{\circ}$, and with the wind speed constant at 200 cm sec^{-1} , transpiration increased from $0.005\text{ ml/dm}^2/\text{hr}$ in the dark to $0.009\text{ ml/dm}^2/\text{hr}$ at a radiation level of 0.5

Figure 7. Daily trend of transpiration from excised branches of black spruce following thawing, under constant temperature (5° C) and radiation (0.5 ly min^{-1}). (a) Wind speed zero. (b) Wind speed 200 cm sec^{-1} .



ly min^{-1} and to $.013 \text{ ml/dm}^2/\text{hr}$ at a radiation level of 1.1 ly min^{-1} . Each increase in transpiration, however, lagged 3 hours behind the increase in evaporation from the wet filter paper disk (Fig. 8). With the leaf boundary layer resistance assumed negligible at a wind speed of 200 cm sec^{-1} , the leaf resistance to transpiration was calculated by the equation on page 8 to be 316 sec cm^{-1} in the dark, 182 sec cm^{-1} at 0.5 ly min^{-1} , and 121 sec cm^{-1} at 1.1 ly min^{-1} .

When the air temperature was lowered to 1° C (leaf temperature approx. 2° C), the change in leaf resistance with increasing light intensity was inhibited. Switching the light intensity from zero to 1.1 ly min^{-1} resulted in an oscillation of transpiration for 6 hours about a mean of $0.003 \text{ ml/dm}^2/\text{hr}$, corresponding to an average leaf resistance of 280 sec cm^{-1} (Fig. 9). Raising the temperature then from 1° C to 10° C , while maintaining constant radiation load and wind speed, resulted in a decline of leaf resistance to 148 sec cm^{-1} . In Figure 9, the dashed line represents the projected course of transpiration as a result of increased evaporative demand (reduced relative humidity) accompanying the temperature increase, had the leaf resistance remained at 280 sec cm^{-1} . The oscillations of transpiration at 1° C were observed again when the temperature was cycled between 0° C and 5° C at 3 hour intervals (Fig. 10). A summary of light and temperature effects on leaf resistance is given in Figure 11.

The net effect of increasing wind speed at constant

Figure 8. Transpiration as a function of radiation intensity under constant temperature (5° C), humidity (35-41%), and wind speed (200 cm sec^{-1}). Light regimes are; darkness (heavy shading), 0.5 ly min^{-1} (light shading), and 1.1 ly min^{-1} (unshaded). Vertical lines indicate standard deviation of the means. Dashed line represents evaporation from the Piche filter disk.

TRANSPIRATION (ML DM⁻² HR⁻¹)

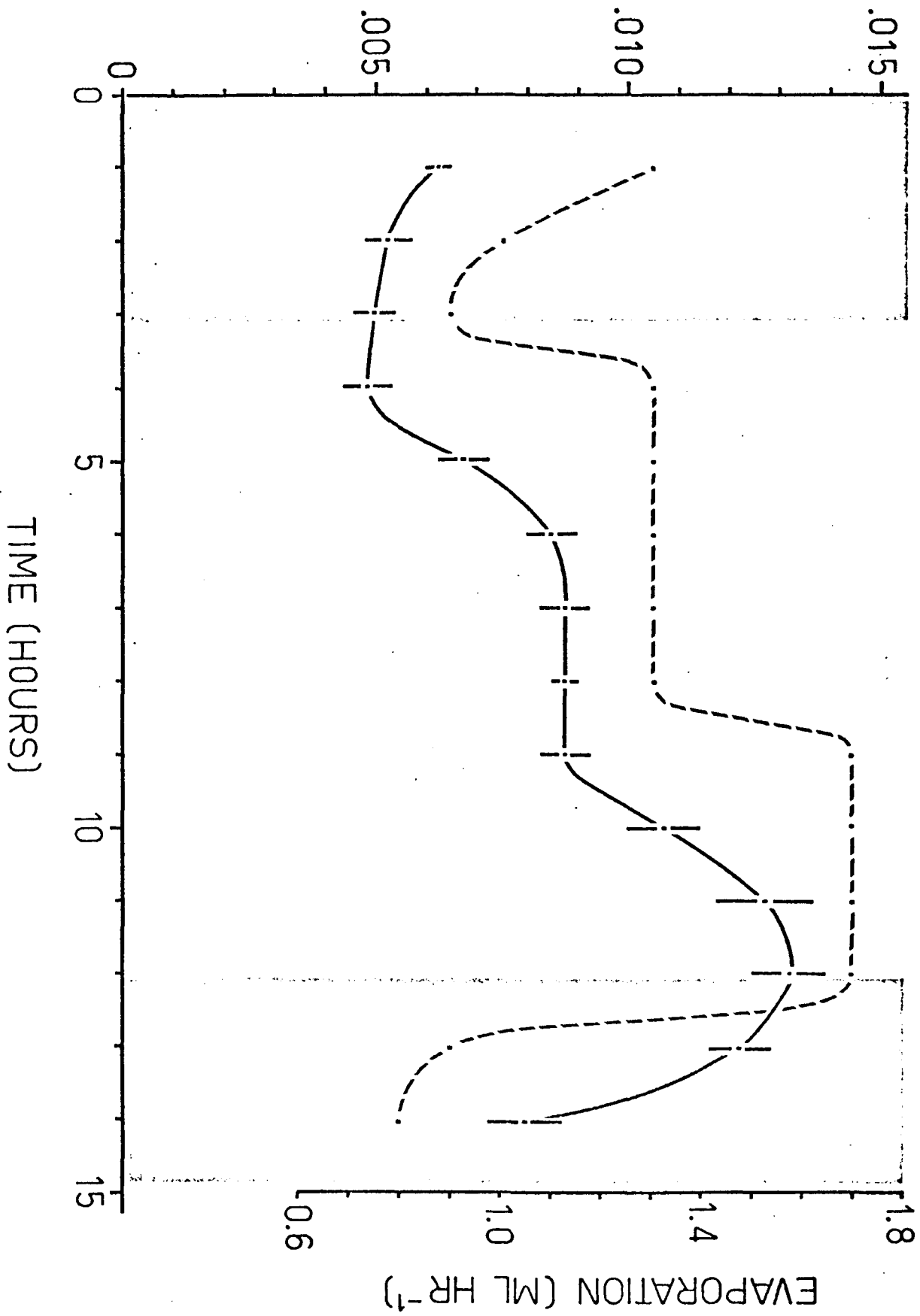


Figure 9. Transpiration as a function of temperature under constant radiation (1.1 ly min^{-1}) and wind speed (200 cm sec^{-1}). Shaded area represents dark transpiration. After 6 hours of light transpiration at 1° C , the chamber temperature was allowed to go to 10° C . Broken line represents the projected course of transpiration following the temperature increase, assuming no decrease in the calculated leaf resistance (see text). Dashed line represents evaporation.

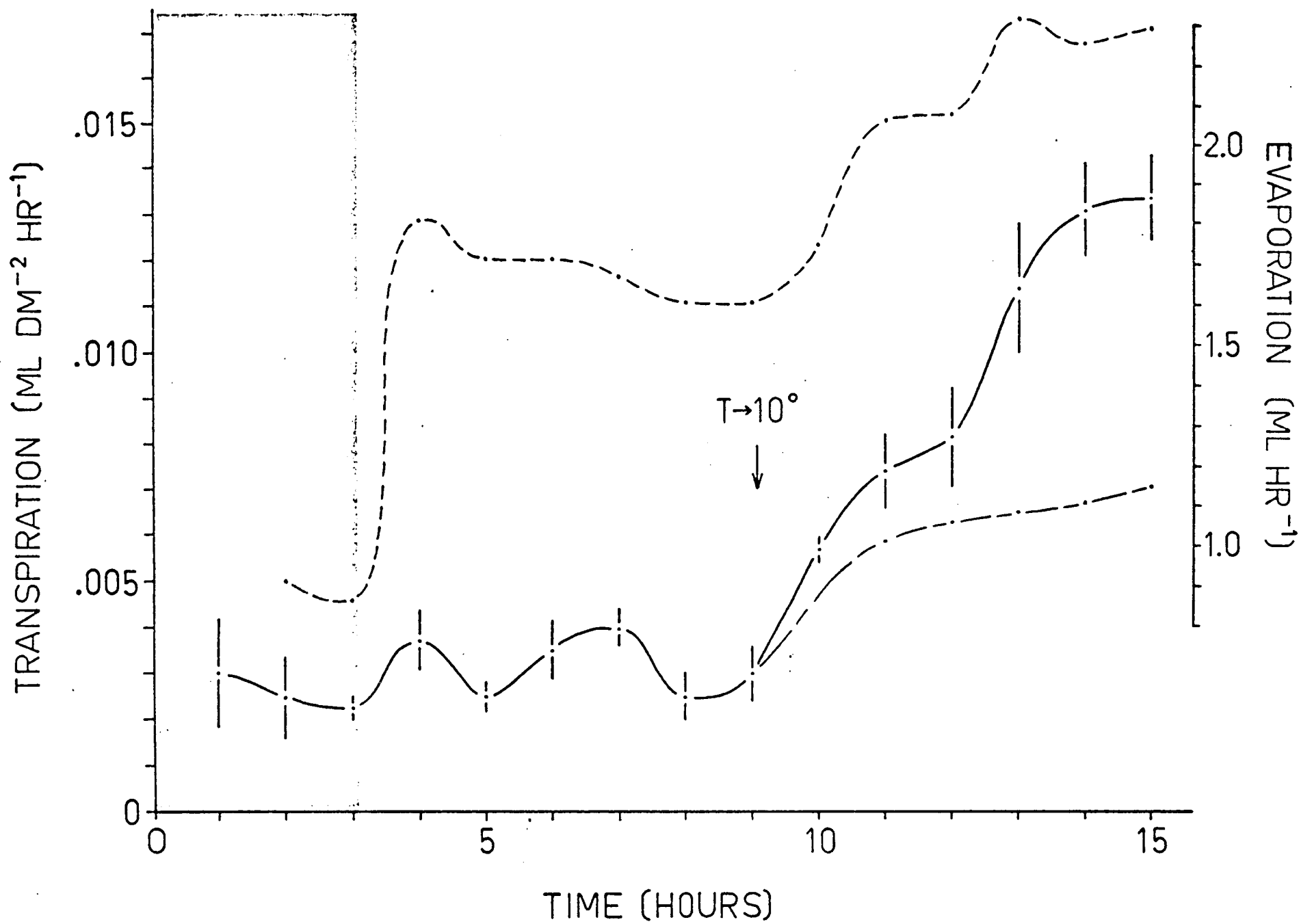


Figure 10. Transpiration with cyclic changes in temperature between 0° C and 5° C. Constants; radiation 0.5 ly min^{-1} , wind speed 200 cm sec^{-1} . Dashed line represents evaporation.

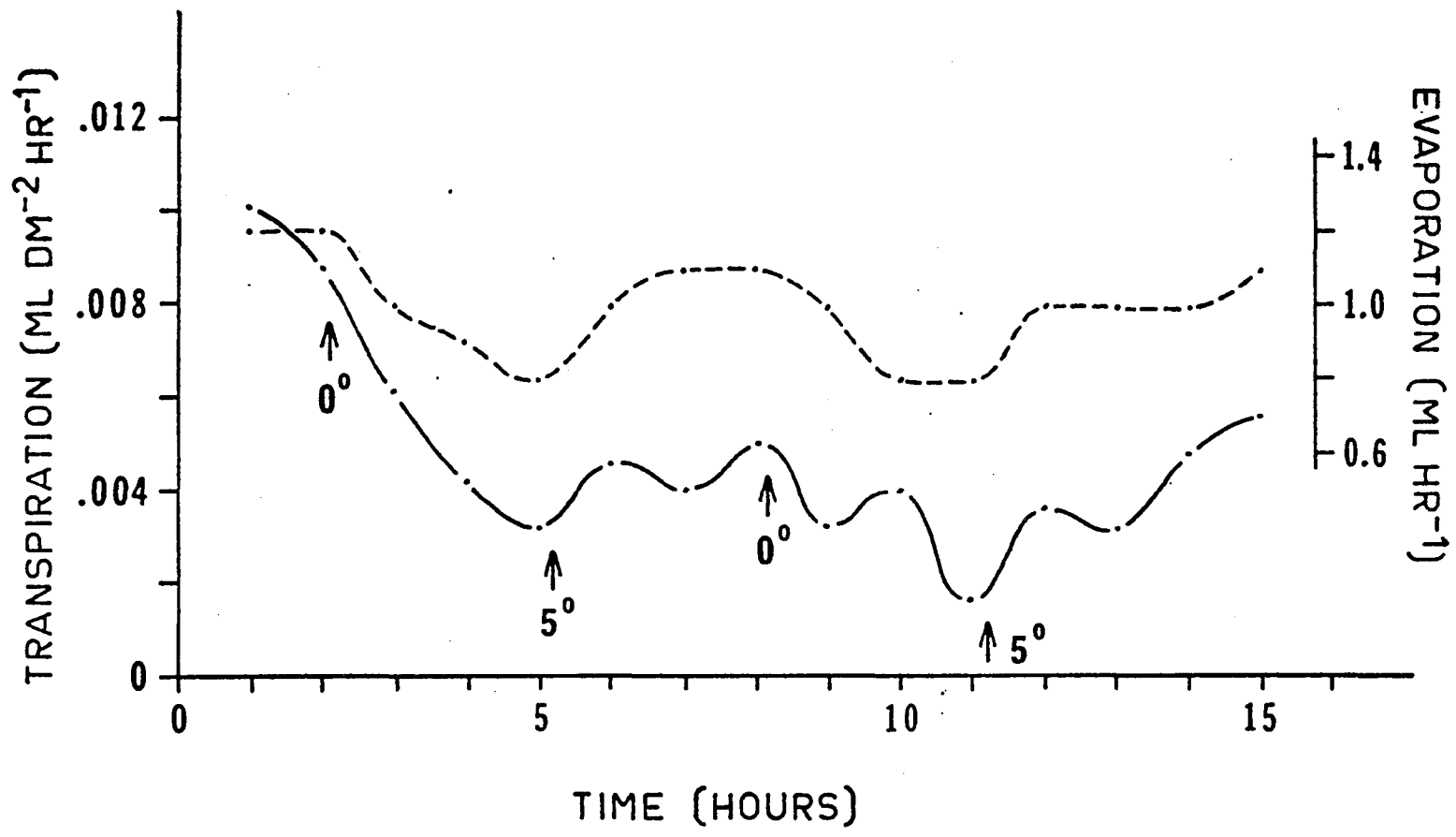
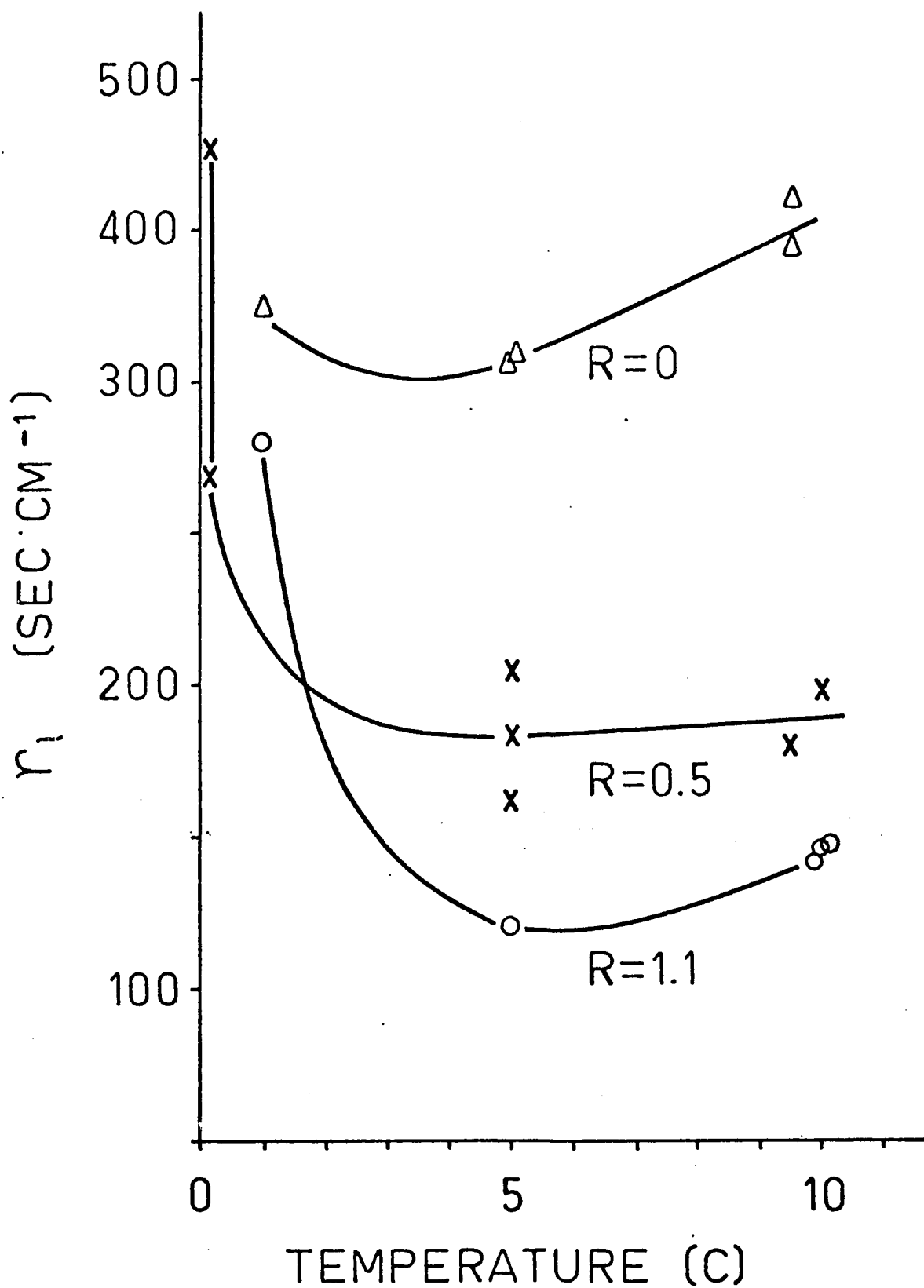


Figure 11. Summary of radiation and temperature effects on calculated leaf diffusion resistance.



temperature, relative humidity, and radiation was to decrease the transpiration rate. Maximum transpiration was found to occur in nearly still air. At a wind speed of 100 cm sec^{-1} , transpiration was reduced slightly more than 50% under radiation intensities of 0.5 and 1.1 ly min^{-1} . Further increase in wind speed to 700 cm sec^{-1} had little effect on transpiration (Fig. 12), while evaporation increased almost linearly. Dark transpiration rates were unaffected by changes in wind speed between 0 and 200 cm sec^{-1} .

The effect of wind on transpiration is apparently related to the heat transfer efficiency of low wind speeds. In still air, leaf temperatures were raised $5.5^{\circ} \text{ C} \pm 1.3 \text{ s.d.}$ above air temperature under a radiation intensity of 0.5 ly min^{-1} and $9.8^{\circ} \text{ C} \pm 2.5 \text{ s.d.}$ above air temperature under a radiation intensity of 1.1 ly min^{-1} . These temperature differentials were reduced, however, to $0.8^{\circ} \text{ C} \pm 0.7 \text{ s.d.}$ and $1.8^{\circ} \text{ C} \pm 1.6 \text{ s.d.}$ for radiation levels of 0.5 and 1.1 ly min^{-1} , respectively, at a wind speed of 90 cm sec^{-1} (Fig. 13). Thermal equilibrium between leaf and air was maintained for both radiation levels at a wind speed of 700 cm sec^{-1} .

Figure 12. Transpiration as a function of wind speed under radiation intensities of 0.5 ly min^{-1} (—) and 1.1 ly min^{-1} (---). Vertical bars indicate standard deviation of the means. Air temperature is 5° C .

TRANSPIRATION
(percent of maximum rate)

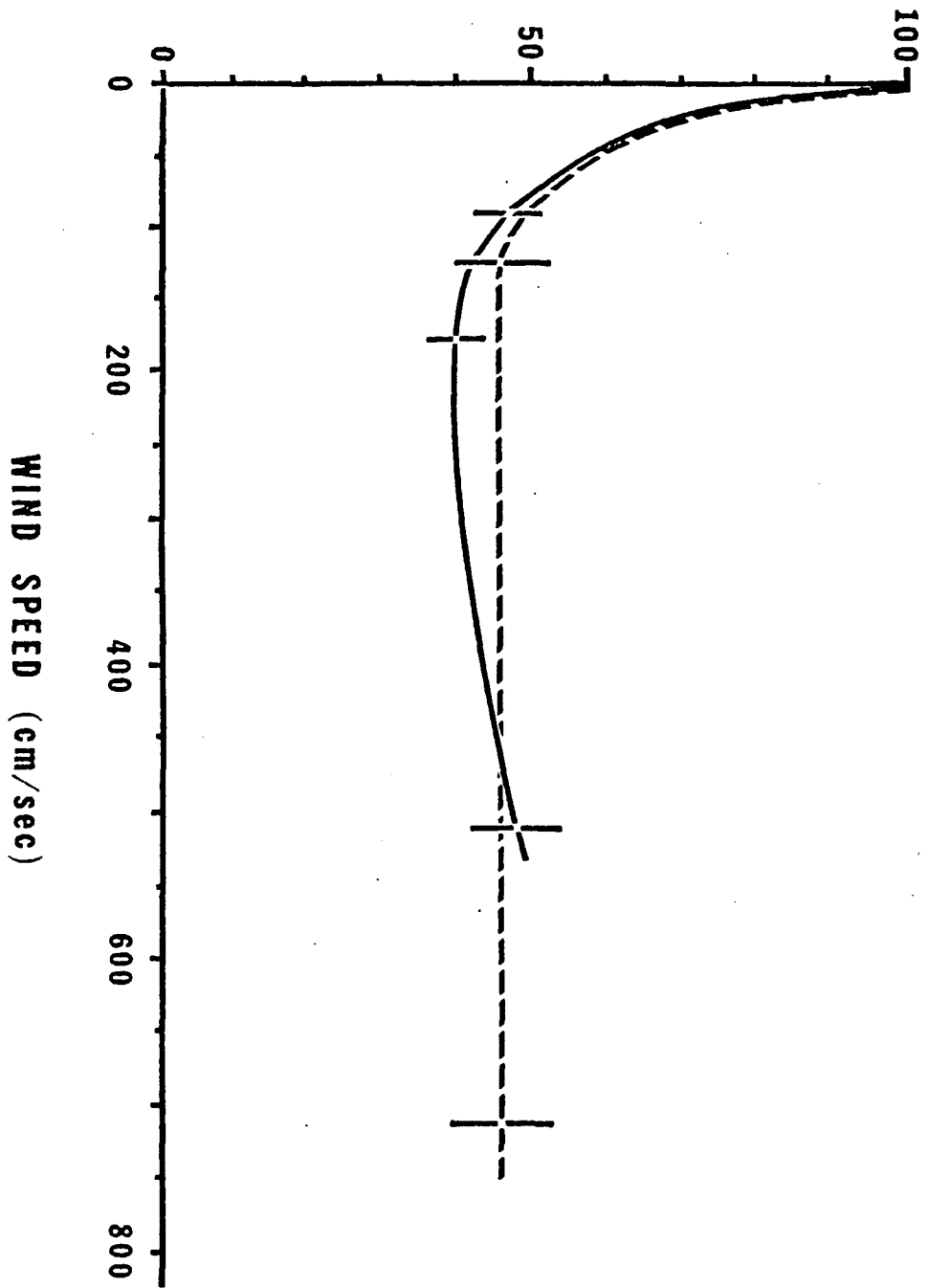
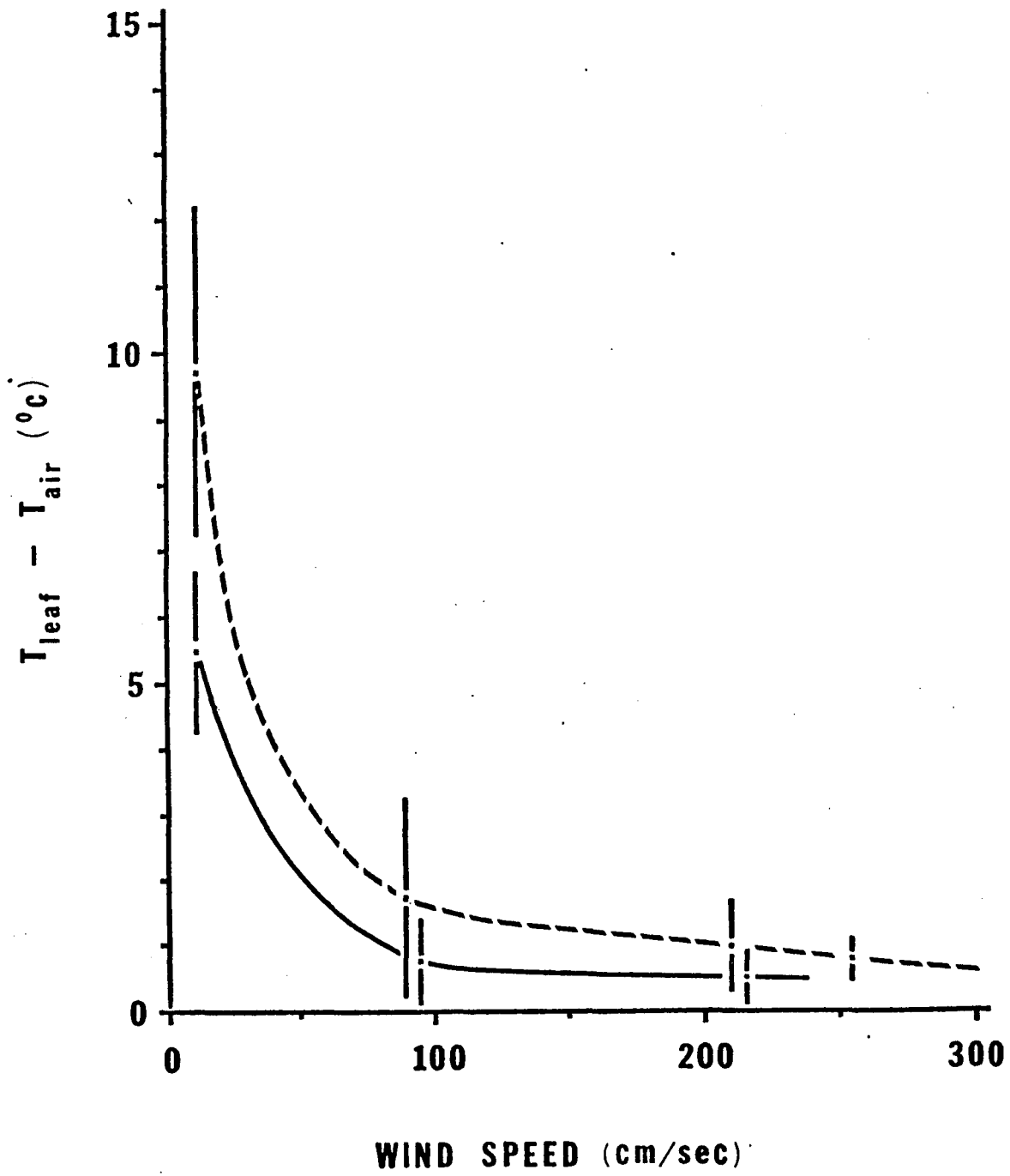


Figure 13. Leaf-air temperature differences as a function of wind speed under radiation intensities of 0.5 ly min^{-1} (—) and 1.1 ly min^{-1} (----). Vertical bars indicate standard deviation of the means.



DISCUSSION

As a conservative estimate, the transpiration rate of black spruce during the winter drops by a factor of 100 from the summer rate, e.g., from 0.4 to 0.004 ml dm⁻²hr⁻¹. This would correspond to an increase in leaf resistance from 16 sec cm⁻¹ to approximately 300 sec cm⁻¹. Khlebnikova, et al. (1963) report that winter transpiration of scotch pine is 200-300 times less than during the summer, at a rate of 25 mg/gm fresh wt/day. Hygen (1963) calculates the minimum water loss from Norway spruce during the winter at 12.5 mg/gm fresh wt/day. For purposes of comparison, the minimum transpiration rate for dormant black spruce in this study is calculated at 21 mg/gm fresh wt/8 hr day at a radiation intensity of 0.5 ly min⁻¹.

Several factors may contribute to transpiration rates in excess of the above. The leaf resistance to vapor diffusion, and hence the transpiration rate, was seen to vary significantly with changing temperature and light intensity. The direction of the light response, i.e., decreasing leaf resistance with increasing light intensity, and the oscillatory nature of transpiration at temperatures between 0 and 5° C is strongly suggestive of stomatal activity, though the magnitude of resistance change would seem to indicate only the slightest movement of the stomatal guard cells. Available data indicate that changes in cuticular resistance would go in the opposite direction with high light intensity increasing the resistance (Holmgren et al., 1965). The Q₁₀ of leaf conductance in

this case, however, is considerably higher than that usually associated with stomatal opening. With a rise in temperature from 1° to 10° C (Fig. 9) the Q_{10} for the increase in $1/r_1$ is 4.9. The plot of leaf resistance vs. temperature for all experiments (Figure 11) shows little temperature sensitivity, however, between 5° and 10° C. If calculated over the range 0° to 5° or 1° to 5° , the Q_{10} exceeds 6.0.

Drake, et. al., (1970) report a Q_{10} of 1.7 to 2.1 for the increase in stomatal conductance of Xanthium between 25° and 35° C. Stalfelt (1962) reports a nearly linear relation between stomatal opening and temperature with a Q_{10} of 1.5 for stomatal conductance at temperatures above 5° C. In any case, there appears to be an important temperature threshold at about 5° C below which stomatal movements, if that is a correct assessment, are prevented regardless of radiation intensity.

As previously discussed, wind has a two-fold effect on the water balance of exposed plants; (1) it facilitates removal of the moist air from the leaf surface, hence lowering the diffusive resistance of the leaf boundary layer, and (2) it increases the rate of advective heat transfer from the leaf, thus tending to maintain temperature equilibrium between the leaf and air. These processes have long been recognized - the question as to which is more important in terms of winter plant-water balance can now be resolved: The importance of elevated plant temperatures on the leaf resistances to vapor transfer has just been described. The transpiration of black spruce was seen to be sub-

stantially greater at 10° C than at 1° C as a direct result of decreased leaf resistance. In addition to its effect on the diffusive resistances of the leaf, however, the heating of exposed plant parts clearly affects the vapor concentration gradient between the intercellular spaces of the leaf and the outside air. The difference in the vapor concentration between the ambient air at 0° C and 50% relative humidity and a saturated leaf in thermal equilibrium with the air is approximately 2.4 ug/cm³. With the leaf temperature elevated to 5° C under the same conditions, the difference in water vapor concentration between the leaf and air increases to approximately 4.4 ug/cm³. By substituting these values into the transpiration equation (page 8) it is readily apparent that when leaf diffusive resistance is very high, reduction of the boundary layer by moving air is far more important in terms of its effect on the vapor concentration gradient than its reduction of the diffusion resistance of the air surrounding the leaf - hence the pronounced increase in transpiration in nearly still air when heating is maximum (figs 12 and 13). Drake et al. (1970) reached a similar conclusion noting that increasing wind reduced the transpiration of Xanthium (having a much lower leaf resistance) at temperatures up to 35° C.

Such heating of plants as occurred under the conditions of the controlled environment experiments have been frequently observed in the field. Tranquillini (1964), for example, has found temperatures of Pinus cembra needles as high as 21.5° above air temperature in April, as a result

of high direct and reflected radiation load. Similar observations have been reported by Sakai (1970) and Salisbury and Spomer (1964). Such heating must occur only under very calm conditions, however, as it appears that even very low wind speeds, e.g., 100 cm sec^{-1} , efficiently reduce the heat load of a conifer needle. It is likely then, that damaging water loss from winter-exposed plants will occur only on calm and cloudless days and that any increase in wind speed would then decrease the rate of water loss. The effectiveness of wind is potentially greatest at air temperatures slightly below 0° C , under high radiation intensity, since the leaf temperature may be reduced from initially above to below the point of any stomatal activity and close to the freezing point of the cell water.

The lack of good correlation between leaf water content changes at treeline and the atmospheric variables of temperature, radiation and wind speed can be related to the nature of the winter climate on Mount Washington. Days on which the maximum temperature exceeds 0° C are infrequent. Cloud cover is persistent and the occurrence of calm days is rare (Table 1). The probability of near zero air temperature, high radiation load, and low wind speeds occurring together, i.e., the probability of strong heating of exposed tissue, is thus quite low. The correlation, insignificant as it is, between RWC and maximum air temperature is probably related to the low atmospheric vapor concentrations (not monitored) at low air temperatures rather than to temperature itself. It is otherwise hard to explain

why maximum water loss should coincide at all with low temperatures. The almost complete insensitivity of RWC to the wind regime of Mt. Washington seems to support the laboratory observations that heat dissipation is complete at very low wind speeds and that further increases in wind speed are ineffective. Were there more frequent calms, the correlation might have been more significant in the negative direction, i.e., lower RWC with decreasing wind speed.

Interpretation of the RWC increases which were observed during the winter is a matter of some difficulty, as the weather patterns associated with the increases do not give a clear indication of the possible causes. The pronounced increase in RWC which occurred during the period from Feb. 25 to Mar. 9, 1973 (Fig. 4) coincided with a definite warming trend, with daily maximum temperatures exceeding 0° C at the study site on each of the last 8 days of that period. During the period from March 9 to March 15, 1974, however, at which time a similarly pronounced increase in RWC occurred (Fig. 5), the study area was under the influence of one of the coldest air masses of the winter. Maximum daytime temperatures during that week dropped from -5° to -22° C (Observatory records) accompanied by high winds and prevalent cloud cover.

The fact that such occasional rapid increases in RWC were parallel in all three species suggests that similar explanations should be sought for the "absorption" gains of each. The data also suggest that more than one mechanism is likely. Passive absorption of surface meltwater by

adventitious roots is the classical explanation for the periodic relief of winter water deficit, but in the case of the birch, this hypothesis has some problems. The evidence of Hammel (1967) indicates that cavitation of the water column of birch occurs upon freezing. This is apparently not the case with most gymnosperms, as evidenced by Hammel's experiments and our own with black spruce. It is not clear, however, just how seriously cavitation impairs absorption and translocation in the angiosperm during the winter. Havis (1971) demonstrated water movement in both a diffuse- and ring-porous angiosperm below the freezing point of the xylem water and at a rate equal to that which occurred at temperatures between $+2^{\circ}\text{C}$ and $+10^{\circ}\text{C}$. He found that translocation stopped only at a second and lower freezing point, at which time, presumably, the symplastic water froze. Nonetheless, the overall decline in the RWC of birch throughout the winter (Figs. 4 and 5) does indeed suggest that water replenishment is more restricted in this species, at least until early spring, at which time renewed cambial activity may begin to restore the xylem water column.

Though translocation may occur in spite of cavitation and at temperatures below 0°C (a possibility suggested by Hygen (1963) and Polunin (1933) as well), it is not known whether or not absorption from frozen soils, as for example through vapor transfer, is significant. The increase in RWC of exposed branch tips might be more feasibly explained in terms of a redistribution of water within the plant. Tranquillini (1963) has suggested

that conifers in particular have a large amount of water in "storage" which may be used to satisfy the water demands when absorption is inhibited. To carry this one step further, the foliar parts of the plant which are buried beneath the snowpack could, in fact, become effective "absorbing" tissue, since these generally remain at full turgor due to the saturated state of the snowpack interstices. The proper water potential gradient would then exist within the plant for the upward movement of water to the exposed branch tips whenever the plant is warmed sufficiently.

Absorption of water from the atmosphere is also possible as long as the proper vapor concentration gradient exists between plant and air (Slatyer, 1960). The probability of this occurrence is slight, however. For a leaf water potential of -10 bars, at a temperature of 0°C , the relative humidity of the mesophyll air spaces is calculated to be 99.2% (see discussion of P.S. Nobel, 1974, p. 320). Thus, for a leaf in thermal equilibrium with the surrounding air at 0°C , absorption of atmospheric water vapor will take place only when the relative humidity of the air exceeds 99.2%. By the same calculation, at a leaf water potential of -20 bars, absorption of water vapor will take place only at relative humidities above 98.4% and only so long as the leaf temperature is not elevated above air temperature. Outside of the interstices of the snowpack such conditions are seldom met, except perhaps for a few hours during the night. For the short periods when the atmosphere around

the exposed plant is saturated, however, the absorption flux is apt to be very small in view of the high cuticular resistance to vapor diffusion. Nonetheless, this does remain a mechanism by which impending water deficit may occasionally be stalled. Each of the above processes are clearly in need of further research.

Treeline and the Winter Environment - The Mt. Washington Case

Winter desiccation cannot be considered a primary cause of the low treeline in the Presidential Range of New Hampshire. During the winter, tissue water content of exposed but undamaged spruce and fir at treeline rarely departs from what could be considered normal levels, in part because of the wind and cloud cover conditions of Mt. Washington and in part because of the occasional opportunity for the partial relief of water deficit.

Continual exposure to high winds during the winter appears to affect the plant adversely only in relation to its susceptibility to sustaining physical damage, particularly that associated with the abrasive force of wind-carried ice particles. In some cases such physical damage appears to be considerable. The shoots of conifers which were most prominently exposed to high winds were often observed to have sustained considerable needle, stem and bud breakage, often with these tissues removed entirely. Such damage was usually most noticeable within 1-3 decimeters of the snowpack and was strongly "directional" as would be expected of particle impact damage. Saville (1963, 1972) described

the development of "mop-head" growth forms from such abrasive removal of foliage from the mid portions of exposed spruce at northern treeline. Similar forms appear locally in the sub-alpine zone of Mt. Washington (Fig. 14) and apparently for the same reason, as close examination reveals strong abrasive wear on the bark tissues of windward sides of stems.

There is no indication, however, that any needles are predisposed to removal by abrasion as a result of prior desiccation, but rather, drying becomes evident only after the breakdown of diffusive resistances through needle breakage or removal. There is no evidence of any wound repair following such winter injury (personal observation), so, as a probable result of the exposure of open-ended vascular tissue, branches which have sustained such damage do become susceptible to increased water loss.

The overall importance of such desiccation as a secondary problem may also be questioned, however. The data indicates that the mobility of water within the plant is sufficiently low so that drying tends to be localized and, if lethal, seldom affects large portions of the tree. It should also be noted that when conditions are favorable, even the damaged branch tips showed marked increase in RWC, approaching normal levels (Fig. 4 and 5). Localized death of branches was sometimes observed where needle removal was excessive, but in many cases axial and terminal buds remained viable (as described by Saville, 1972), resuming growth in the summer (Fig. 15). Thus, while it is obvious that the growth forms at treeline are shaped by the differential

Figure 14. Black spruce in the subalpine zone on Lion Head, Mt. Washington. Characteristic "mop-head" form results from the removal of foliage by wind-carried ice particles in the zone of maximum transport above the snow-pack.



Figure 15. Balsam fir in the subalpine zone on Chandler Ridge, Mt. Washington, showing recovery from the effects of winter damage: Top, April 29, 1974; Center, July 3, 1974; Bottom, overview showing development of characteristic "mop-head" form.



success of wind-exposed vs. wind sheltered shoots, the process appears to be primarily mechanical, having little to do with differential drying of exposed and sheltered parts.

The overall importance of winter abrasion, in terms of its influence on treeline position in the Presidential Range, might best be argued by considering the case of birch wintering in the subalpine zone. The data in figures 4 and 5 indicate that birch, even with its greatly reduced evaporative surface, may be expected to share the same fate as the conifers with respect to winter water balance - a statement which points out the effectiveness of the dormant conifer needle in reducing water loss. Surprisingly, the deciduous habit in this case appears to be neither of advantage nor disadvantage in terms of winter water balance. Birch, however, is much less vulnerable to sustaining physical damage, a fact which, in view of the foregoing discussion, may be expected to confer some considerable advantage on the species. However, the fact that birch is only a co-dominant at treeline, ie. that it does no better than the conifers with which it shares this position, suggests that it is not the occurrence of physical damage alone which restricts growth at treeline, that perhaps some other factor such as restrictive summer temperatures is of controlling influence.

Thus, while Saville (1972) maintains that the significance of abrasive forces in winter is underestimated, and while wind is seen to be an environmental force of some consequence on Mt. Washington, it cannot be concluded that it is a controlling force by its mechanical effects alone.

Wind may be considerably more important in terms of its effect on temperatures at the metabolic sites of the plant during the growing season.

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