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Cold Period Plant-Water Relations Affecting Consumptive Use of Soil and Wastewater Reuse

Brian F. Chabot
University of New Hampshire

Peter J. Marchand
University of New Hampshire

Russell S. Kinerson
University of New Hampshire

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by

Brian F. Chabot
Peter J. Marchand
Russell S. Kinerson

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Summary

This report concerns the interactions between biological and environmental factors which affect the rate of water use from evergreen plants during the winter. Black spruce (Picea mariana) and balsam fir (Abies balsamea) were used as test species with paper birch (Betula papyrifera) serving as a control in some tests. The following analytical methods were employed:

1. Transpiration measured in laboratory experiments with excised branches under controlled conditions of temperature, light, water vapor pressure, and wind speed. These tests emphasized transpiration occurring at 0-10°C.

2. Evaporation rates from potted seedlings during the summer with close environmental monitoring.

3. Annual monitoring of plant water status and anatomy, particularly during the winter, as a means of extending laboratory-derived data to the field.

Branches of black spruce brought into the laboratory during the winter had initially low transpiration rates with several hours to days required to reach a steady and high water loss rate. Transpiration proved to be very sensitive to radiation loads at temperatures above 1°C. Maximum water loss at a radiation intensity of 1.1 ly/min was 0.013 $ml/dm^2/hr$ at an air temperature of 5°C, wind equal to 200 cm/sec, and water vapor pressure deficit of .150-.165 mm Hg. The leaf resistance to water loss under these conditions was 121 sec/cm. There was a significant lag of about 3 hrs between change in radiation load and stabilization of transpiration. Transpiration was also highly temperature sensitive with a Q_{10} of 6 from 1-5°C and 4.9 from 1-10°C. At 1°C and below there was an inhibition of transpiration, loss of sensitivity to radiation, and an undamped oscillation of water loss. Increased wind speeds decreased transpiration through convectional cooling of the needles.

Summer evaporation from potted seedlings reached a maximum of 0.42 $ml/dm^2/hr$ for spruce, 0.40 for fir, and 1.19 for birch. Highest rates occurred early in

the season at maximum leaf expansion and declined throughout the summer. Water loss dropped off rapidly in the fall in paper birch with leaf senescence. For the conifers water loss was most related to daily maximum air temperatures, while for birch a combination of average relative humidity and total daily radiation was correlated most closely with total daily water loss.

Field studies during the winter indicated that transpiration was very low to not measurable using the techniques employed. Relative water content (RWC) of healthy branches averaged 90% for spruce and 91.4% for fir, corresponding to a water potential of -11 bars. The lowest RWC was 87.4% for spruce (-17.5 bars) and 84.7% for fir (-28 bars). Change in RWC during the winter was not correlated with air temperature, wind speed, or radiation.

Anatomical studies throughout the season indicated that maturation of the needle and especially cuticle formation occurred early in the season with some development continuing throughout the summer. By fall, the needles are covered with waxy materials which partially "plug" stomatal openings and increase resistance to water loss. Between November and March, the needles appear to be physiologically dormant. Physiological dormancy could be responsible for low rates of water loss during the winter and the lag times for transpiration noted above.

Winter water transport by conifers is likely to be several hundred times less during the winter than during the summer due to a combination of both biological and environmental controls. The total quantity of water used by a stand during winter will depend upon total leaf area in the stand, but may be appreciable even with the restricted rates of water loss noted here. However, water loss by broad-leaved species during the growing season would be substantially greater than for conifers.

Introduction

Studies directed toward the management of watersheds during the winter have, for the most part, focused on the role of vegetation in snow accumulation and melt processes (Kittredge, 1956; Martinelli, 1965; Miller, 1965). Little attention has been given to the transfer of water from the soil to the atmosphere by the transpiration process during the winter. Because of the generally low atmospheric vapor pressures associated with low winter air temperatures, the atmosphere may serve as a strong sink for water vapor transfer from plant surfaces. Transpiration might therefore be important anytime during the winter period when the translocation pathways are not frozen, particularly in areas heavily forested with coniferous species. Whether or not this process is significant in terms of watershed management objectives is simply not known. Transpiration may also be important in certain managed situations. In particular, where spray irrigation is used as a means of water treatment, water and soil temperatures may be kept above freezing. In these cases, a functional vegetation cover may be necessary for proper operation of the filtration system through transpiring excess water and recovering nutrients. Both environmental and biotic controls on water use under near freezing temperatures need to be explored.

Physical models describing evaporation have been developed for both plant communities and individual leaves (Penman, 1963; Gates, 1968; Penning de Vries, 1972; Rouse and Stewart, 1972). Transpiration from a single leaf is most conveniently expressed as a direct function of the water vapor concentration gradient between leaf and air and inversely related to resistances in the diffusion pathway as follows:

$$T = \frac{c_l - c_a}{r_l + r_a}$$

where T is the transpiration rate, $c_l - c_a$ is the vapor concentration difference between leaf intercellular spaces and the bulk air outside the leaf boundary layer, and r_l and r_a are the leaf and boundary layer resistances to water vapor diffusion. Environmental variables such as temperature, wind speed, radiation load, and water vapor cover affect all terms of this equation. Leaf resistance, r_l, is primarily a biological variable influenced by leaf development, light, external humidity, and CO_2 (see Meidner and Mansfield, 1968; Lange et al., 1971). Boundary layer resistance occurs in a layer of air next to the leaf surface and is proportional to the thickness of this layer. Boundary layer thickness is a direct function of leaf size and inversely related to wind speed. The water vapor concentration gradient is affected by temperature since saturation vapor pressure increases greatly with rising temperature. The gradient steepens as leaf temperature increases above air temperature. Leaf temperature, in turn, depends upon the incident radiation load as well as the cooling effect of transpiration and convection (Gates and Papain, 1971). We see these subtle interactions between biological and physical variables. The biological functions are the least well known.

Variable leaf resistances to the outward diffusion of water vapor account for most of the departure of transpiration rates from physical models based on potential evaporation. With the onset of the cold period it is generally assumed that leaf resistances increase significantly due to stomatal closure and remain high throughout the dormant season. There are several reports of limited photosynthetic activity in winter (e.g. Parker, 1961; Schulze et al., 1967) but stomatal opening has not been observed (Tranquillini, 1964), though this may be the result of insensitive experimental techniques. If vapor diffusion is limited to cuticular pathways, the leaf resistance may indeed become very high. This would have the effect of greatly reducing transpiration rates.

Significant increases in leaf resistance also can be expected to alter the relative importance of environmental variables affecting the transpiration rate, particularly with respect to the significance of wind and the processes of heat and water vapor transfer. When the diffusive resistance of the leaf is very high relative to the boundary layer resistance, reduction of the latter by high winds may become insignificant in terms of increasing vapor transfer. The dominant effect of wind might instead shift toward the consequences of forced convection, e.g. reduction of leaf-air temperature differences and consequent reduction of the vapor concentration gradient between the leaf interstices and the bulk air. These relationships have never been systematically investigated under controlled conditions, though it is clearly important that they be understood before any attempt is made at modeling winter plant-water use. This study therefore focuses on the interaction of environmental and biotic factors, particularly the role of leaf resistances, affecting the rate and quantity of water loss via the plant pathway during the winter.

Methods

Experimental Plan

This study focused on the water relations of conifers. The year-round maintenance of leaf surfaces by evergreen species initially suggests a more important role in watershed hydrology during rhe winter and spring than would be the case for deciduous trees. Our study focused on two principal questions: (1) what environmental factors regulate transpiration at low temperature, and (2) what is the extent of biologic control over water loss under winter conditions. These questions were answered from three basic approaches. First, transpiration was measured in the laboratory with excised branches under controlled conditions of temperature, light, water vapor pressure, and wind speed. These tests emphasized transpiration occuring at 0-10°C and were intended to explore basic environmental controls over transpiration. Second, evaporation rates were determined for potted seedlings during the summer with close environmental monitoring. This permitted a seasonal compariosn of transpiration rates. Third, plant water status and anatomy were monitored throughout the year on naturally growing trees. This served as a means of extending laboratory-derived data to the field.

Growing-Season Transpiration

As a basis for evaluating winter transpiration rates, the growth-season transpiration of potted seedlings of yellow birch (*Betula alleghaniensis* Britt.), balsam fir (*Abies balsamea* (L.) Mill.), and black spruce (*Picea mariana* (Mill.) BSP.) 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. 1). 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. Environmental variables monitored were wind speed, total solar

radiation (YSI Integrating Pyranometer), temperature, and relative humidity. Additionally, evaporation was monitored with both a black, flat-surfaced Livingston Atmometer and a Piche Evaporimeter. Leaf area for yellow birch was determined by establishing a relationship between leaf lenght and area as measured with a dot grid, and thereafter measuring the leaf lengths for 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 alos for later controlled-environment experiments. The seasonal course of transpiration was thus obtained and correlated with atmospheric variables by a stepwise multiple regression analysis for the period June to October, 1973.

Winter Transpiration: Laboratory Experiments

With the onset of dormancy, the gravimetric technique became too insensitive for transpiration studies. Sealing the pots with paraffin 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 the potted seedlings. Therefore a system of potometers, six in all 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 using silicone rubber (General Electric 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.

Fig. 1. Experimental setup for growth-season transpiration study.

The potometer system was then positioned in a wind tunnel such that only the plants protruded into the airstream. Wind velocities up to 715 cm sec^{-1} (16 mph) were controlled by changing fan speed with a variac transformer. Wind speeds were measured with a hot-wire thermistor-type anemometer (Hastings-Raydist). 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°. Relative humidity was not controlled but was stable ($\pm$ 5%) throughout any given experiment. General Electric 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 in the chamber, from the lamps, remained constant, contributing to the stability of the relative humidity. Radiant load on the plants was measured with a silicon cell pyranometer (Lambda Instruments). Very fine copper-constantan thermocouples were embedded in the leaf tissue allowing 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 in order to monitor evaporation simultaneously with transpiration.

Winter Transpiration: Field Methods

In the field, winter transpiration losses were related qualitatively to fluctuations in tissue relative water content (RWC).* Two sites were visited frequently, one at treeline on Mt. Washington (Fig. 2), representing a severe winter climate (Table 1), and the other at a lower elevation in Madbury, N.H. 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

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* $RWC = \frac{\text{weight fresh} - \text{weight dry}}{\text{weight turgid} - \text{weight dry}} (100)$

Fig. 2. Chandler Ridge field site, Mt. 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.

	Average Daily Maximum (°C)	Number of Days Maximum Above 0°C	Average Daily Minimum (°C)	Number of Days Soil Above 0°C	Precipitation as Snow or Ice (cm)	Total Precipitation - Water Equivalent (cm)	Average Hourly Wind (m sec^{-1})	Average Hourly Wind (mph)	% of Possible Sunshine
1972-73									
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
1973-74									
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

transported in a cooler to minimize water loss. At the lab, a fresh weight to an accuracy of 4 decimal places was obtained. 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 arising from differences in the temperature of the leaf tissue when collected and the temperature at which water uptake is allowed (Millar, 1966) were 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 thus 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 versus water potential as determined by thermocouple psychrometer and pressure bomb. Fluctuations in tissue RWC were then related, again by stepwise multiple regression, to variations of air temperature, wind speed, and radiation load. These data were obtained in part from the records of the Mt. Washington Observatory and in part from recording soil and air thermographs at the study site (Fig. 2). Attempts at maintaining a recording pyrheliometer at the Mt. Washington site failed so daily insolation was estimated by the method of Hamon et al. (1954) from the Observatory records of daily sunshine duration. Records for the two years of study are summarized in Table 1.

Seasonal Anatomical Studies

Tissue samples were obtained from balsam fir and black spruce grown under three conditions: at timberline (1250 m) on Mt. Washington, N.H.; in a transplant garden near Durham, N.H.; and from individuals propagated in a cool greenhouse (10-20°C). Collections were made on a monthly basis. Samples were taken from the middle of the needle and were immediately fixed in either 5% glutaraldehyde

or 2% glutaraldehyde and 1% formaldehyde (from paraformaldehyde) in 0.1 M Na-K phosphate buffer, pH 7.2, for 2-4 hrs. The tissue was washed and stored in buffer before post-fixation in 1% OsO_4 in Na-K phosphate buffer (0.05-0.1 M), pH 7.2, for 1-2 hrs. After rapid dehydration in acetone and passage through propylene oxide, the material was embedded in an Epon-Araldite mixture or a low viscosity resin (Spurr, 1969). Sections were cut on a Sorvall Porter-Blum MT-1 microtome. Thick sections for light microscopy were stained with toluidine blue. Thin sections were mounted on copper grids and stained with uranyl acetate and lead citrate. Grids were examined with a Phillips 200 or 300 electron microscope.

Surface features of the needles were studied with scanning electron microscopy. Fresh needles were quickly frozen in liquid nitrogen and freeze-dried. Specimens attached to stubs with silver paint were coated with gold-palladium. Observations were made with an I.S.I. Mini-SEM.

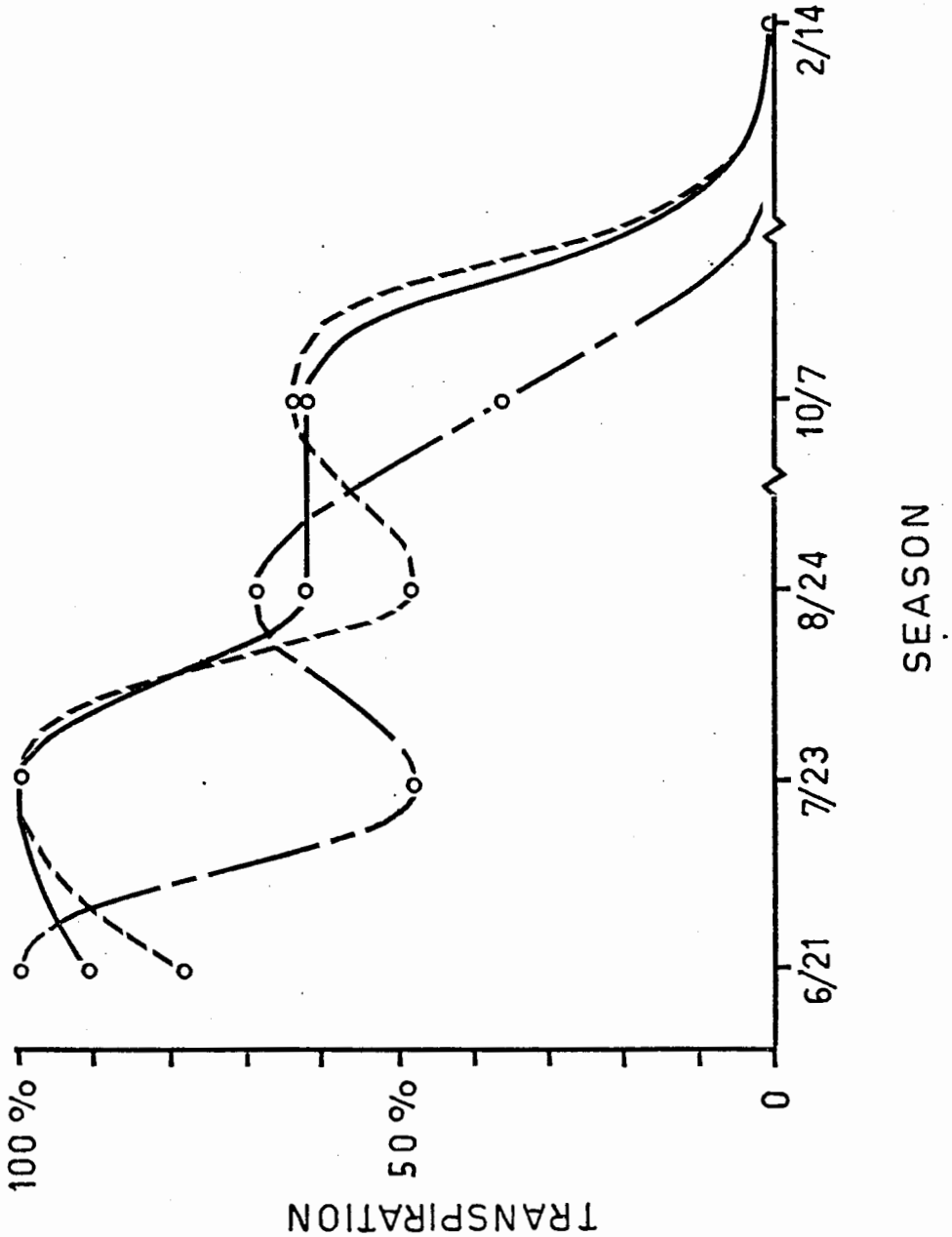
Results

Summer Growing Season

The time of maximum transpiration per unit area of leaf surface for yellow birch occurred in late June (Fig. 3). Bud burst and needle elongation were slower in the two conifers so that their maximum transpiration occurred fully one month later. At their maxima, transpiration rates were 1.19, 0.40, and 0.42 $ml/dm^2/hr$ 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). Results from the same gravimetric procedure used in midwinter (in the greenhouse) showed no significant difference at the 95% confidence level between water loss from the spruce and fir seedlings and that from the soil controls.

Correlations of summer transpiration rates with 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) with mean relative humidity, wind speed, and radiation load accounting for very little of the variation in transpiration. In the case of paper birch, mean relative humidity appeared to account for most of the variation but with an insignificant correlation coefficient of 0.16. When combined with radiation, however, the correlation coefficient was improved considerably ($R = .69$), i.e. the two variables taken together were many times more significant than either one alone. Evaporation from bare soil was most sensitive to radiation ($R = .81$) but with each added variable improving the regression equation considerably.

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



	Variable	S.S. Reduced	Adjusted R	Reg. Coef.
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)

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.

All four variables taken together accounted for 96% of the variation in soil-water loss.

The use of either the Livingston atmometer or the Piche evaporimeter as an indicator of "transpiration demand" does not appear satisfactory.

Winter Transpiration: Laboratory Experiments

Several factors were found to affect plant water use during the winter. Indications are that with freezing at least some disruption of the water column occurs in black spruce 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 3-4 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. 4). Initially the transpiration rate (averaged for four branches over the first 4 hrs) was just under 0.006 $ml/dm^2/hr$ 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 preceding 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. 4).

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°C $\pm$ 0.5°, and with the wind speed constant at 200 cm sec^{-1}, transpiration increased from 0.005 $ml/dm^2/hr$ in the dark to 0.009 $ml/dm^2/hr$ at a radiation level of 0.5 ly min^{-1} and 0.013 $ml/dm^2/hr$ at a radiation level of 1.1 ly min^{-1} (Fig. 5). Each increase in transpiration, however, lagged 3 hrs behind the increase in evaporation from the wet filter paper disk (Fig. 5). With the leaf boundary layer resistance assumed negligible at a wind speed of 200 cm sec^{-1}, the leaf resistance to transpiration was

Fig. 4. 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}.

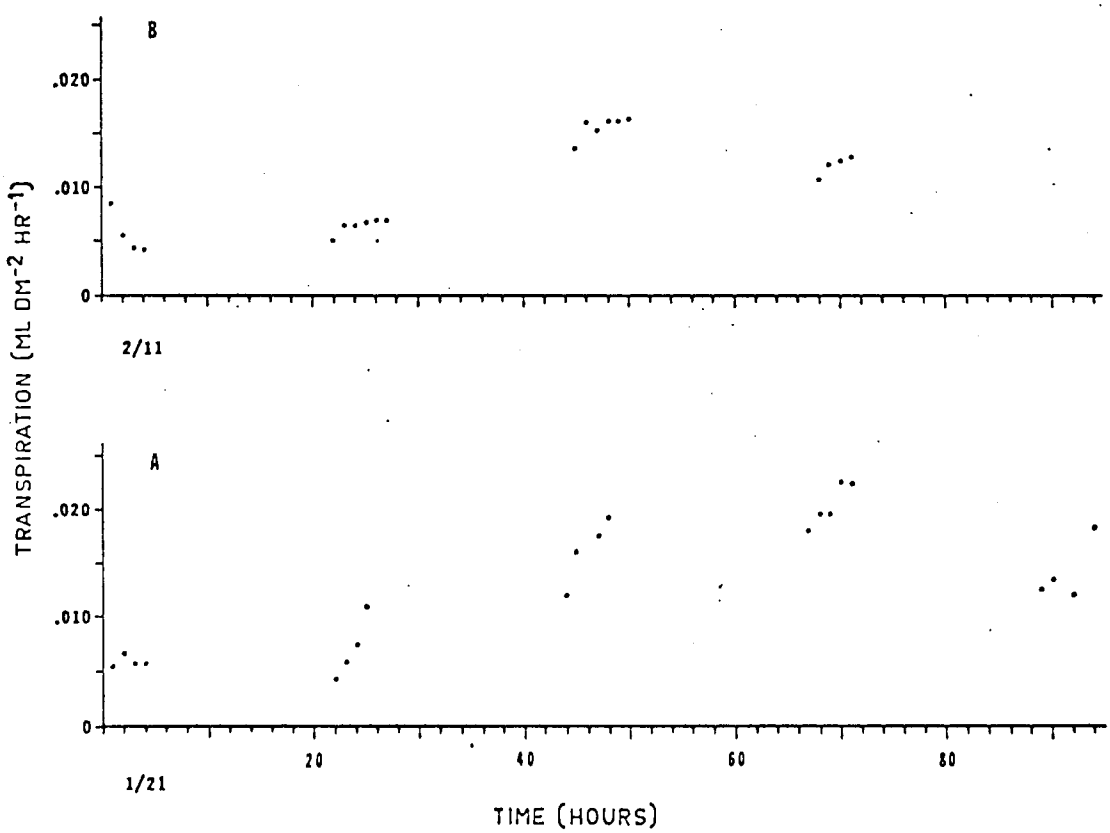
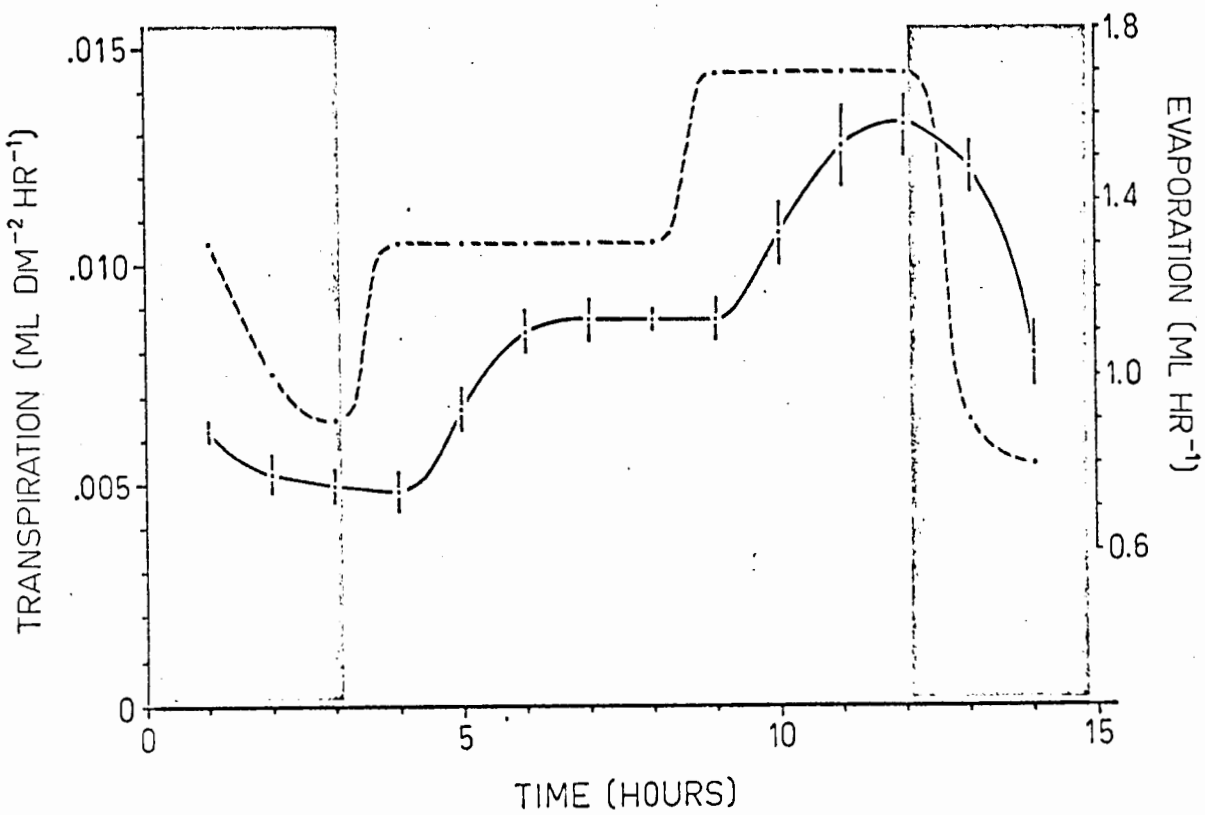


Fig. 5. Transpiration as a function of radiation intensity under constant temperature (5°C), humidity (35-41%), and wind speed (200 cm sec^{-1}). Light regimes are: darkness (heavy shading), 0.5 ly min^{-1} (light shading), and 1.1 ly min^{-1} (unshaded). Vertical lines indicate standard deviation of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



calculated* 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 approximately 2°C), however, the change in leaf resistance with increasing light intensity was inhibited. Switching the light intensity from 0 to 1.1 ly min^{-1} resulted in an oscillation of transpiration for 6 hrs about a mean of 0.003 $ml/dm^2/hr$, corresponding to an average leaf resistance of 280 sec cm^{-1}, only slightly lower than the average dark leaf resistance of 346 sec cm^{-1} (Fig. 6). 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 Fig. 6, the dashed line represents the predicted 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-hr intervals (Fig. 7). A summary of light and temperature effects on leaf resistance is given in Fig. 8.

The net effect of increasing wind speed at constant 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. 9), while evaporation increased almost linearly. Dark transpiration rates were unaffected by changes in wind speed between 0 and 200 cm sec^{-1}.

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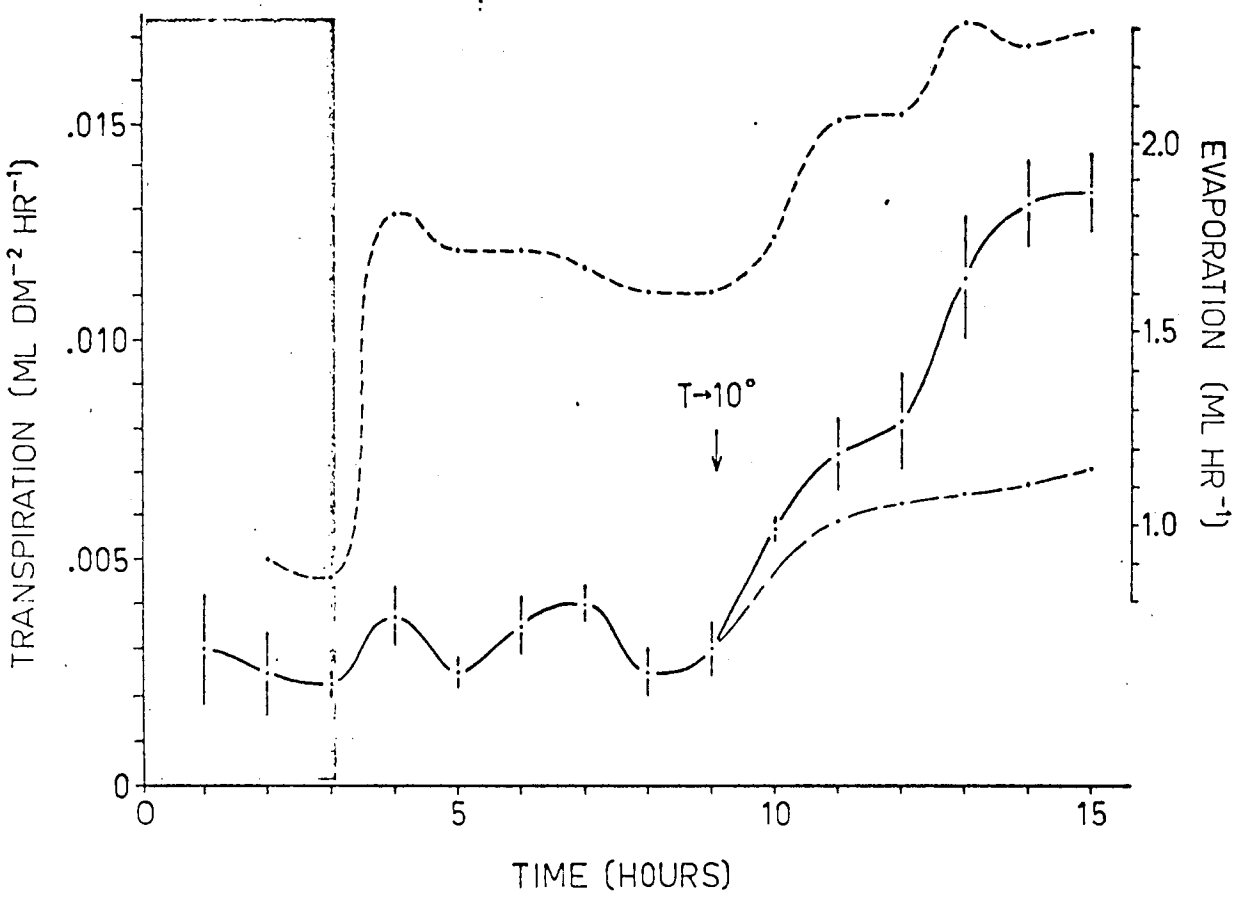
* Leaf Resistance = $\frac{C_L - C_a}{T + r_a}$ where C_L and C_a are the vapor concentrations of leaf and air respectively. T is the transpiration rate, and r_a is the boundary layer resistance (Ehrler and van Bavel, 1968).

Fig. 6. 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 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.



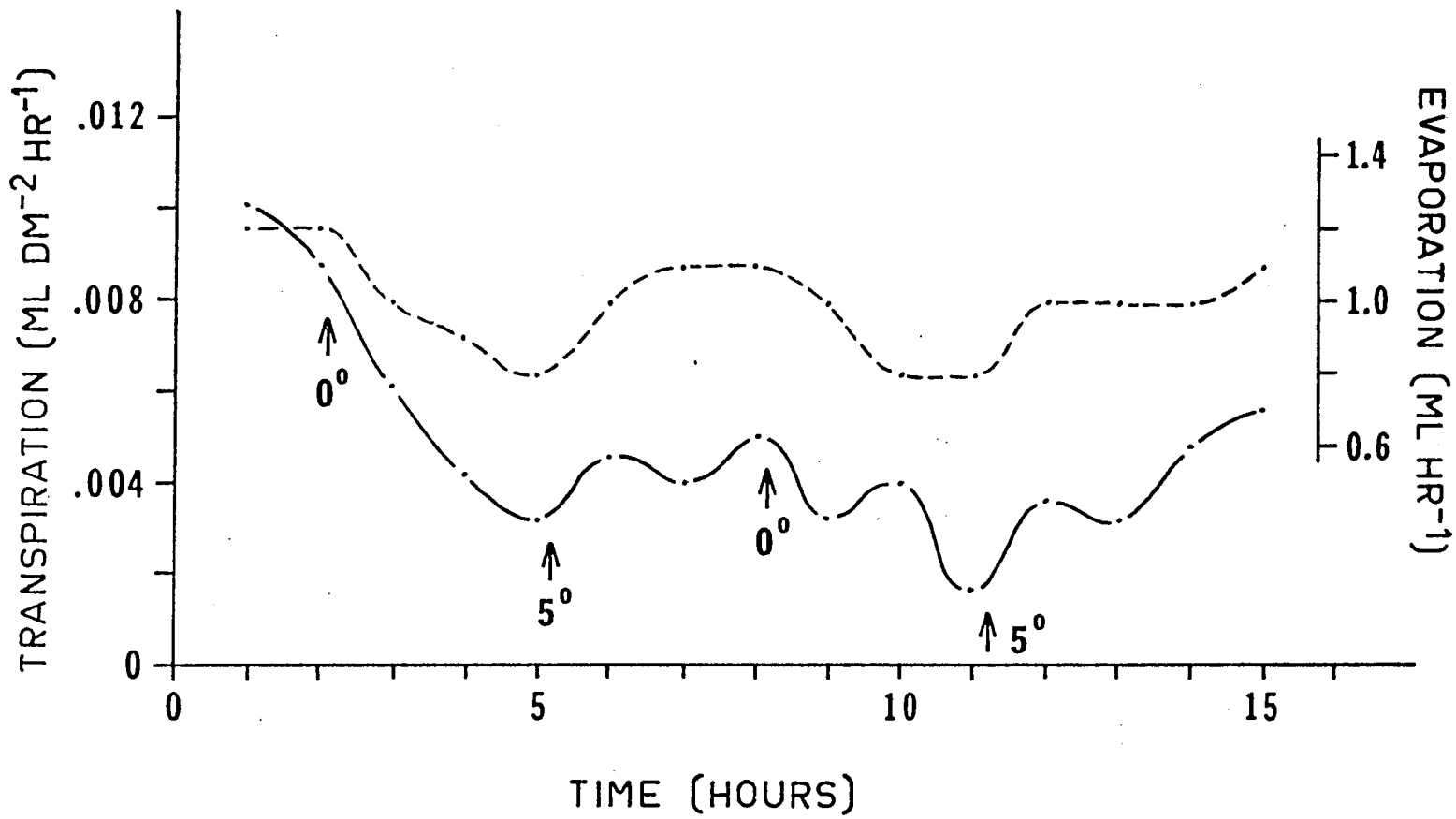


Fig. 7. Transpiration with cyclic changes in temperature between 0°C and 5°C. Constants: Radiation 0.5 ly min^{-1}, wind speed 200 cm sec^{-1}. Dashed line represents evaporation.

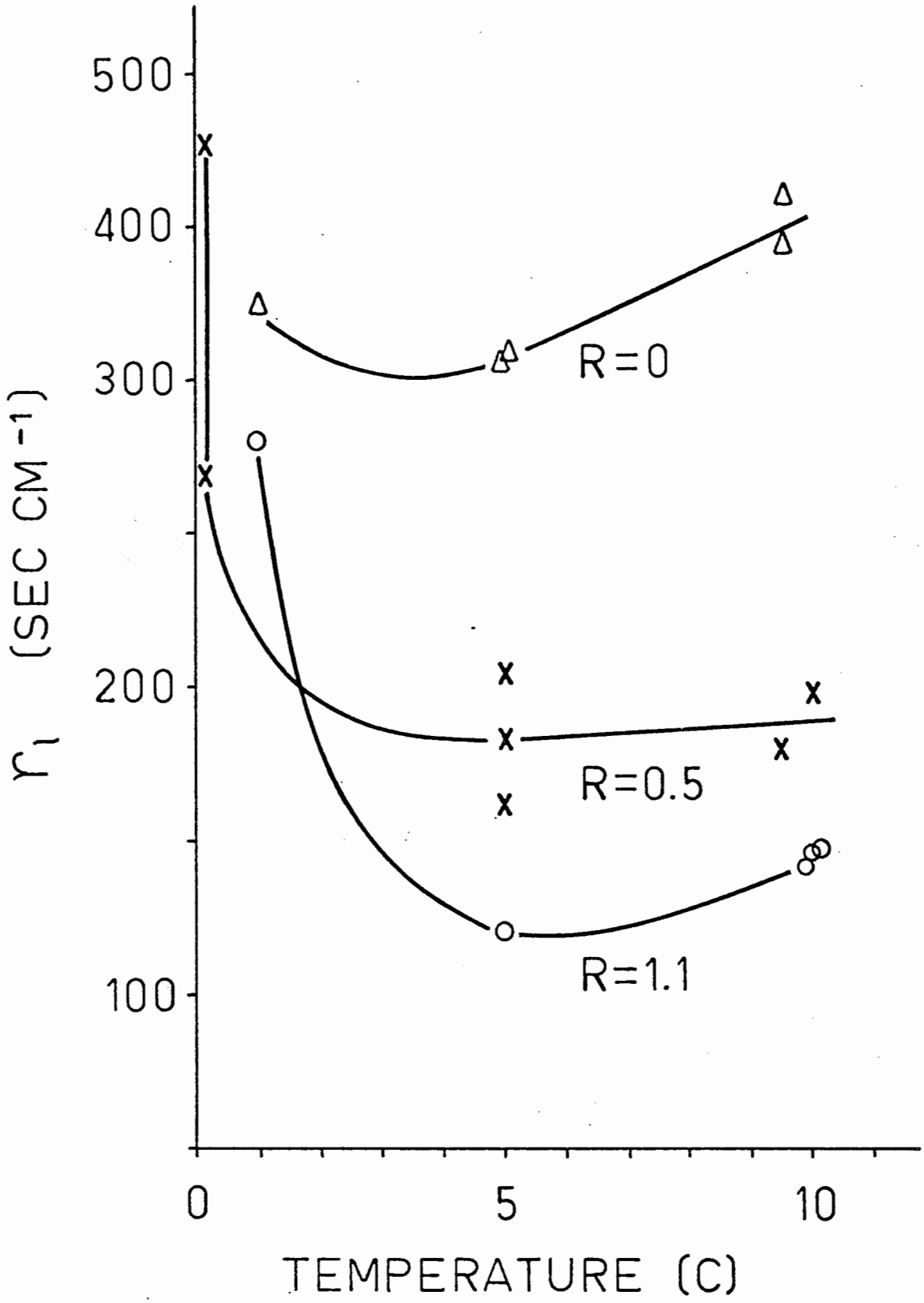


Fig. 8. Summary of radiation and temperature effects on calculated leaf diffusion resistance.

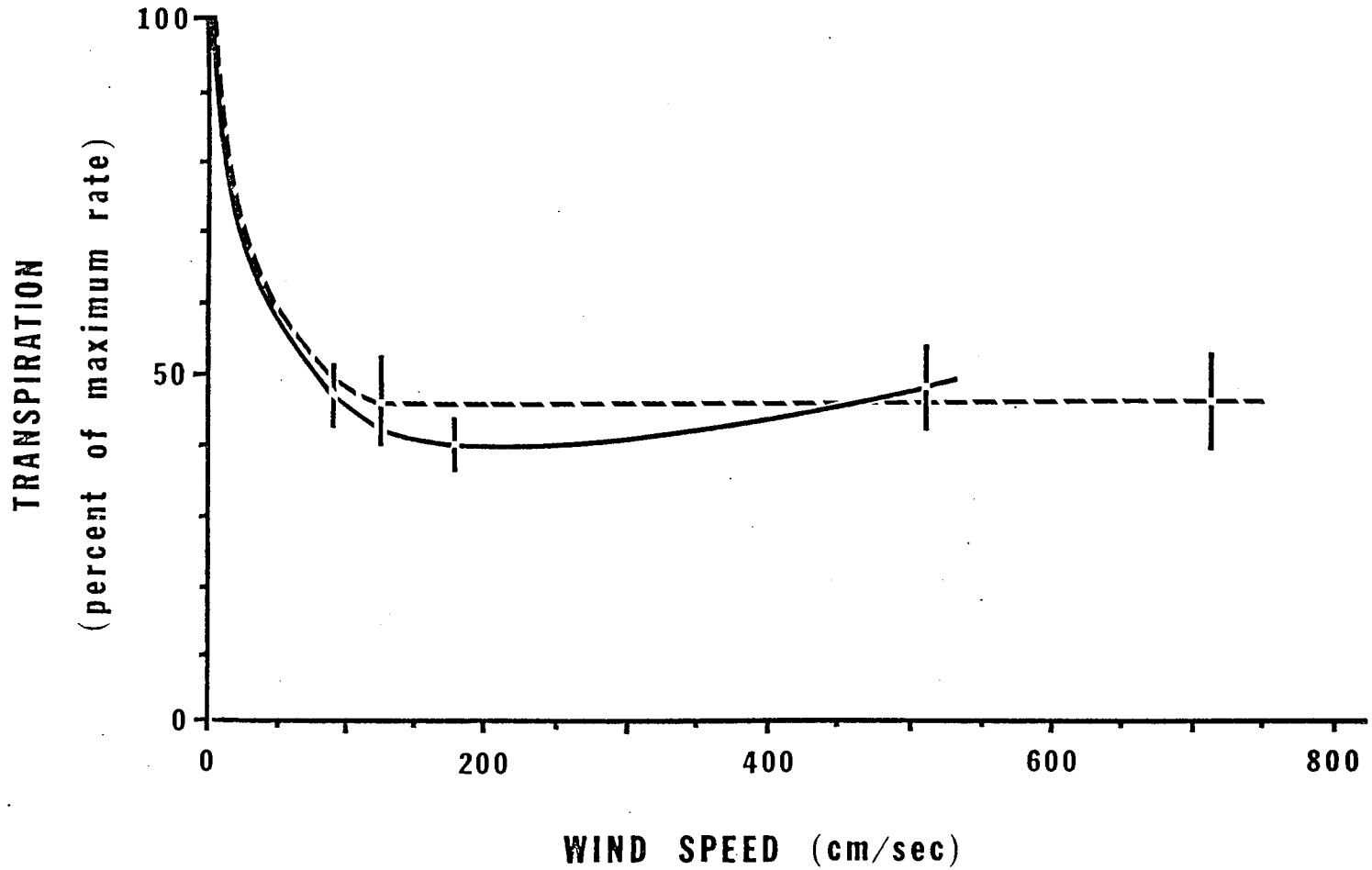


Fig. 9. Transpiration as a function of wind speed under radiation intensities of 0.5 ly min^{-1} (————) and 1.1 ly min^{-1})(— — —) . Vertical bars indicate standard deviation of the mean.

The effect of wind on transpiration is apparently related to the energy transfer efficiency at low wind speeds. In still air, leaf temperatures were raised 5.5°C ± 1.3°C (s.d.) above air temperature under a radiation intensity of 0.5 ly min^{-1}, and 9.8°C ± 2.5°C (s.d.) above air temperature under a radiation intensity of 1.1 ly min^{-1}. These temperature differentials were reduced, however, to 0.8°C ± 0.7°C and 1.8°C ± 1.6°C for radiation levels of 0.5 and 1.1 ly min^{-1} respectively at a wind speed of 90 cm sec^{-1} (Fig. 10). Thermal equilibrium between leaf and air was maintained for both radiation levels at a wind speed of 700 cm sec^{-1}.

Winter Transpiration: Field Observations

At the Mt. Washington field site, the relative water content of undamaged tissue fluctuated about a mean of 90.0% for black spruce and 91.4% for balsam fir over both 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) (Fig. 11). These values appear normal for the species (compare, for example, the data points of September and October, 1973) and correspond to a plant-water potential of approximately -11 bars in each species (Fig. 12). The lowest mean 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 10 sampling dates of 91.3% (Fig. 12).

Tissue which had suffered mechanical damage, e.g. needle breakage, showed similar fluctuations but consistently lower relative water contents than the undamaged samples (Figs. 11 and 12). During the 1972-73 winter, the RWC of damaged spruce and fir averaged 88.3% and 84.4% respectively. Over five sampling

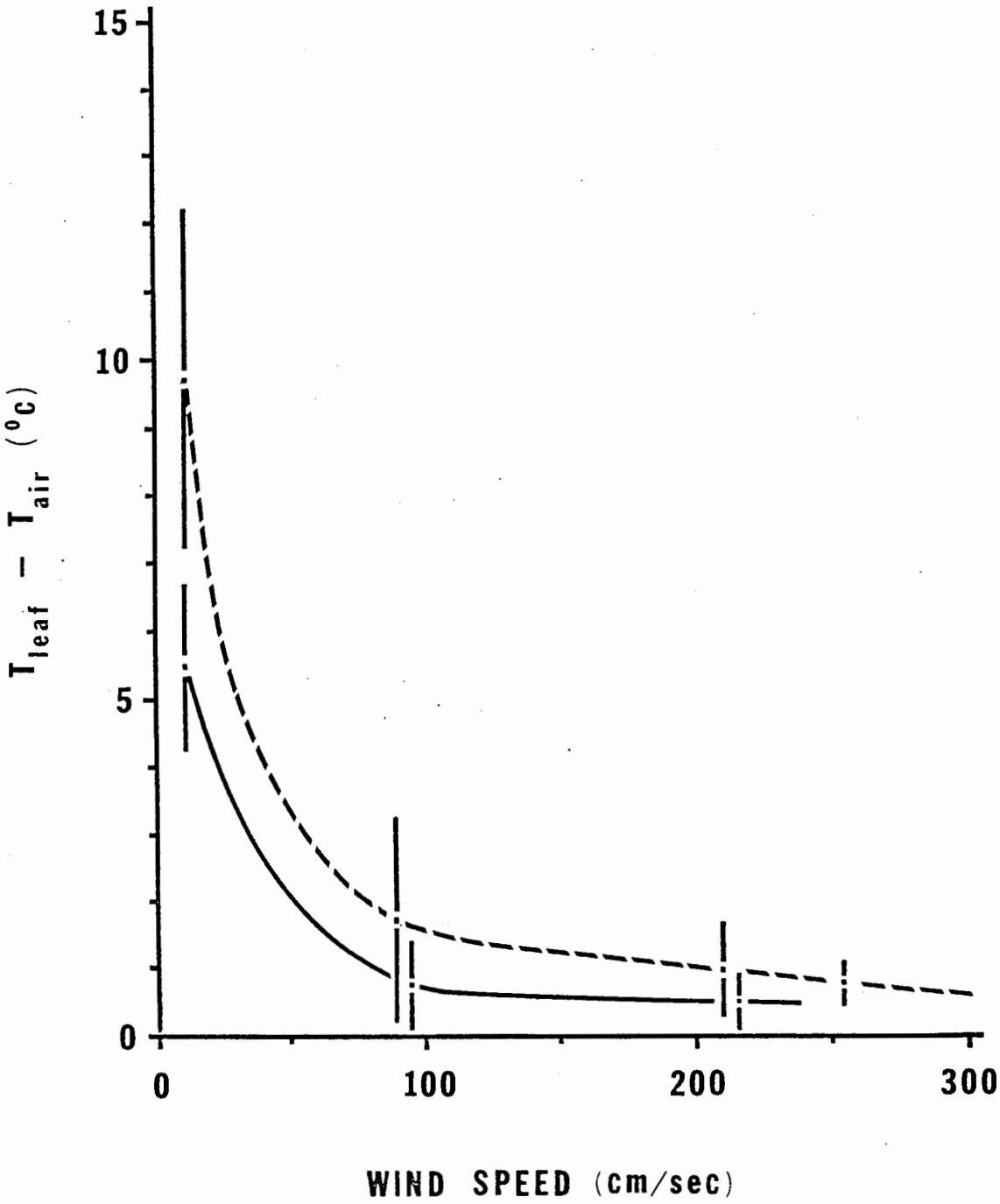


Fig. 10. Leaf-air temperature differences as a function of wind speed under radiation intensities of 0.5 ly min^{-1} (————————) and 1.1 ly min^{-1} (— — — —) Vertical bars indicate standard deviation of the means.

Fig. 11. 1972-1973 seasonal course of relative water content in exposed branches of paper birch (Δ), black spruce (•), and balsam fir (o) from treeline, Mt. Washington, N.H. Dashed line represents damaged samples.

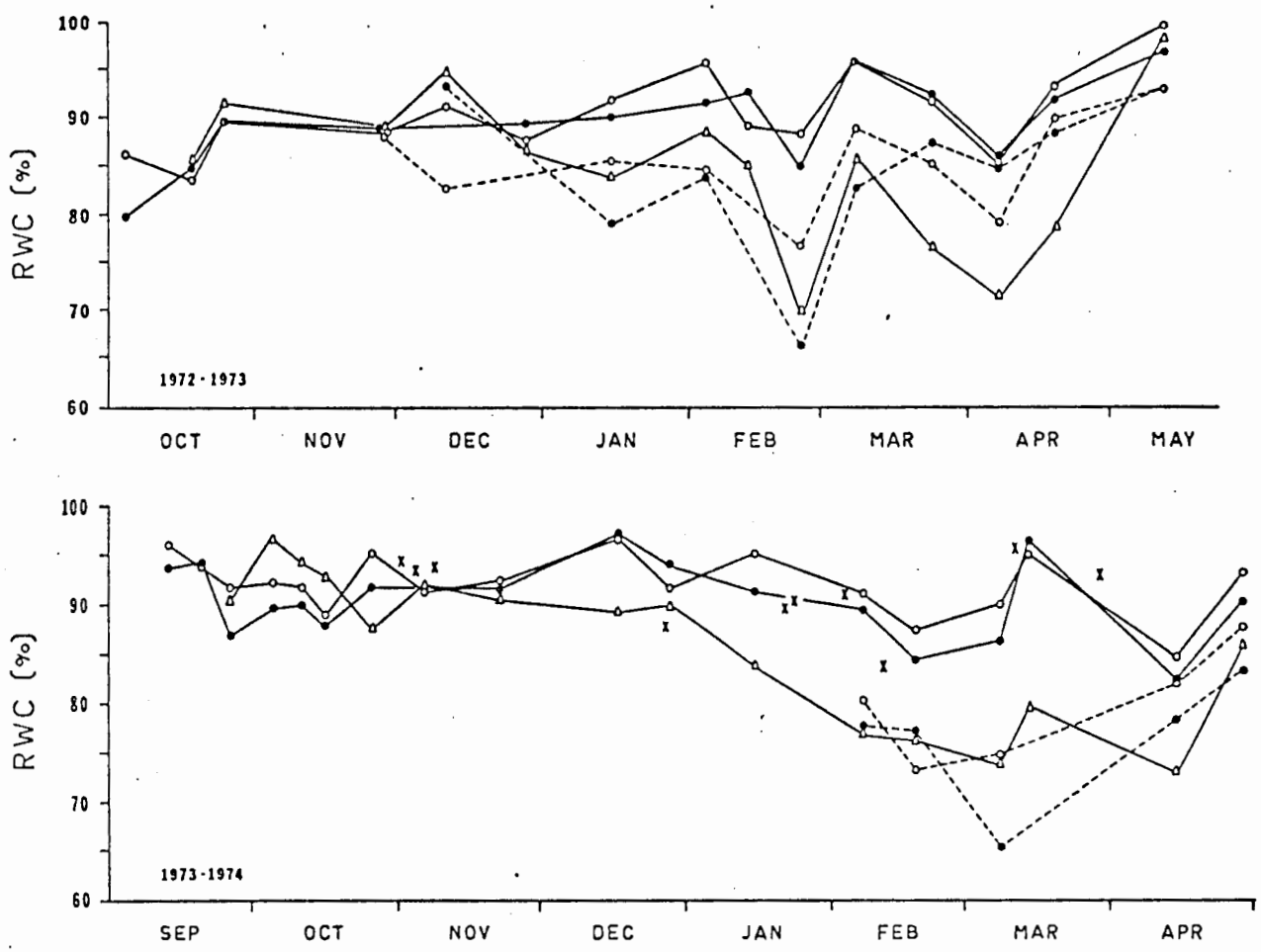
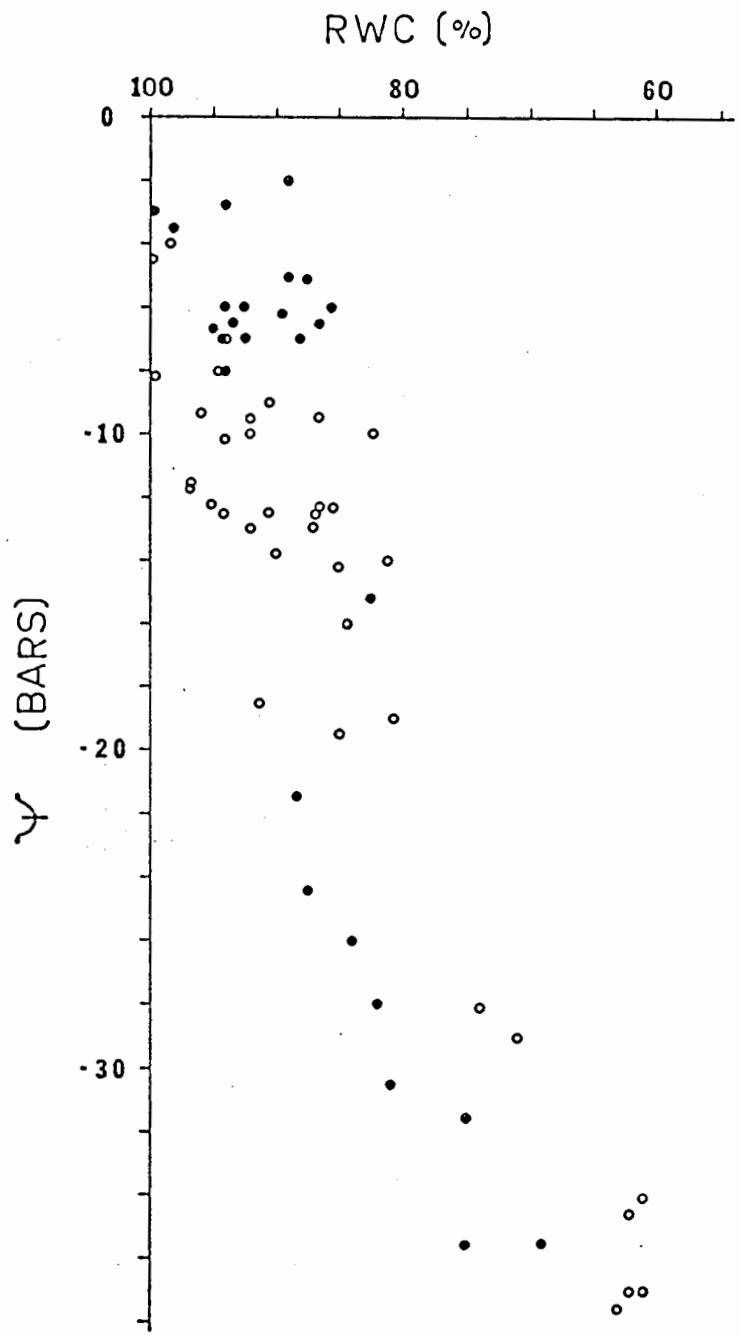


Fig. 12. Plant-water potential (Ψ), determined by thermocouple psychrometer and pressure bomb, as a function of relative water content (RWC) for balsam fir (o) and black spruce (•).



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 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%. Within either damaged or undamaged samples there was no significant difference in RWC between different age class needles. By early May the differences between damaged and undamaged samples had mostly disappeared (Fig. 11).

The seasonal trend of RWC in leafless birch stems somewhat paralleled that of the two conifers except that the water content 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 12.2 for samples of 6 stems on each of 3 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 (Fig. 11).

Fluctuations of tissue RWC in the field did not correspond to changes in temperature, wind speed, and radiation with the same sensitivity indicated in the controlled-environment studies. Results of a stepwise multiple regression analysis are given in Table 3. The average maximum air temperature of the 2 days prior to sampling accounted for the greatest amount of variation in the RWC of the conifers but showed a correlation coefficient of only 0.21 for spruce and 0.32 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 3 days prior to sampling accounted by itself for most of the sample variation, but again the correlation

	Variable	S.S. Reduced	Adjusted R	Reg. Coef.
Fir	2-day Max. Temp. (°)	33.550	0.322	0.144
	4-day $\overline{m}$ Wind	3.974	.272	0.036
	3-day Tot. Radiation	1.941	.172	0.001
			(Y intercept = 87.189)	
Spruce	2-day Max. Temp. (°)	28.218	0.208	0.122
	3-day Tot. Radiation	1.429	0	-0.001
	2-day $\overline{m}$ Wind	0.309	0	0.015
			(Y intercept = 87.471)	
Birch	3-day Tot. Radiation	181.726	0.349	-0.009
	3-day $\overline{m}$ Temp.	154.488	.479	0.291
	4-day $\overline{m}$ Wind	22.912	.457	0.085
			(Y intercept = 80.343)	

Table 3. 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.

coefficient was a low 0.35. Adding temperature and wind speed data into the regression improved the correlation only slightly (Table 2).

Seasonal Anatomical Studies

A complete description of developmental and seasonal changes in the mesophyll ultrastructure of balsam fir has been summarized elsewhere (Chabot and Chabot, 1975). Both black spruce and balsam fir behave in similar ways such that a description of the latter will suffice.

Dominant buds of balsam fir were conical in shape and covered with a translucent resinous material which turned whitish during the winter or early spring. Bud break occurred in May for trees grown at Durham and in June on Mt. Washington. Needles elongated to about 5 mm at the time of bud break. Externally, differentiation of the needles was seen to be more advanced at the tips and less mature at the base as indicated by the presence of wax-filled stomatal pores.

The youngest tissue examined was from a needle still in the bud in a region that had not yet formed stomata (Fig. 13). The epidermis consisted of large cells, some of which were still dividing. These cells contained poorly developed vacuoles, chloroplasts which appeared weakly photosynthetic, and a thin cuticular layer. Within the mesophyll, major cell types had differentiated. Differentiation of mesophyll advanced from the vascular tissue towards the sides of the leaf. Stomata had differentiated and substantially matured at bud break.

Mature cells (Figs. 14 and 16) had a large central vacuole, a spherical nucleus to one side with one to several small nucleoli, and a thin layer of cytoplasm around the wall. Changes in the organelles included a reduction of ribosomes and rough endoplasmic reticulum in the cytoplasm, great increase in the number and size of chloroplasts, decrease in the mitochondrial cross-sectional area per area occupied by chloroplasts, and an increase in the number of

Fig. 13. Epidermal cells in very young leaf from bud. Chromatin (Cr) in the nucleus (N) is visible. Vacuole (V), cuticle (Cu), and chloroplasts (C) are poorly developed. UA/PbC. 9000x.

Fig. 14. Mature epidermal cells. Cell walls (W), cuticle (Cu), and surface wax deposits (Wx) are well developed. Nucleus (N) and chloroplasts (C) surround the vacuole (V). UA/PbC. 9000x.

Fig. 15. Cross section of mature needle. Cuticle (Cu), epidermis (Ep), and hypodermis (H) surround loosely organized mesophyll cells (M). Stomata (St) are present on lower surface. UA/PbC. 100x.

Fig. 16. Mature mesophyll cell showing well-developed starch grains (S), mitochondria (Mi), and microbodies (Mb). Lipid deposits (L) occur in vacuole (V). UA/PbC. 13000x

Fig. 17. Chloroplasts aggregated in winter. Long lamellae are appressed in regions. Plastoglobuli are present, but no starch. A dense deposit is present on the tonoplast. Small lipid droplets are seen along the wall. UA/PbC.]3,000x.

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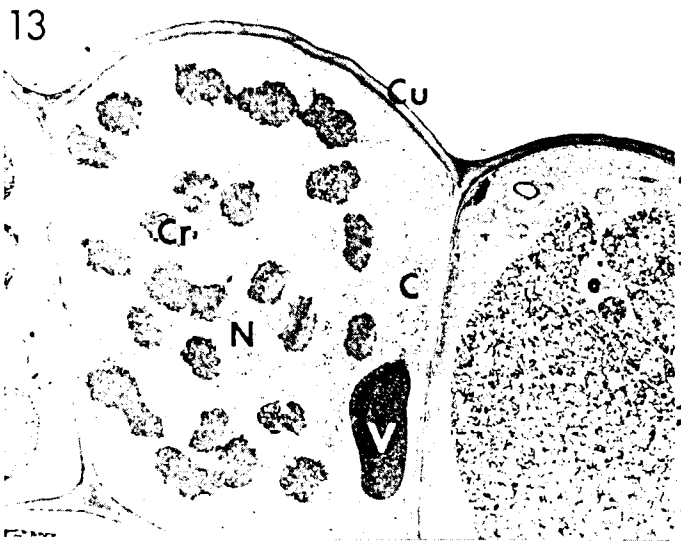

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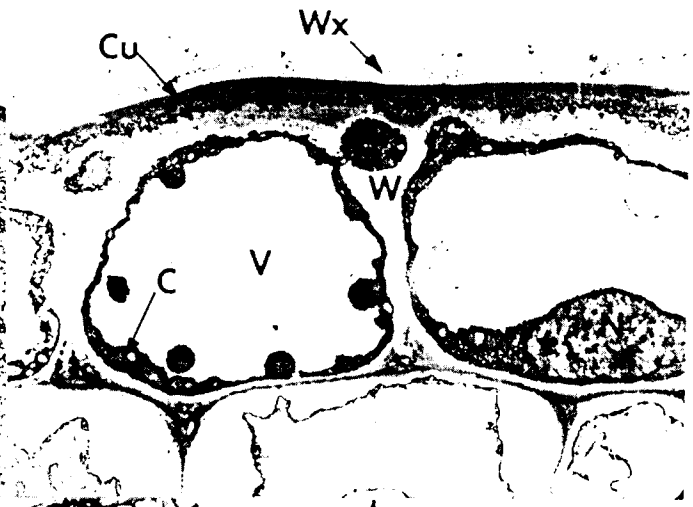

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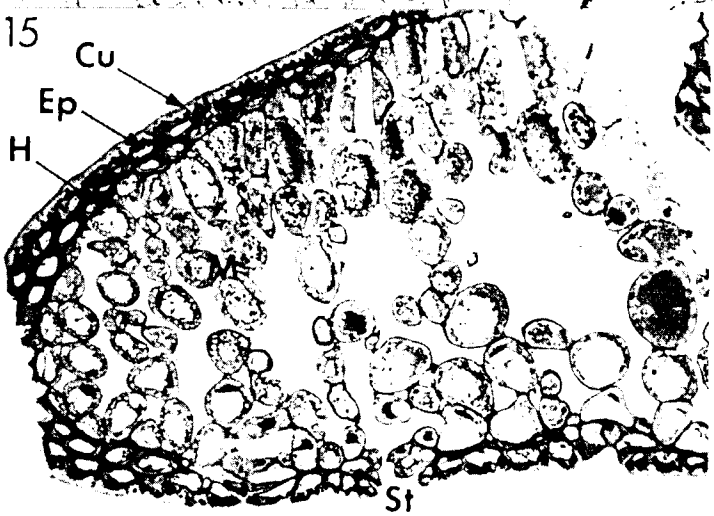

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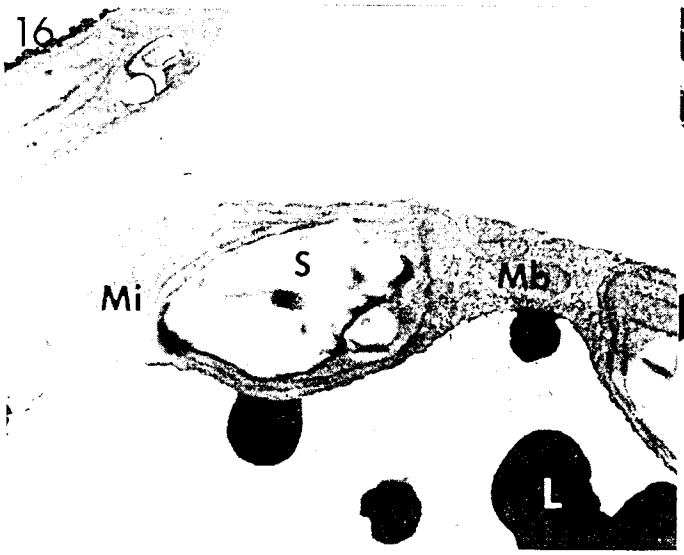

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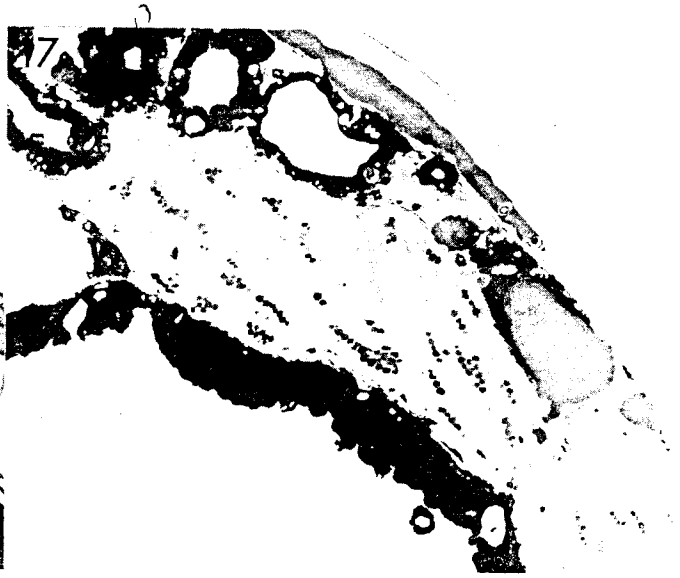

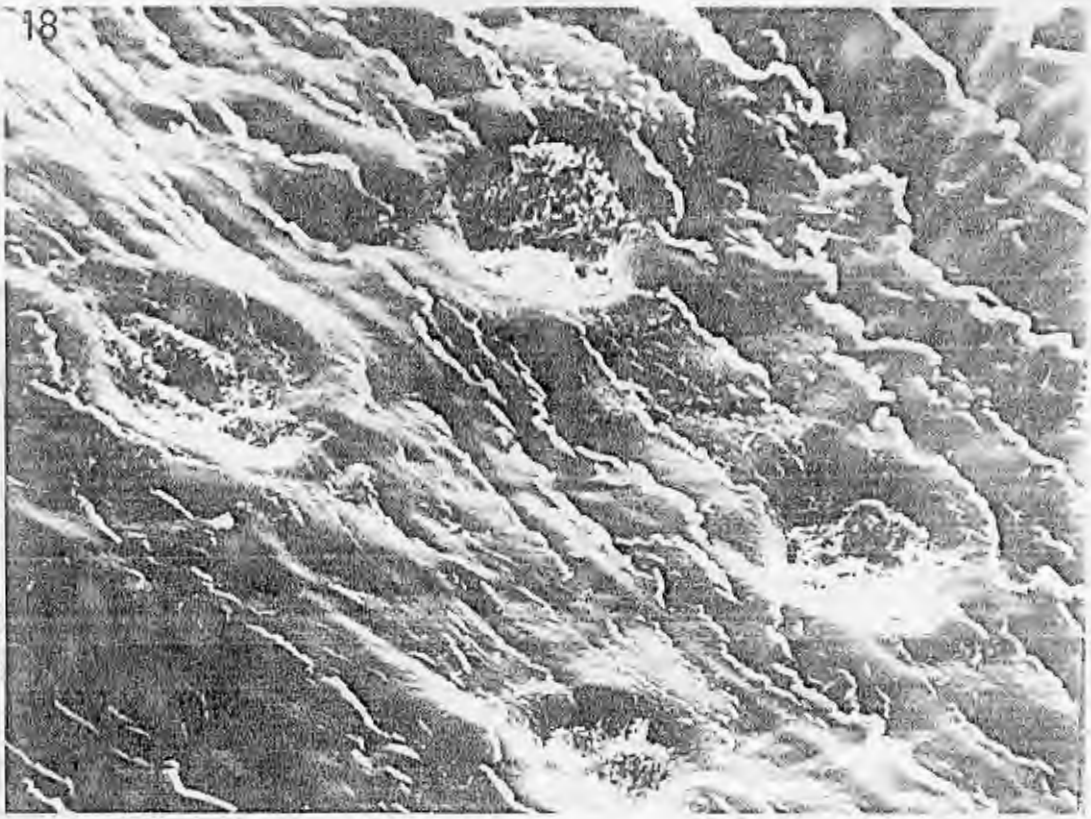

Fig. 18. Lower surface of needle with sunken stomatal pores filled with wax.

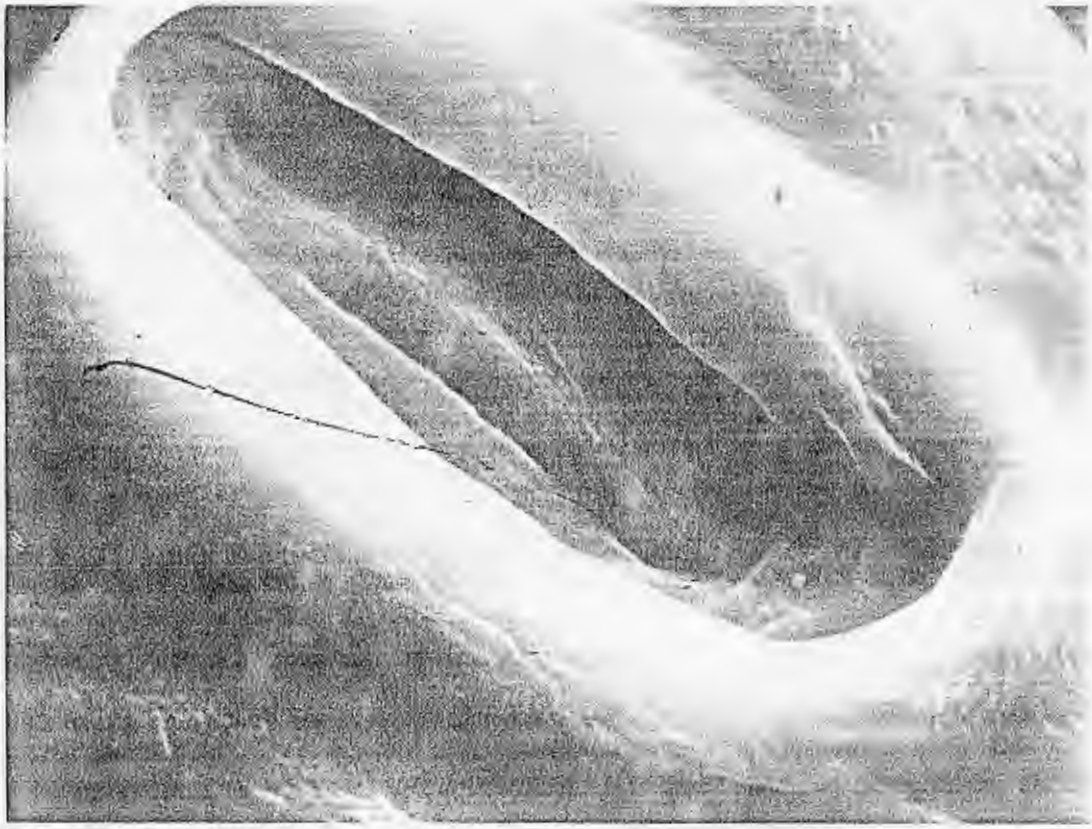

Fig. 19. External stomatal chamber with wax plug removed by chloroform to show guard cells.

microbodies. Chloroplasts were spread in a single layer around the wall and on favorable days they accumulated starch. Needles collected from naturally growing trees in exposed locations had only rudimentary grana. Granal formation was more extensive in trees grown in a shaded greenhouse. Wall development was particularly active in young tissue but proceeded rapidly following bud break. Mature needles had thick cell walls and a multilayered cuticle with surface wax deposits (Fig. 14). Trees grown naturally had extensive development of a subepidermal layer of cells known as a hypodermis (Fig. 15). The surface of mature needles was covered with a waxy material (Fig. 18). This appeared as platelike extrusions which filled even the stomatal pore. The wax could not be removed by washing with water. However, a brief soaking in chloroform (30 sec) did displace wax from the stomatal pore (Fig. 19). The wax coating was evident even as needles emerged from the bud and did not seem to disappear during the remainder of the life of the needle.

In late fall and winter cytoplasmic organelles tended to clump together (Fig. 17), often around the nucleus. The chloroplasts were several layers deep and stacked against each other rather than spread out evenly against the cell wall. The other parts of the cell, from which these organelles had migrated, had only a very thin layer of cytoplasm, mainly small lipid bodies and mitochondria, between the tonoplast and cell wall.

From November through March no starch was found in the chloroplasts of plants grown outdoors even when samples were taken on bright, sunny days from exposed branches. The amount and type of other storage products varied. In particular, the trees in the transplant garden did not develop the large lipid reserves seen in the Mt. Washington samples. Many of the organelles had a disrupted appearance which coincided with the needles developing a yellowish appearance. Starting in March, starch production was again noted in the

chloroplasts and organelles began to relocate around the periphery of the cell, suggesting a release from dormancy.

Discussion

As a conservative estimate, the transpiration rate of black spruce during the winter drops by a factor of 100 from the summer rates, e.g. from 0.4 $ml/dm^2/hr$ to 0.004 $ml/dm^2/hr$. Khlebnikova et al. (1963) report winter transpiration of Scotch pine is 200-300 times less than during the summer at a rate of 25 mg/g fresh wt/day. Hygen (1963) calculates the minimum water loss from Norway spruce during the winter at 12.5 mg/g fresh wt/day. On the basis of Hygen's calculations, and assuming an average leaf biomass of 8.4×10^3 kg/ha for a mature stand of Norway spruce (Ovington, 1962), the consumptive use of soil water from mid-November to mid-March could be expected to exceed 31,000 liters per hectare for that species if the water is available. The expression of transpiration on the basis of needle fresh weight is not advisable, but for purposes of comparison with these data the minimum transpiration rate for dormant black spruce is calculated at 21 mg/g 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 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 Q_{10} 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. 4), the Q_{10} for the increase in conductance is 4.9. 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 Q_{10} of 1.5 for stomatal opening. The plot of leaf resistance vs temperature for all experiments (Fig. 8) shows little temperature sensitivity between 5° and 10°C. If the Q_{10} is then calculated over the range of 0 to 5° or 1 to 5° the values exceed 6.0, indicating perhaps that membrane permeability sharply decreases at temperatures approaching 0°C.

Plant temperatures under the conditions of the controlled-environment experiments (Fig. 10) were consistent with leaf-air temperature differences reported in the literature for field conditions. Tranquillini (1964), for example, has found temperatures of Pinus cembra needles as high as 21.5°C above air temperature in April as a result of high direct and reflected radiation. Similar heating of plants is reported by Salisbury and Spomer (1964). The effect of this heating can be readily appreciated. As the leaf temperature is elevated above air temperature, the vapor concentration gradient between the intercellular spaces of the leaf and the outside air steepens. For example, the difference in 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 $\mu g/cm^3$. With the leaf temperature elevated to 5°C under the same conditions, the difference in water vapor concentration increases to approximately 4.4 $\mu g/cm^3$. By entering these numbers into the transpiration equation, 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 is its reduction of the diffusion resistance of the air surrounding the leaf. Drake et al. (1970) reached the same conclusion working with plants having much lower leaf resistance, noting that increasing wind reduced transpiration of Xanthium at temperatures up to 35°C.

At some temperature between 5° and 0°C, the data indicate an important temperature threshold below which stomatal movements are prevented regardless of radiation intensity. This same effect has been recently noted in two other conifer species (Reed and Drew et al., cited in Running et al., 1975). Heating the leaf of black spruce above 5°C resulted in a substantial decrease in diffusion resistance. The effectiveness of wind in reducing transpiration would therefore be greatest at air temperatures near or below freezing, especially under high radiation intensity. For example, if the ambient air were at -5°C with the leaf heated to +5°C under calm conditions and moderate to high radiation intensity, then an increase in wind speed to 200 cm/sec could be expected to reduce transpiration more than the 50% reported (Fig. 9). In this case, lowering the plant temperature would not only reduce the vapor concentration gradient and maintain high leaf resistance, but all parts of the transpiration pathway, i.e. both symplast and apoplast, may approach freezing (see, for example, Havis, 1971), further reducing transpiration. The amount of soil water use during the winter in a given area might therefore be strongly dependent on the normal air temperature, radiation load, and wind speeds as these affect plant temperatures.

An additional factor revealed in the microscopical study was the period of winter dormancy. For a period from November to March spruce and fir tissue lacked the cytological organization or the ability to synthesize starch that is typical of summer needles. This apparent dormancy perhaps underlies the response seen in Fig. 4 where stomatal activity changed over a period of several days after branches had been brought into the laboratory. Clark (cited in Little, 1970) and Schwarz (1971) have shown for several species of conifers that gas exchange during winter months is negative and that photosynthesis is resumed only after warming for several days. This lapse may be related to the reestablishment of chloroplast orientation and structure. It may be concluded

that stomatal regulation is fundamentally different under summer and winter conditions partly as a function of ambient temperature and partly as a result of intrinsic dormancy. Together these account for the extremely low rates of water loss found in the winter.

The lack of good correlation between leaf water content changes and the above environmental variables can be related to the nature of the winter climate on Mt. 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 February 25 to March 9, 1973 (Fig. 11), 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. 11), 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°C and +10°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 (Fig. 11) does indeed suggest that water replenishment is more restricted in this species, at least until early spring at which time perhaps renewed cambial division begins to restore the xylem water column.

Though translocation may occur in spite of cavitation and at temperatures below 0°C, it is not known whether or not absorption from frozen soils, as for example through vapor transfer, is significant. Even where soils remain unfrozen, the increased viscosity of water (nearly twice as great near 0°C as at 25°C) and

the decreased permeability of cell membranes at low temperature greatly restrict absorption (Jensen and Taylor, 1961; Kramer, 1969).

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. 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 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 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 atmospheric water vapor will take place only at atmospheric 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. Furthermore, for the short periods when the atmosphere around the exposed plant is saturated, 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 is clearly in need of further research.

In the controlled-environment experiments, transpiration from excised branch tips in the potometers was allowed to proceed without restriction, an unnatural situation indeed. As the dormant conifer needle has proved not entirely passive, it is not known how differently an intact plant might respond to the same environmental manipulations. One limitation to winter transpiration losses in the field may be the development of highly negative water potentials where water uptake is severely limited. It is not known, however, at what level negative water potential by itself will inhibit winter stomatal movements. Rottenburg and Koeppner (1972) found that beyond a water deficit of 10% (RWC = 90%) the stomates of *Taxus baccata* closed rapidly while those of *Abies alba* closed more gradually. It is probably reasonable to assume, at least for *Abies balsamea* and *Picea mariana*, that in this region the development of low water potentials is not an important factor, since the mean RWC of 90% over the past two winters corresponds to a water potential of approximately -11 bars, a value which appears to be the normal "operating" level during the summer. For the sake of conservatism, however, the rates and responses observed under controlled conditions must be considered optimum and extrapolation to the field situation should be done with caution.

Application

Forested areas have had a traditional role in water supply. Management studies begun in the early part of this century have been directed toward improving yield from watersheds while maintaining water quality. Recently, increasing problems with disposal of human and animal wastes have led to the concept of spraying sewage on vegetated areas in an effort to recycle both the nutrients and water. The pioneering studies by Sopper (1971) demonstrated the feasibility of such practices. In all cases vegetation cover remains an important factor in management designs.

The use of watersheds for both water supply and sewage processing creates conflicting goals as far as determining the appropriate vegetation cover is concerned. On the one hand, plants with low yearly water use would lead to increased water yield. On the other hand, in the presence of "excess" water and nutrient inputs, plants which had a high rate of water and nutrient use would improve the nutrient recovery process. This problem is potentially solvable. Forest cover in New Hampshire ranges from deciduous species to evergreen conifers, each presenting very different hydrologic characteristics. Sewage disposal sites will probably cover only limited areas of a watershed and may be managed for a species composition different from the general forest if necessary.

Several properties of the vegetation must be considered. Data from this study suggest that water loss from deciduous leaved species is approximately twice as great as from conifers during the growing season. However, conifers maintain twice as much foliage biomass and leaf area as deciduous trees (Nicholson, 1975). This increased area for transpiration plus the longer duration of the foliage with associated interception losses would make conifers less suitable where high water yield is an objective. In fact, lower water yields from pine- vs deciduous-covered watersheds have been reported (Swank and Douglass, 1974).

These features which lead to increased transpiration may be advantageous for nutrient recovery operations. While water absorption and transpiration are not closely linked over short time intervals (Kramer, 1937), equilibrium is established on a daily basis and high transpiration rates indicate a greater volume of water moving through the plant. Associations between transpiration and solute absorption have not been entirely resolved (see Kramer, 1969). It seems clear that ions will be absorbed differentially (Hoagland, 1944), that active accumulation is significant particularly at low transpiration rates (Russell and Barber, 1960), but that mass flow may account for much of the ion movement away from the absorbing zone of the roots (Lopushinsky, 1964; O'Leary, 1965). A reasonable conclusion would be that high total transpiration plus greater biomass in conifers would make such species effective nutrient concentrators, especially during early growth stages when biomass accumulation is greatest. It therefore would be most worthwhile at this point to conduct field tests of the influence of sewage spray irrigation on different forest types. Particular attention should be given to growth rates of trees and shrubs (biomass accumulation), nutrient concentration in the plants, and the rate of nutrient return through leaf fall. If the additional problems of low soil temperatures affecting absorption can be solved, conifers would seem to be the most reasonable cover for sewage disposal sites in New England.

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