Winter Water Relations at the Upper Elevational Limits of Hemlock on Mt. Ascutney, Vermont

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Abstract

Winter water relations have been monitored in hemlock (*Tsuga canadensis* (L.) Carr.) at their upper elevational limits for three winters, 1997, 1998, and 1999, on Mt. Ascutney, Vermont. Hemlock and white pine trees (*Pinus strobus* L.) reach their elevational limit on Mt. Ascutney at 640 m (2100'), while the summit has an elevation of 960 m (3150'). Relative water contents (RWCs), water potentials, and cuticular conductances were monitored in combination with micrometeorological weather information on both species. These data were incorporated into a winter water relations model which predicts relative water contents based on climate information.

Measured RWCs and water potentials of hemlock fell below those of white pine. Although RWCs were generally above 60%, considered a threshold of desiccation damage for conifers, foliage was damaged in the winter of 1998. Possibly the January ice storm of 1998 damaged and killed a portion of foliage by the end of that winter. Hemlock cuticular conductances were consistently greater than white pine conductivities, most markedly in second year foliage and when damaged. White pine trees did not experience high cuticular conductivities during any winter nor did they lose older foliage from the ice storm. Results from this hemlock study could lend support to the hypothesis that upper elevational limits are determined by winter water relations.

Introduction

Timberline is a prominent vegetation boundary, where woody plants often experience shoot death related to winter desiccation. Drying of conifer needles during winter is considered to be the defining factor for tree distribution at upper elevational limits (Sakai 1970, Wardle 1971, Tranquillini 1979). Excessive water losses occur through the cuticles and bark due to abrasion (Hadley and Smith 1983, Maruta 1996), inadequate cuticle development during short cool summers (Wardle 1971, Hadley and Smith 1986, 1990, 1994), or lack of water availability due to frozen soil or stem tissues (Sakai 1970, 1982). Some timberline species do not experience winter drought (Marchand and Chabot 1978, Cochrane and Slatyer 1988, Grace 1990) and some species experience shoot dieback without winter desiccation (Slatyer 1976, Kincaid and Lyons 1981). Research has often focused on alpine treeline without looking at forces that cause upper elevational limits of trees in general.

Tranquillini (1976) stated that "...probably all evergreen conifers at timberline are subject to marked winter desiccation...the degree of this desiccation increasing with increase in altitude." Challenges to this statement have clearly been made by Cochrane and Slatyer's (1988) work in the Snowy Mountains of Australia, which demonstrated that water potential and RWC did not cause shoot dieback at treeline. Water content and water potential in cembran pine and mountain beech at timberline did not change over the winter, even though mountain beech experienced increased cuticular conductivity (McCracken et al. 1985). Poor cuticular development does not explain treeline in Scotland as Wardle (1971) suggested, rather stomates seem to dysfunction due to mechanical abrasion.

It is important to examine current assumptions of winter damage on low elevational species at their upper elevational limits. Damage caused by factors related to upper elevational limits reduce plant productivity and further limit the geographical range where such species can grow (Sakai, 1970). Knowledge of winter damage and the process of establishing upper elevational limits could lead to the development of new strategies to improve plant drought and freezing tolerances. Discovering the mechanisms that cause damage could be used by forest managers to increase forest productivity and survival when confronted by multiple stresses.

Present understanding of winter drying and subsequent injury in conifers at treeline is derived from empirical studies as well as mathematical models (Sowell et al. 1996, Boyce et al. 1991, Boyce et al. 1992). Empirical studies are intermittently sampled over an entire winter season. Gaps in the season's data can be predicted through modeling. The purpose of this study is to examine desiccation stress of two low elevational conifers at upper elevational limits by utilizing physiological measurements and a winter water relations model (WINWAT). Environmental and plant factors will be identified that affect current assumptions regarding winter water relations at treeline.

Materials and Methods

Study Area

The study site was located at 640-m elevation on the north facing slope of Mt. Ascutney (43°27' N, 72°27'W) in Eastern Vermont. The mountain rises to an elevation of 960 m (3150'). The research site is located along the Brownsville Trail and is accessible only by this hiking trail. The vegetation on the Mt. Ascutney north facing slope changes from predominantly hardwood species at lower elevations to conifers at higher elevations, while the summit is populated by red spruce and balsam fir. White pine extend from 490 to 665 m on Mt. Ascutney while hemlock is found in a wider range of 230 to 650 m elevation (Boyce, 1998). The site's canopy consists of white pine, red pine, red spruce and hemlock trees. The mid-canopy is mostly balsam fir and red spruce trees and the under story is red spruce, balsam fir and hemlock seedlings. Snow cover remained throughout

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the sampling period at depths of 20-40 cm, which dissipated by the end of April.

Microclimate Measurements

A meteorological tower was installed at the site and positioned so instruments measured within the canopy. A 10-m telescoping tower with mounted instruments reaches into the upper half of each mature conifer forest stand. Shielded thermistors (Campbell Scientific) measured air temperature and relative humidity. Cup anemometers (R. M. Young) measured wind speeds greater than 0.2 ms^{-1} and wind direction was measured by a wind vane. Instrumentation also included a soil temperature probe (Campbell Scientific), a pyranometer (Licor) to measure irradiance (%), and leaf wetness sensors (Campbell Scientific). To monitor needle temperature, thermocouples were constructed of 40-gauge (0.0799 mm) copper-constatan loops which were placed on individual needles of well exposed south-facing branches. Four thermocouples were placed on an individual tree, two on first year needles and two on second year needles of white pine and hemlock trees. Hourly measurements were stored on a programmable Campbell Scientific CR-10 data logger as mean, maximum, and minimum values.

Water Relations

From January through April of each winter season over the course of three winters, shoots were removed from four individuals of each species on a weekly basis. Foliage was removed from the same trees throughout the entire study, with the exception of 1 hemlock and 1 white pine tree which were removed from the study in 1999 due to lack of obtainable foliage. Sun exposed shoots were removed using a telescoping pole pruner and kept in sealed plastic bags over ice and in darkness while transported to the laboratory. Measurements were conducted within 6 hours after collection. First and second year shoots were used to determine the relative water content and cuticular conductances of each species. To measure shoot relative water contents, shoots were weighed (w_f) then floated on deionized water for 24 hours at 4 °C in the dark (Koides, 1991). The shoots were blotted dry, reweighed (w_t), and oven dried at 60 °C for three days before weighing again (w_d). Shoot relative water contents were calculated as:

RWC (%) = 100 x $w_f - w_d / w_t - w_d$

Cuticular conductances were determined on a monthly basis for the same shoots that were used to calculate RWC and water potential. Procedures followed those described by (Herrick, 1991) and (Boyce et al. 1991, Boyce et al. 1992). After turgid weights of shoots sampled on those dates had been determined, shoots were placed in a dark chamber at approximately 4 °C and 20% relative humidity. Temperature and relative humidity were monitored and recorded by a temperature and relative humidity probe connected to a CR-10 data logger (Campbell Scientific). The shoots were weighed at approximately 12 hour intervals for 3 days. The shoots were then oven dried and weighed. Foliar surface area was determined from a dry weight-surface area relationship developed for mature trees from this site (R.L. Boyce, unpublished data).

Water potential measurements were made following the procedure developed by Scholander et al. (1965) using a pressure bomb (PMS instruments, Corvallis, Oregon). After stripping off a portion of bark, xylem pressure measurements were made for white pine shoots. It was not necessary to remove bark from the slender hemlock shoots. Measurements were averaged using four water potential measurements per tree and four trees per species.

WINWAT Model

The WINWAT model was used according to procedures developed by Boyce et al. (1992) for red spruce RWCs. Measured meteorological parameters were used to simulate changes in hemlock and white pine first and second year shoot RWCs during the three winters. The single state variable in the model is the water content of an average shoot per unit area. Stomata are assumed to remain closed and shoots are assumed to remain connected to a reservoir of water available in the stem above -4 °C. The rate of loss of water to the atmosphere is driven by: air temperature, needle temperature, relative humidity, and cuticular conductance. Relative water content, recharge, and the vapor density difference between air inside the leaf and outside the boundary layer are auxiliary variables.

Results

Microclimate

Micrometeorological weather information is summarized on Table 1. Usable data were collected in January and February in 1997, December through April in 1998, and December through March in 1999. The warmest winter of the three occurred in 1998 (average temperature of -2.5 °C), probably due to an early spring warming trend which began in March. The coldest temperatures occurred in January of 1999 (-27.6 °C) when the average monthly temperature was -9.7 °C. Soil temperature fluctuated with air temperature within a much smaller range. The warmest soil temperatures were recorded in December of 1999 (1.9 °C). Average monthly soil temperatures were below zero for all other months monitored.

The wind speed and direction sensors were destroyed by the ice storm (1998), and were often frozen during January of 1998. Values from the other three months which data were collected indicate a mean wind speed of 1.1 ms^{-1}, with maximum speeds of 5.3 ms^{-1} (Table 1). The surface of the leaf wetness sensor was often frozen, especially during the ice storm. In this condition, it is not wet, and is a poor indicator of wetness experienced by foliage. However, the relative humidity sensor provided a more reliable indicator of general moisture at the site. The most humid month occurred in January of 1998 (93.8%) which was also the most humid year on average (82.8%). The wettest month of all the winter seasons was January. The least humid month

Table 1.—Summary of micrometeorological infomration collected on Mt. Ascutney. Values are for 24-hour day measurements. Data were collected in January and February in 1997, December through April in 1998, and December through March in 1999.

	White Pine and Hemlock Site				
Parameter	Min.	Max.	Mean	Std. Dev.	n
1997					925
Air T (°C)	-19.0	12.1	-4.5	5.8	
Soil T (°C)	-16.4	4.5	-2.6	2.1	
% Relative humidity	20.7	100	76.1	18.6	
Wind velocity (ms^{-1})	0	5.3	1.2	0.84	
Pyranometer	0	417	10.9	20.3	
1998					2349
Air T (°C)	-22.4	25.2	-2.5	7.1	
Soil T (°C)	-7.1	0.0	-1.0	1.2	
% Relative humidity	19.3	100	82.8	21.0	
Wind velocity (ms^{-1})	0	4.4	0.49	0.06	
Pyranometer	0	579	12.8	24.2	
1999					2782
Air T (°C)	-27.7	17.3	-4.3	7.1	
Soil T (°C)	-2.9	6.5	0.27	1.5	
% Relative humidity	8.74	100	72.2	22.9	
Wind velocity (ms^{-1})	NA				
Pyranometer	0	729	11.7	22.8	

occurred in February of 1999 (64.7%) which also was the most variable of the three winters.

Water Relations

The greatest RWCs were measured in the winter of 1998, when RWCs were often greater than 100% (Figures 1 and 2). The foliage was coated with ice and became supersaturated in transport to the laboratory. The highest RWCs for hemlock (Figure 1) occurred in January of 1998, above 100%, and the lowest average monthly RWC occurred in April of 1998 (81.3%). Over the three winters, foliar RWCs ranged from 30.7% to >100%. Generally, second year foliage have lower RWCs than first year foliage and follow a similar seasonal trend. The winter of 1998 is the most variable year for RWCs in hemlock while 1999 is the least dynamic.

The most variable year for white pine RWCs is 1999 (Figure 2), while both 1997 and 1998 are relatively static. The highest mean monthly RWC occurred in February of 1998 (93.0%) and the lowest in January of 1997 (81.5%). The range of RWCs for foliage during the three winters was 48.2% to >100%. Generally second year foliar RWCs were less than first year foliar RWCs, and were the lowest in 1999.

Hemlock first and second year foliage always had greater conductivity values than white pine foliage (Table 2). The highest conductivity occurred for both species in 1998. Hemlock second year foliar cuticular conductivity averaged 0.20 m/ks in January and in March, while the first year foliage averaged 0.12 m/ks in January and dropped to 0.04 m/ks there after. Hemlock cuticular conductivity increased over the winter of 1999 for first year foliage, while the second year foliage cunductivities generally remained the same (0.08 m/ks). White pine cuticular conductivity for the first year foliage was greatest in March of 1998 (0.04 m/ks). This value is close to the lowest cuticular conductivity experienced by hemlock. During 1999, first and second year white pine foliage have the same monthly mean cuticular conductivity (0.02 m/ks) for all months.

Water potentials of hemlock shoots were more negative and more variable than white pine shoots (Figure 3). Hemlock shoots were the most negative during 1998, when the most negative water potential occurred in April (-5.1 MPa). Water potentials varied the least in 1997, rising from -1.04 to -0.6 MPa over that winter. The average water potential for the entire winter of 1997 and 1999 did not differ (-0.8 MPa) while the yearly average for 1998 was -1.0 MPa. White pine shoots in general varied little over any winter, 1999 being the most variable. Yearly averages during 1998 and 1999 were -0.5 MPa, and -0.7 MPa in 1997. The most negative water potential occurred in February of 1998 (-1.9 MPa) for white pine shoots.

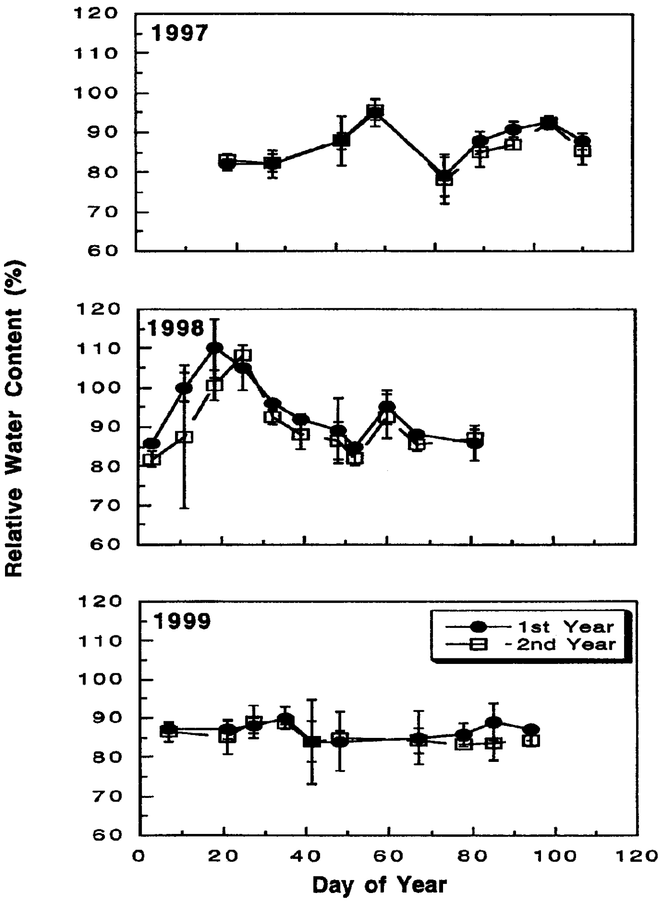

Figure 1.—Relative water contents of hemlock fist and second year foliage during the winters of 1997, 1998, and 1999. Error bars are 1 standard deviation from the mean (n=32).

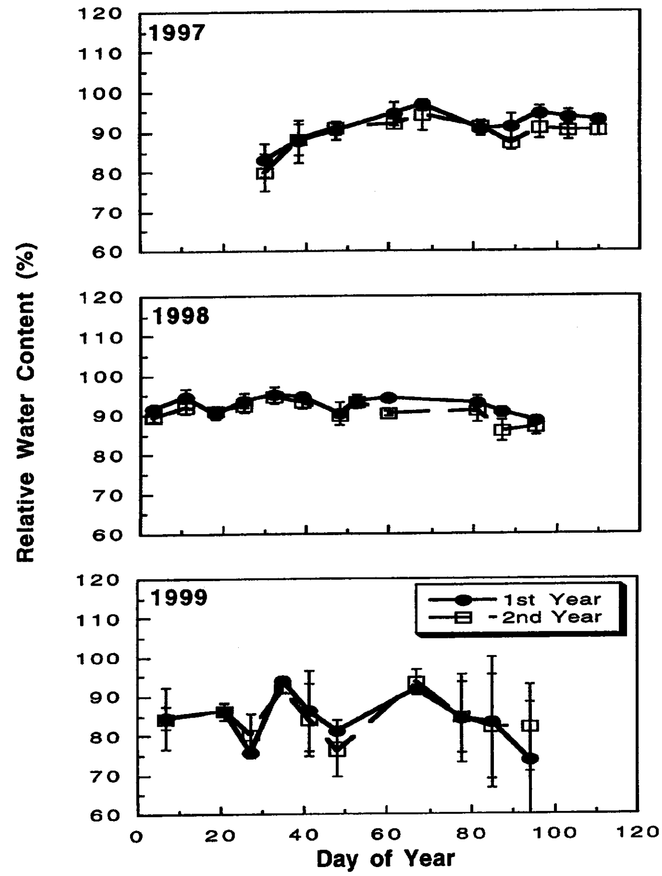

Figure 2.—Relative water contents of white pine fist and second year foliage during the winters of 1997, 1998, and 1999. Error bars are 1 standard deviation from the mean (n=32).

WINWAT Model

The WINWAT model accurately predicted RWCs for the winters with the least variability in measured RWCs (Table 3). RWCs with the most seasonal variablity, in 1998 for hemlock and 1999 for white pine, are poorly predicted. Accuracy was assessed by calculating mean square errors, which is the sum of squares divided by the number of RWCs measured. The sum of squares is the sum of measured minus modeled RWCs squared. WINWAT predicted first year better than second year foliar RWCs, and white pine more accurately than hemlock RWCs (Figures 4 and 5). There are periodic dips and peaksin modeled RWCs which measured RWCs do not show.

Discussion

The purpose of this study is to examine desiccation stress of two low elevational conifers at upper elevational limits by utilizing physiological measurements and a winter water relations model. Hemlock trees from this study experienced lower relative water contents, higher cuticular conductivities, and more negative water potentials than white pine at upper elevational limits. Older foliage was damaged and a portion died by the end of 1998, possibly from the January ice storm. White pine trees did not experience foliage death during any winter. This study quantified microclimatic data of an upper elevational site for hemlock and white pine trees. During the winters of 1997, 1998, and 1999, air temperature, wind speed and direction, relative humidity, solar irradiance, leaf wetness, soil temperature, and needle temperature were monitored on Mt. Ascutney in Eastern Vermont. Relative water content, cuticular conductivity, and water potential in combination with the WINWAT model were used to develop a clear understanding of water relations of two conifers at their upper elevational limits not at treeline.

Controversy surrounds measurements of plant water status used in comparative studies. Many inconsistencies are associated with water relations due to the involvement of additional often opposing factors that may mask or compensate a presumed relationship, and the difficulty of capturing through point samples the dynamic nature of plant responses (Uta Maier-Maircker, 1998). These difficulties are compounded by the fact that conifers during winter alter solute concentrations, membrane permeability, ice crystal

Table 2.—Monthly average cuticular conductivities of hemlock and white pine first and second year foliage measured in 1998 and 1999.

	Mean Cuticular Conductance (m/ks)				
	First Yr. Foliage	Standard Deviation	Second Yr. Foliage	Standard Deviation	n·
Hemlock					
1998					
January	0.12	0.04	0.20	0.03	32
February	0.04	0.01	0.17	0.01	32
March	0.04	0.03	0.20	0.03	32
1999					
January	0.03	0.01	0.08	0.02	24
February	0.04	0.02	0.09	0.02	32
March	0.05	0.03	0.08	0.03	32
White Pine					
1998					
January	0.03	0.004	0.03	0.01	32
February	0.03	0.002	0.02	0.01	32
March	0.04	0.01	0.03	0.01	32
1999					
January	0.02	0.01	0.02	0.002	24
February	0.02	0.003	0.02	0.003	24
March	0.02	0.004	0.02	0.01	24

formation, and the level of drought and freezing tolerances in ways that have not been elucidated. Variation in RWC or water potential individually are unlikely to describe a response to water imbalance (Zobel, 1996). This study draws upon several water relations parameters to confirm similar trends and analogous results. Cuticular conductivity, relative water content, and water potential are used simultaneously to represent the water balance of a plant. If desiccation occurs, the effect should be apparent in all of the parameters used in this study.

Hemlock trees may be considered more susceptible than white pine trees to winter damage, possibly from desiccation. Hemlock experience higher cuticular conductivities, more negative water potentials, and lower relative water contents than white pine trees at 640 m elevation on Mt. Ascutney. The winter of 1998 resulted in the highest cuticular conductivities, indicating the ice storm may have damaged hemlock cuticles. However, cuticular conductivity did not increase over the winter for first year foliage, suggesting that deterioration of the cuticles was not a permanent or continuous condition. Cuticular conductivities remained high throughout that winter for second year foliage (0.2 m/ks). Generally RWCs and water potentials were not lethal during this winter (1998), and it seems unlikely that desiccation alone resulted in shoot death. The WINWAT model did not predict RWCs below 60%, the threshold for desiccation damage in conifers, and measured RWCs seldom fell below 60%. Damage was short-term, over a single winter season and related most to the ice storm. If the effect is damage and needle loss, the specific cause is not revealed by this study.

White pine trees did not experience desiccation at upper elevational limits, with low cuticular conductivities, higher RWCs of both first and second year needles than hemlock, and analogously high water potentials. It has long been noted that white pine trees are susceptible to winter injury less frequently than hemlock trees (Curry and Church, 1952). Winter data from Mt. Ascutney support this observation and do not reveal damage. The WINWAT model predicted RWCs well for white pine, except in 1999. During 1999, RWCs were the most variable and lowest of the three years. Needles appeared chlorotic, but remained viable with low cuticular conductivities and high water potentials. Discolored needles may contribute less to the next season's photosynthesis, and it would be interesting to determine how this would contribute to the following winter's water relations.

The winter climate on Mt. Ascutney at 640 m is characterized by low temperatures and constant snow cover. On average, monthly air temperatures remained below 0 °C in all months except April of 1998 (1.8 °C). Soil temperatures also remained below 0 °C in all months except December of 1999 (1.9 °C). There is little sun exposure at this north facing and heavily shaded site. Needle temperatures seldom

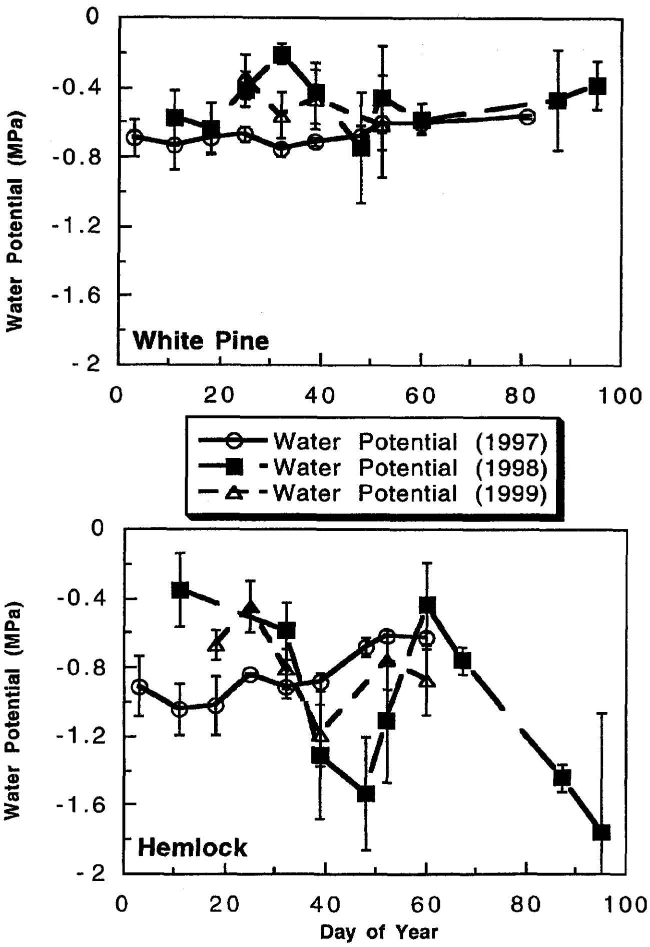

Figure 3.—Water potential (MPa) measured on hemlock and white pine shoots during the winters of 1997, 1998, and 1999.

exceeded air temperatures (data not shown), noted in conifers at other upper elevational limits (Sakai 1970, Hadley and Amundson 1991). On calm and sunny days, needle temperatures can exceed air temperature by 10 and 20 °C, optimizing water loss (Marchand 1987). Drought occurs because soil water, when frozen, is unavailable to the plant yet transpiration proceeds at a finite, minimal rate even in winter. Since needle temperatures did not deviate from air temperatures in this study, and rehydration is possible even when roots are frozen and the ground is covered in snow (Scott and Hansell 1992), it seems unlikely that the relationship between the soil, plant, and air caused desiccation.

The success of regeneration at treeline is vital in an environment which is characterized by limitations. Considering that hemlock trees are shade tolerant, mesic conifers which prefer to establish seeds in moist and decaying logs, it is of little surprise that hemlock would not have developed mechanisms to tolerate drought. White pines grow on rocky cliffs as well as sandy soils, tolerate high levels of irradiance, and are more able to tolerate water shortages. Since mechanisms to tolerate drought are behavioral as well as genetic, it is reasonable that white pines could have developed better mechanisms to deal with desiccation. White pines have been witnessed at other New England summits (personal observation), and hemlock trees seldom if ever reach the upper limit of tree growth.

Hemlock needles may have experienced water and foliage loss during the ice storm through mechanical failure. Ice particles may have impacted the cuticle, disrupted turgor relations of the epidermis and prevented proper stomatal closure. Perhaps as ice formed on the foliage, ice crystals penetrated inside vulnerable needles, resulting in freezing damage and death. Direct mechanical damage has previously been implicated for winter water imbalances (Marchand and Chabot 1978, Hadley and Smith 1983 and 1986, Maruta 1996) and may very well be the cause of damage experienced by hemlock from the ice storm of 1998. The upper elevational limits of hemlock on Mt. Ascutney may establish from severe and sporadic events, such as the 1998 ice storm, rather than symptoms which occur each winter. This study shows that the ice storm damaged hemlock trees, not white pine trees, and was related to elevation since the duration and quantity of ice increased with elevation. This study explored water relations only at upper elevational limits and a study which looks at water relations along an elevational gradient could support these findings.

Stem recharge is assumed to occur at temperatures greater than -4 °C (Sowell 1996, Boyce et al. 1992), and average monthly temperatures remained above -4 °C for half of each winter studied. More information is needed to understand stem recharge during the winter for hemlock and white pine species which may experience stem recharge at a different threshold. Differences in sapwood water storage capacity could have an important influence on winter water relations, and little is known about capabilities of species in this study. Xylem embolism has been noted to result in winter damage in other conifers (Sperry and Tyree 1988,Cochard 1992) but the propensity of hemlock to experience embolism over pine is not known. Differences in rooting architecture have been implicated to take advantage of available soil water (Day et al. 1989) and root distribution may explain elevational distribution of hemlock and white pine trees.

Damage in winter constitutes the greatest limiting factor for growing plants in cold climates and high mountains (Sakai, 1970). Woody plants at their upper elevational limits experience stress from seasonal and sporadic events that can reduce plant productivity and increase susceptibility to injury from other stresses. Researching winter damage and the process of establishing upper elevational limits may elucidate how conifers survive severe conditions.

Table 3.—Calibrated values of recharge parameter A in 1997, 1998, and 1999 for first and second year shoots of hemlock and white pine at their upper elevational limits on Mt. Ascutney.

	Validation of the WINWAT Model								
	1997			1998			1999		
	A	SS[1]	MS[2]	A	SS	MS	A	SS	MS
Hemlock									
First Year Foliage									
	90	191.0	23.9	45	274.1	24.3	45	104.3	13.0
Second Year Foliage									
	140	334.2	42.0	455	1415.8	118.0	95	89.1	11.1
White Pine									
First Year Foliage									
	105	85.5	10.7	40	188.2	17.1	20	346.6	43.3
Second Year Foliage									
	70	139.5	17.4	35	215.4	19.6	20	309.5	38.7

SS[1] = Sum of squares = Σ (measured RWC - modeled RWC)^2
MS[2] = Mean square error = SS / (# measured RWC values)

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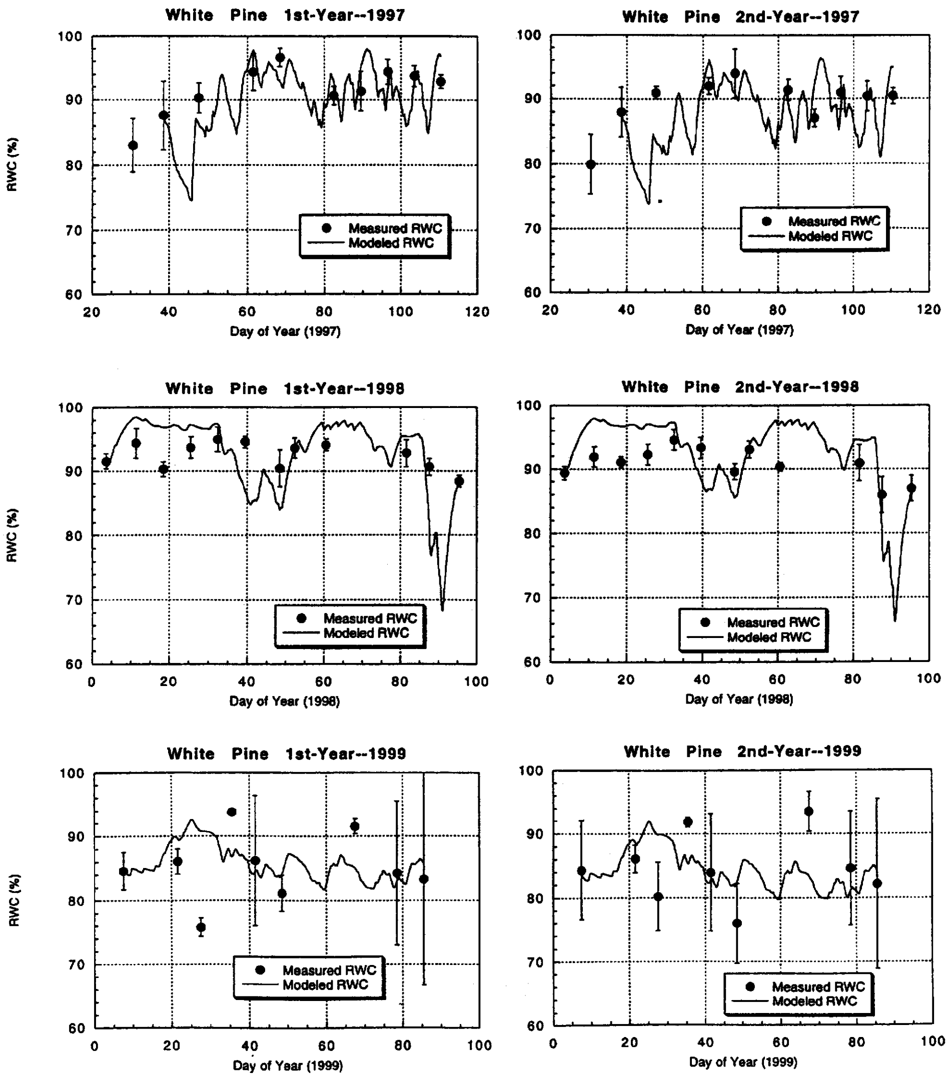

Figure 4.—WINWAT model predictions of Relative Water Contents for White Pine for 1997, 1998, and 1999.

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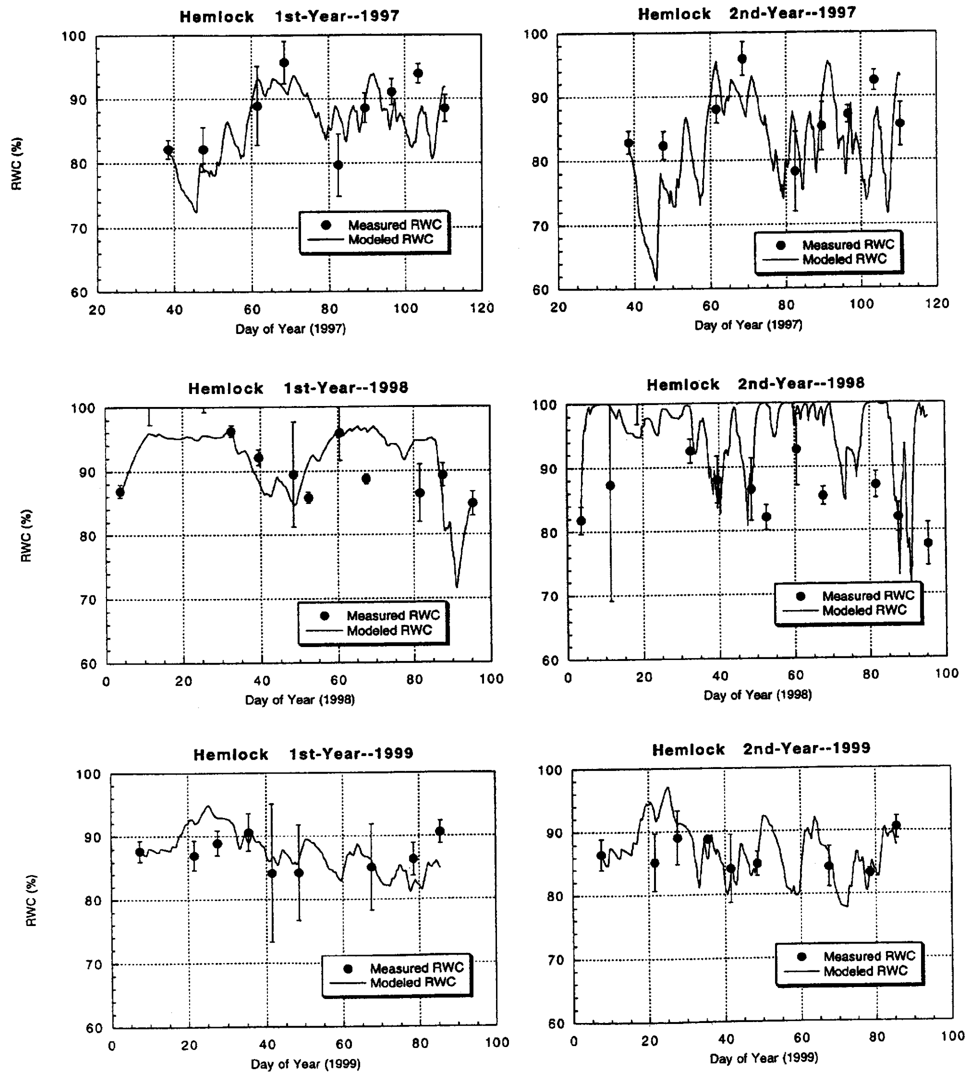

Figure 5.—WINWAT model predictions of Relative Water Contents for Hemlock for 1997, 1998, and 1999.

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